A new crustacean clam shrimp (Spinicaudata: Eosestheriidae) from the Upper Triassic of Argentina and its importance for 'conchostracan' taxonomy

OSCAR FLORENCIO GALLEGO

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A new species of a fossil crustacean clam shrimp (Spinicaudata: Eosestheriidae) *Menucoestheria wichmanni* is described from the lower Upper Triassic Vera Formation (Los Menucos Complex) in Río Negro Province, southern Argentina. This discovery represents the first record of this family in the Triassic of Argentina and the southernmost record of South American Triassic 'conchostracans' (Spinicaudata). The new species shows close affinities with Middle Jurassic faunas from Antarctica and offers important data on the taxonomy (notably the use of ornamentation characters), palaeobiogeography (as South America hosts the oldest-known fossils of this family) and evolution of the Gondwanan faunas. Other South American eosestheriid species are tentatively recognized. *Menucoestheria* is hypothesized to be the ancestral form of the Triassic–Jurassic Gondwanan eosestheriids. Relationships between European and Gondwanan eosestheriids remain unresolved.

Oscar Florencio Gallego [ofgallego@live.com.ar], Micropaleontología (Facultad de Ciencias Exactas y Naturales y Agrimensura—Universidad Nacional del Nordeste) y Área Paleontología (Centro de Ecología Aplicada del Litoral—CONICET), Casilla de Correo 128, 3400 Corrientes, Argentina. *Received 18.5.2009; revised 12.10.2009; accepted 15.10.2009.*

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TRIASSIC spinicaudatans from Argentina have been known since the second half of the 19th century from the descriptions given by Jones (1862, 1897) and Geinitz (1876) and the contributions of Phillipi (1887), Kurtz (1921), Rusconi (1948a, 1948b), Camacho (1995) and others. Recently, new studies carried out by the author and co-workers (Gallego 1992, 1999a, 2001a, 2001b, 2005, Gallego & Melchor 2000, Shen *et al*. 2001, Gallego *et al*. 2004) have yielded new records and provided detailed descriptions of Argentinian Triassic spinicaudatan faunas, mainly from the Cuyana and Bermejo basins. In this paper, *Menucoestheria wichmanni* sp. nov. (Eosestheriidae) is described from lower Upper Triassic strata of the Vera Formation (Los Menucos Complex) in Río Negro Province, southern Argentina.

Geological setting

The sedimentary and volcanic rocks exposed around the Los Menucos locality (Río Negro Province) are located in the 'Macizo Nordpatagónico' or 'Macizo de Somún-Curá' (*sensu* Page *et al*. 1999, Kokogian *et al*. 2001) geological province (Fig. 1). Stipanicic (1967) and Stipanicic *et al*. (1968) defined the Los Menucos Basin based on geological and palaeontological data. The rocks bearing spinicaudatans and a typical *Dicroidium* flora are included in a volcaniclastic unit, known previously as the Los Menucos Formation (*sensu* Stipanicic 1967) and recently as the Los Menucos

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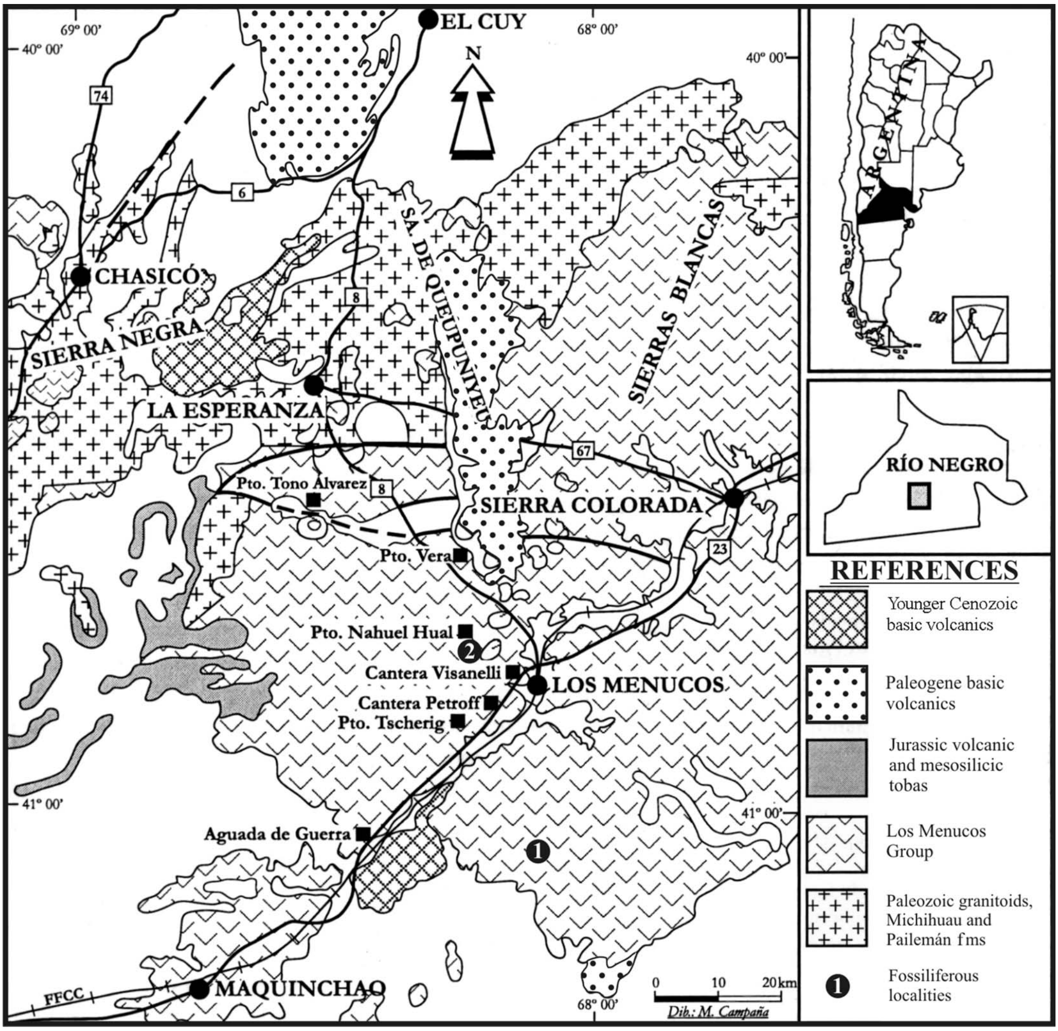

Fig. 1. Geological map of the Los Menucos area showing fossil localities, Río Negro Province, Argentina (adapted from Kokogian *et al.* 2001): **1**. Bajo de Caltrauna, **2**. Puesto Visanelli.

Group (*sensu* Labudía *et al.* 1995, Labudía & Bjerg 2001) or included in the Los Menucos complex (*sensu* Cucchi *et al.* 2001, Lema *et al.* 2005). According to Labudía *et al.* (1995) and Labudía & Bjerg (2001), the Los Menucos 'Group' is 150 m thick and divided into two formations: the Vera and Sierra Colorada formations (Kokogian *et al.* 2001, Labudía & Bjerg 2001, Labudía *et al.* 2002a).

The Vera Formation is characterized by interstratified yellowish-brown conglomeratic lenses, greenish-white cross-bedded sandstones, wackes, reddish-brown to red pelites, laminated tuffites (with plants, fish, spinicaudatans and ichnofossils) and amalgamated pyroclastic flow deposits (ignimbrites and dacitic breccia). The overlying Sierra Colorada Formation (previously known as the Nahuel Hual Formation;

Stipanicic 1967) is composed of pyroclastic flow deposits (rhyolitic ignimbrites) that are 40 m thick (Kokogian *et al.* 2001; Fig. 2).

Labudía *et al.* (1995) suggested that the region was subjected to the influence of explosive volcanic activity during deposition of these units (Los Menucos 'Group'). The landscape incorporated braided and low-gradient fluvial systems associated with marshes and shallow ephemeral lakes, influenced by a seasonal climate with alternating wet and dry conditions. Correspondingly, the palaeoflora through much of the Middle and Late Triassic of Argentina was dominated by mixed forests with meso-xerophytic adaptations, i.e. seasonally dry subtropical forests (Kokogian *et al.* 2001, Brea *et al.* 2008).

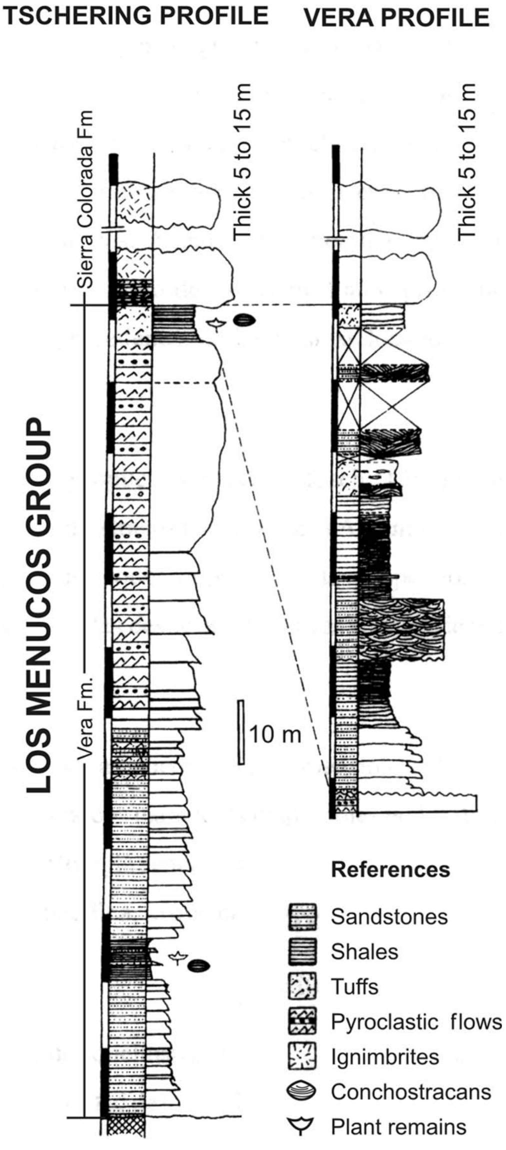

Fig. 2. Stratigraphic section at two localities exposing the Los Menucos Group (Río Negro Province, Argentina), showing the fossiliferous levels (adapted from Labudía *et al.* 1995).

Claudio Iglesias (pers. comm. 1994) indicated that sedimentary facies and facies associations suggest a lacustrine environment, with smooth relief generally dominated by gently settled sediments (as shown by the plant remains preserved parallel to stratification). Pyroclastics (tuffs) deposited in this environment during the dry season would be periodically covered by sandy sediments during humid-season flooding. Dry-season desiccation is reflected by the presence of abundant mud cracks.

The age of this complex, 215–222 ± 2 Ma (Norian), was established by radiometric dating of lava flows in the Sierra Colorada Formation (Kokogian *et al.* 2001, Labudía *et al.* 2002b). The *Dicroidium* flora recorded in the Vera Formation also supports a Late Triassic age (Labudía *et al.* 2002c).

Historical background

According to Manceñido & Damborenea (1984), Wichmann (1927) was the first to record spinicaudatans in the Mesozoic of Río Negro province, in the 'Cerro Colo-Niyeu' among other localities, which allowed him to propose a Late Triassic age for those deposits. Previously, Feruglio (1949) and Casamiquela (1964) concluded the strata were of Middle Jurassic to Early Cretaceous age based on sedimentological, stratigraphical and ichnological evidence. Casamiquela (1975) reinterpreted the ichnological assemblage as Late Triassic.

Manceñido & Damborenea (1984) assigned the Triassic spinicaudatans from Río Negro province to the extant genus *Cyzicus* Audouin, 1837. These authors indicated that the specimens needed detailed studies to confirm whether they represent more than one species and to elucidate their stratigraphic value.

Fossils of the Vera Formation include plants, ichnofossils, scarce actinopterygian fish (first reported here) and 'conchostracans'. Among the abundant megafossil plants are species of *Phyllotheca*, *Cladophlebis*, *Dicroidium, Zuberia*, *Pteruchus*, *Lepidopteris*, *Scytophyllum*, *Dejerseya*, *Pseudoctenis*, *Yabeiella*, *Pterophyllum*, *Taeniopteris*, *Sphenobaiera* and *Heidiphyllum* (Stipanicic & Archangelsky 2002). Artabe *et al.* (2001) defined two palaeocommunities based on this flora from the lower and upper sections of the Vera Formation. Both are included in the BNP Biozone (*Yabeiella brackebuschiana*, *Scytophyllum neuburgianum* and *Rhexoxylon piatnitzkyi* Biozone of Artabe *et al.* 2001), which corresponds to the Cortaderitian stage (ranging from the upper Middle Triassic to the middle Upper Triassic) as defined by Spalletti *et al.* (1999). Artabe *et al.* (2001) characterized the palaeoflora from the Vera Formation as a seasonal subtropical forest.

The ichnofauna includes tetrapod footprints and trackways summarized by Melchor *et al.* (2001) and Domnanovich *et al.* (2008). The ichnological association was named by Casamiquela (1984) as 'Ichnofauna local de Los Menucos' and is dominated by a high diversity of small therapsids, and secondarily includes crurotarsi archosaurs, 'lepidosaurs,' and probable temnospondyls. This ichnological assemblage characterized a fauna endemic to northern Patagonia.

Material and methods

The material described in this paper was collected by Claudio Iglesias during field trips in 1987, 1993, 1994 and 1995. It derives from two localities: Puesto Visanelli, 10 km to the west of Los Menucos town (40°50′31.92″S; 68°4′35.73″W); and Bajo de Caltrauna, 30 km to the south of the latter. Specimens are stored in the Paleozoological Collection, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina (CTES-PZ). Scanning electron micrographs were taken using a JEOL JSM-5800LV Scanning Microscope (of the SECyT-UNNE, Corrientes, Argentina).

Systematic palaeontology

The taxonomy adopted here follows mainly that of Chen & Shen (1985) and Martin & Davis (2001). Measurement abbreviations follow the scheme of Tasch (1987).

Order DIPLOSTRACA Gerstaecker, 1866

Remarks. The name 'Conchostraca' has been widely employed in the literature on the Diplostraca. Recently, however, molecular and morphological analyses have indicated that the 'Conchostraca' is not a monophyletic group and has no taxonomic meaning. It is, therefore, abandoned as a strict taxonomic unit (Fryer 1987, Olesen 1998, Stenderup *et al.* 2006, Li *et al.* 2009a, b,c). Martin & Davis (2001) divided the order Diplostraca into four suborders: Laevicaudata, Spinicaudata, Cyclestherida and Cladocera. Two extinct suborders should be added to this order: Leaiina Kobayashi, 1972 and Estheriellina Kobayashi, 1954 (Shen 2003, 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 EOSESTHERIIDAE Zhang & Chen in Zhang *et al.*, 1976

Menucoestheria Gallego in Gallego & Covacevich, 1998

Type species. *Menucoestheria terneraensis* Gallego in Gallego & Covacevich, 1998. Cerro La Ternera-Atacama region (Chile), La Ternera Formation, Upper Triassic.

Other species. *Menucoestheria puquenensis* Gallego in Gallego & Covacevich, 1998, El Puquén-Coquimbo region (Chile), Pichidangui Formation?, Upper Triassic. *Menucoestheria bocki* Olempska (2004), Krasiejów (Poland), Upper Triassic (late Carnian). *Menucoestheria*? sp. of Olempska (2004), Krasiejów (Poland), Upper Triassic (late Carnian).

Occurrence. La Ternera Formation, Upper Triassic, Quebrada del Carbón (Cerro La Ternera), and La Coipa beds (here considered probably Upper Triassic), La Coipa mine (La Coipa area), both from Atacama region, Chile. Upper Triassic strata of the Biobío River, Santa Juana, Biobío region, Chile. ?Pichidangui Formation, Upper Triassic, El Puquén and Salto del Diablo, Coquimbo region, Chile. ?Profeta Formation, Upper Triassic, Sierra de Varas, Antofagasta region, Chile. Vera Formation, lower Upper Triassic, Bajo de Caltrauna and Puesto Visanelli, Río Negro Province, Argentina. Krasiejów (Poland), Upper Triassic (late Carnian).

Discussion. This genus was informally defined by Gallego (1999a) based on the specimens described here. The previous publication of the material from the Triassic of Chile (*Menucoestheria terneraensis* and *Menucoestheria puquenensis*: see Gallego & Covacevich 1998, Gallego *et al.* 2005) forced the author to designate *M. terneraensis* as the type species of the genus. Kozur & Weems (2007) synonymized *Menucoestheria* with *Anyuanestheria* from the Upper Triassic of China. I disagree with that proposal since *Anyuanestheria* (*sensu* Zhang & Chen in Zhang *et al.*, 1976, original diagnosis) differs in some diagnostic characteristics such as the subquadrate outline and wider growth bands ornamented with moderate reticulations (areolae about 0.03 mm in diameter) that change to linear arrangement in the post-ventral region of the valve, and cross-bars filling in lirae. These features differ clearly with the statement by Kozur & Weems (2007) that '.... The reticulation may be totally replaced by radial lirae, very indistinct, or not present at all'. *Menucoestheria* differs markedly from all other genera of the family Eosestheriidae (see Gallego & Covacevich, 1998, table 2). *Carapacestheria* Shen, 1994 (Early to Middle Jurassic, Antarctica) is the most similar genus. It resembles *Menucoestheria* in the presence of the transitional ornamentation changing laterally from reticulation to radial lirae in the same middle growth band (see Figs 3, 4F this paper; fig. 4b of Shen 1994). It differs slightly in the smaller dimensions of the carapace, polygonal reticulation (areolae 0.02–0.036 mm in diameter) and about 40 radial lirae per millimetre, and with minute punctae filling areolae and occurring between radial lirae, which are lacking in *Menucoestheria* (Fig. 5A). *Abrestheria* Wang, 1981 (Upper Jurassic to Lower Cretaceous, China) resembles *Menucoestheria* in the reticulate-radial lirae ornamentation pattern, and the claviform and triangular tubercle end of the radial lirae when they meet the growth lines. They differ by the presence of the transitional ornamentation changing laterally from reticulation to radial lirae in the same middle growth band and the weakly evident claviform radial lirae in *Menucoestheria*,

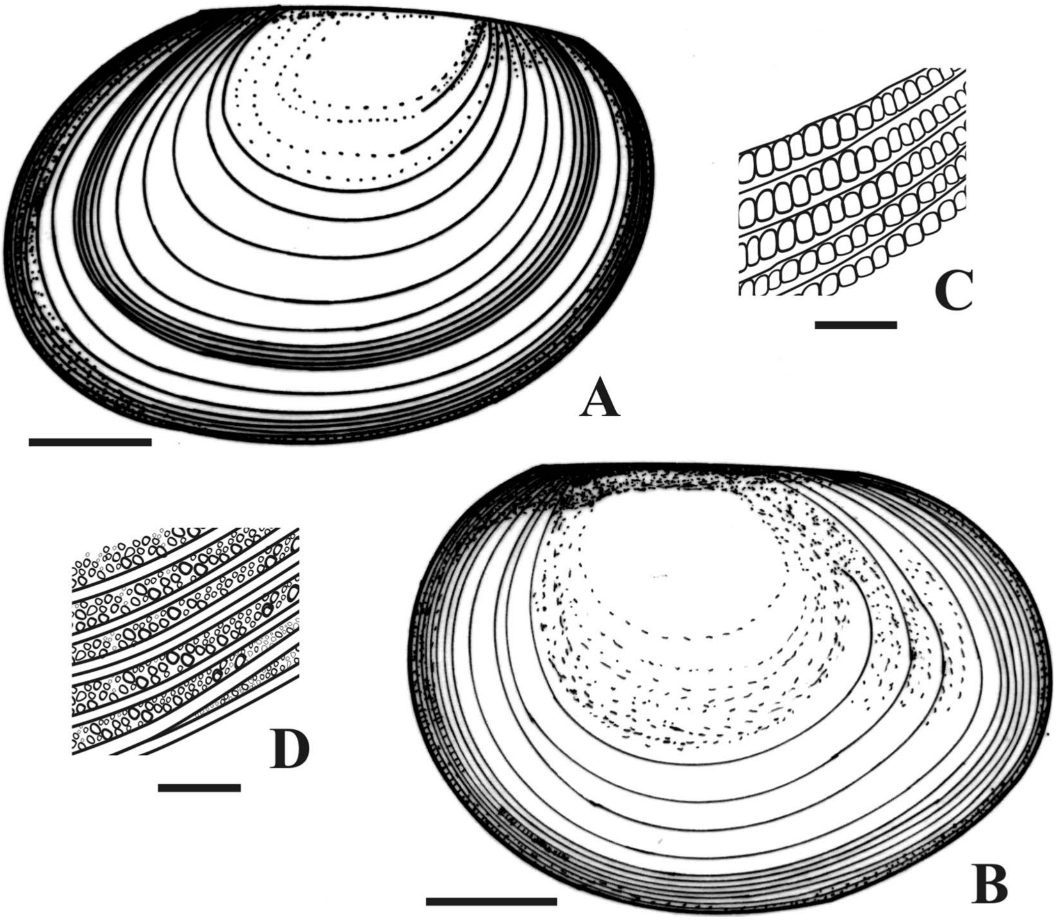

Fig. 3. Menucoestheria wichmanni sp. nov., Bajo de Caltrauma-Puesto Visanelli localities, (Río Negro Province, Argentina). **A**, CTES-PZ 5714, schematic drawing of a right valve with ovate outline. **B**, CTES-PZ 5717 (holotype), schematic drawing of the left valve with subcircular outline. **C–D**, Antero-ventral details of the radial lirae and reticulate ornamentation between growth lines (**C**, CTES-PZ 5713 and **D**, CTES-PZ 5716). Scale bars: A–B = 1 mm, C–D = 0.2 mm.

and fine punctate lumina and growth lines with weak serration in the lower margin of *Abrestheria* (absent in *Menucoestheria*).

Menucoestheria wichmanni sp. nov. (Figs 3; 4A–F; 5A)

Holotype. CTES-PZ N° 5717. Measurements: L (length) 3.8 mm, H (height) 3.0 mm.

Paratypes. CTES-PZ N° 5713 to 5721; 7289 and 7294 (SEM microslides) (50 specimens and hundreds of complete and incomplete carapaces).

Type stratum, age and locality. Vera Formation (lower Upper Triassic); Bajo de Caltrauna and Puesto Visanelli, Río Negro Province, Argentina.

Etymology. In honour of the geologist Dr Ricardo Wichmann (1880 – 1930) for his great contribution to the geology of Patagonia, Argentina.

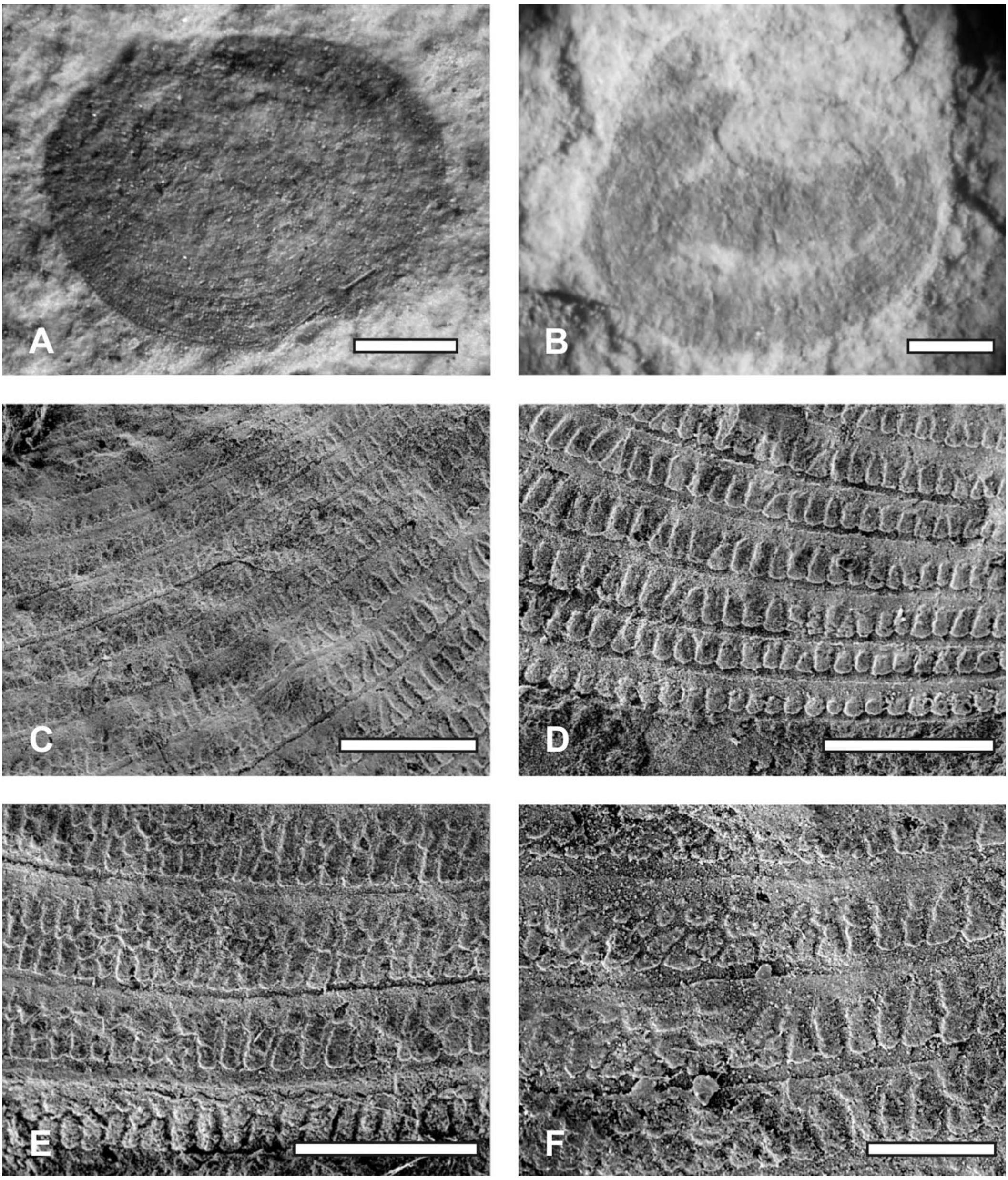

Fig. 4. Menucoestheria wichmanni sp. nov., Puesto Visanelli-Bajo de Caltrauma (Provincia de Río Negro, Argentina). **A**, CTES-PZ 5717, holotype, left valve, subcircular outline (external mould). Scale bar = 1 mm. **B**, CTES-PZ 5714, right valve, ovate outline (external mould). Scale bar = 1 mm. **C**, CTES-PZ 7289, detail of middle region with reticulate ornamentation and the transition to radial lirae. Scale bar = 0.12 mm. **D**, CTES-PZ 7289, anteroventral detail with relatively few radial lirae. Scale bar = 0.25 mm. **E**, CTES-PZ 7289, middle-ventral detail with reticulate ornamentation and the transition to radial lirae. Scale bar = 0.12 mm. **F**, CTES-PZ 7289, detail of middle region with reticulate ornamentation and the transition to radial lirae. Scale bar = 0.06 mm.

Diagnosis. Polymorphic carapace with ovate, elliptical to subcircular outline. Dorsal margin straight to slightly convex. Subterminal umbonal region slightly raised above dorsal margin. Anterior margin shorter and less convex than the posterior, the latter elongated postero-ventrally. Maximum height in middle region of carapace. Ornamentation between growth lines composed of irregular to isodiametrical reticulum (distributed in anterior to mid-dorsal region, areolae with diameters of 0.012–0.050 mm) and radial lirae (reaching ventral and postero-ventral area; lirae 0.012–0.050 mm apart, or 20–80 lirae per mm). Middle region of carapace shows transition between these ornament types.

Occurrence. Vera Formation, lower Upper Triassic, Bajo de Caltrauna and Puesto Visanelli, Río Negro Province, Argentina (Fig. 1, loc. 1).

Description. Small spinicaudatan with polymorphic carapace, with ovate (?females), elliptical (?males) or subcircular (?females) outlines, telliniform and posteriorly elongated. Dorsal margin straight to slightly convex, merging gradually with the anterior and posterior margins (some specimens with a postero-dorsal angle of 125°–130°). Subterminal umbonal region (commonly not preserved) slightly raised above dorsal margin. Anterior margin shorter and less convex than the posterior, the latter elongated postero-ventrally. Ventral margin slightly convex. Maximum height at the middle region of the carapace. Growth lines 16–45, pronounced to indistinct, clearly preserved at the external border of the valve. Growth bands in two incremental categories: those in the medium-dorsal region (0.07–0.19 mm) and those in the ventral area (0.05–0.17 mm; Fig. 4A–F). Ornamentation between growth lines is composed of radial lirae and a reticulum with irregular to isodiametrical areolae. Reticulate ornamentation is distributed in the anterior to mid-dorsal region (mainly in younger moulting stages) with areolae of 0.012–0.050 mm diameter (Fig. 4C). The middle region of the carapace shows the transition between ornamentation types. Two successive growth bands with the irregular reticulum and the radial lirae are evident (Fig. 4F). Radial lirae are present in the ventral and postero-ventral area, perpendicular to the growth lines and separated from each other by 0.025 mm (40 radial lirae per mm). Ultimate growth bands are broader with radial lirae 0.037–0.050 mm apart (or 30–20 radial lirae per mm). The posterior region has radial lirae 0.012 mm apart (80 per mm).

Measurements (in mm). L: 2.94–5.24, H: 1.93–3.58, H/L: 0.58–0.80, Ch: 1.84–3.22, Cr: 0.73–2.11, Av: 0.27–1.10, Arr: 0.55–1.65, a: 0.73–1.56, b: 0.82–1.65, c: 1.38–2.57.

Remarks. *Menucoestheria wichmanni* sp. nov. is similar to *M. terneraensis* and *M. puquenesis* both from the Upper Triassic of Chile. The new species shares the dimorphism or polymorphism of the carapace with *M. terneraensis*, but differs in being smaller and more ovate with a less elongate postero-ventral margin. Although the ornamentation is similar, the Chilean species differs in its great variation in areolae diameter (0.01–0.05 mm) and fewer radial lirae per millimetre (30–75). *Menucoestheria terneraensis* differs further in its rounded reticulate ornamentation, occupying nearly the whole valve surface, and the transition between reticulate-radial lirae ornament being in the ultimate growth bands.

Menucoestheria puquenensis differs from the new species by its elliptical outline and the large range of the ‘Arr’ morphometric parameter (distance from the posterior end of the dorsal margin to the posterior end of the valve). It also differs by its smaller areolae diameter (0.012 mm) and fewer striae per millimetre (40–80).

Of the two species of this genus described by Olempska (2004) from the Upper Triassic (late Carnian) of Poland, *Menucoestheria bocki* differs from the Argentine species by its strongly convex oval outline and convex umbonal region clearly raised above the dorsal margin. The radial lirae are very similar (see Olempska 2004, fig. 9C_4), but the areolae are polygonal not rounded (see Olempska 2004, fig. 9B_3).

Cyzicus (*Lioestheria*) *maugerensis* Tasch, 1987 from the Lower Jurassic of Antarctica, differs from the new species in the location of the umbo and its smaller carapace size; both forms have a similar outline, shape of the anterior and posterior margin and 'hachure type marking' (*sensu* Tasch 1969, 1987) combined with a 'pseudocancellate' ornamentation. *Cyzicus* (*Euestheria*) *taschi* Vallati, 1986 from the Cañadón Asfalto Formation (Middle to Upper Jurassic) of Chubut, Argentina (Vallati 1986), is probably referable to the Eosestheriidae. It differs from *M. wichmanni* by its subovate outline, more convex dorsal margin, larger carapace, more numerous growth lines and reticulation that decreases in areolae diameter towards the hinge.

Development, ontogeny and taphonomy

The spinicaudatan assemblages from both localities are monospecific. The number of specimens per square centimetre ranges from an average of 2.3 (complete specimens) and 5 (fragmentary ones) in Puesto Visanelli locality (levels V_1, V_2 and V_{12}) and 2.8 and 6.3 respectively from Bajo de Caltrauna (levels C_1, C_2 and C_3). The juvenile/adult ratio is 1:1.5. The low diversity/high density assemblage is typical of ephemeral waters with stressed conditions (wet/dry seasonal climate and pyroclastic deposits). The population structure includes male forms (elliptical outline), female forms (ovate and subcircular outlines) and juvenile (ovate outline with an average length of 3 mm) and early immature stages (with lengths < 2.5 mm). The sex ratio is approximately 1:5 (male/female).

The presence of growth bands with variable widths in spinicaudatans and their biological (linked to sex, growth rate, life span and senility) and ecological (associated with food resources, environmental stability, permanent or ephemeral pools) causes 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 growth to reproductive phase. The new species 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 the unfavorable 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.

Ontogenetically, the ornamentation of *Menucoestheria wichmanni* sp. nov. developed from reticulate meshes with a diameter of 0.012 mm in the mid-anterior younger growth bands to reticulation with 0.05 mm areolae in the anterior area; retaining the reticulation with 0.012 mm diameter areolae in the middle carapace region of middle moulting-stage growth bands. In the middle and posterior regions of the same middle moulting-stage growth bands, radial lirae (separated by 0.025 mm) develop by opening the reticulation and developing perpendicular lines. In the antero-ventral region (late moulting stage), the radial lirae are 0.025 mm apart; in the same growth bands the middle region of the carapace shows both the reticulate ornamentation with areolae of 0.012 mm diameter and radial lirae 0.012 – 0.025 mm apart. More ventrally, the latest moulting stage has more widely spaced radial lirae (0.05 mm apart). The space between the radial lirae in the middle region of the carapace is 0.025 mm.

Spinicaudatan taxonomy and ornamentation characters

Species of *Menucoestheria* are the first spinicaudatans in South America that combine both reticulate and radial lirae ornamentation. Traditionally, non-ribbed spinicaudatans (or species without other conspicuous morphological features) are included in the extant genus *Cyzicus*, which has been defined on the basis of soft part characters. The generalized application of the name *Cyzicus* resembles the excessive usage of the name *Estheria* (invalid by homonymy because it is preoccupied by the name of an extant insect) in the 19th century. I agree with Shen (1994) that the classification of living spinicaudatans is based mainly on soft part characters, hence it is very difficult to assign fossil specimens confidently to any modern taxa. Taxonomists have a limited range of simple carapace features to define fossil spinicaudatan taxa. For that reason, it is necessary to consider all carapace features to adequately resolve the identity of fossil spinicaudatans. The Middle Jurassic ‘conchostracan’, *Euestheria luanpingensis* Shen & Niu in Zhang *et al*., 1990, was described with preserved soft parts. If the authors had simply considered the morphology of the carapace, it would have been assigned to *Cyzicus*. However, the soft parts were found to clearly differ from *Cyzicus* and other extant spinicaudatan families. Their contribution gave credence to the idea that it is impossible to identify fossil spinicaudatan taxa (using extant spinicaudatan taxonomy) below the subordinal taxonomic rank.

According to Tasch (1969), *Cyzicus*-type spinicaudatans with reticulate ornamentation (euestheriid type) are referable to the subgenus *Euestheria* and those with radial lirae ornamentation (lioestheriid type) to the subgenus *Lioestheria*. Tasch (1969, 1987) never considered the co-occurrence of these ornamentation types as a diagnostic character to define fossil species. Since the contributions of Zhang *et al*. (1976) and Chen & Shen (1985), ornamentation has been considered one of the main diagnostic features. However, opinions diverge about whether or not ornamentation is a meaningful taxonomic character. For example, Baird (1849), Novozhilov (1954, 1958a,b) and Rohn (1986) favoured its use, whereas Mattox (1957), Defretin (1958), Tasch (1969), Webb (1980) and Stigall Rode *et al*. (2005) claimed otherwise.

Spinicaudatans that combine both types of ornamentation were assigned by Zhang *et al*. (1976) to the superfamily Eosestherioidea and family Eosestheriidae. This family includes *Eosestheria*, *Yanjiestheria*, *Yumenestheria*, *Allestheria*, *Abrestheria*, *Guiestheria*, *Shouchangestheria*, *Turfanograpta*, *Pseudograpta*, *Carapacestheria* and *Menucoestheria*. It ranges from the Upper Triassic to Lower Cretaceous of China, Mongolia, Russia, Korea, Japan, Poland, Germany, Antarctica and South America.

West Gondwanan eosestheriids

West Gondwanan eosestheriids comprise five recorded species: *Menucoestheria puquenensis* (northern and central Chile) and *M. terneraensis* (southern and central Chile), both of Late Triassic age (Gallego & Covacevich 1998, Gallego *et al*. 2005); *M. wichmanni* sp. nov. (from the Late Triassic of southern Argentina, this paper); and

Carapacestheria disgregaris Tasch, 1987 (Shen 1994) and *C. balli* Shen, 1994 from the Middle Jurassic of Antarctica. Other probable members of the Eosestheriidae have also been mentioned (Shen 1994, Gallego & Covacevich 1998, Gallego & Rinaldi 2001, Gallego *et al.* 2005). These Middle to Upper Jurassic taxa from Argentina include *Cyzicus* (*Lioestheria*) *patagoniensis* Tasch in Tasch & Volkheimer, 1970 and *Cyzicus* (*Euestheria*) *taschi* Vallati, 1986 from the Cañadón Asfalto Formation and *Cyzicus* (*Euestheria*) sp. 1 from the Manantial Pelado Formation (Vallati 1986), all from the extra-Andean region of Chubut Province, Argentina.

Furthermore, Shen (1994) suggested that *Cyzicus* (*Lioestheria*) *malacaraensis* Tasch, 1987 from the La Matilde Formation (Middle-Upper Jurassic) of Santa Cruz Province, Argentina, could be an eosestheriid. Current studies, however, suggest that at the type locality of this species (El Malacara farm) '*Cyzicus' malacaraensis* (possibly a fushunograptid or 'lioestheriid' *sensu* Tasch 1969) coexists with a true eosestheriid (probably belonging to *Carapacestheria balli*).

Vallati (1986) mentioned some characters of *Cyzicus* (*Euestheria*) sp. 1 that resemble *Yanjiestheria xiaoxiaensis* Wang, 1983 from the Upper Jurassic to Lower Cretaceous of China. Preliminary observations of new material from the Cañadón Asfalto assemblage confirm this proposal, and also suggest the presence of three species of eosestheriids: *Cyzicus* (*Euestheria*) *taschi* and two new forms.

Other probable members of the family are *Cyzicus* (*Lioestheria*) *maugerensis* and *Cyzicus* (*Euestheria*) *crustapatulus* Tasch, 1987 both from the Middle Jurassic of Antarctica (Shen 1994). According to Shen (1994), the latter species needs re-analysis with scanning electron microscopy for confident identification.

With the exception of *Nigerestheria lamberti* Defretin in Defretin *et al.*, 1956 from the Lower Cretaceous of Africa (Shen 2003), there are no other Gondwanan records of Eosestheriidae. Their presence in other Gondwanan localities should be checked in future research. These diverse Jurassic–Lower Cretaceous records in the Southern Hemisphere suggest the presence of this family since Late Triassic times.

Evolutionary implications

The oldest record of spinicaudatans belonging to the Eosestheriidae in West Gondwana offers new possibilities for understanding the evolution and distribution of this group. The early eosestheriids probably evolved from the 'euestheriid–loxomegaglyptid' group, as proposed by Chen & Hudson (1991), based on studies of Middle Jurassic spinicaudatans from Scotland. This hypothesis for euestheriid ancestry is supported by several characters shared by these forms, such as the reticulate ornamentation with small areolae (around 0.02 mm diameter). In the earliest forms such as *Menucoestheria*, however, the reticulate ornamentation occupies more than 50% of the carapace surface and radial lirae are restricted to the marginal zone of the valve (last five growth bands in *M. terneraensis*). In *Carapacestheria* the reticulate ornamentation occupies more than 85% of the carapace surface and radial lirae are restricted to the last three growth bands, mainly in the middle region of the carapace. It is not clear why, but on the anterior and posterior zones of the carapace in these eosestheriids, the radial lirae occupy more space than that mentioned above. These features are probably related to the growth habit of the carapace, the shape of the valve and the available space between growth lines in the different carapace regions. *Menucoestheria bocki* (Upper Triassic, Poland) resembles *Carapacestheria* in the polygonal reticulum more than other species of *Menucoestheria*, but this does not mean that the latter genus is not a natural taxon. In these features, *M. bocki* also resembles the ornamentation of the *Laxitextella* from the same levels. This supports the hypothesized euestheriid origin of the eosestheriids. Kozur (1982) suggested that the typical Argentine Triassic euestherid *Euestheria forbesi* (Jones, 1862) is a species of *Laxitextella*. This, however, needs to be verified through detailed SEM studies. Research carried out by the author to date does not agree with such a proposal, given that the ornamentation in *E. forbesi* is composed of small rounded areolae (Gallego 1992, 1999a; see Fig. 5C), though more studies are needed to clarify this species' affinities. Kozur & Weems (2007) synonymized *Menucoestheria* with *Anyuanestheria* from the Upper Triassic of China and suggested its evolution from a lineage within *Euestheria*.

A 'loxomegaglyptid' origin is supported by the relatively large number of species (around five) of this group recorded in Triassic sequences of Argentina and Brazil (Gallego 1999a). These records are not yet described but were assigned to *Triasoglypta* by Gallego (1999b). One of these species (*Triasoglypta* sp. 3 from the Potrerillos and Cacheuta formations, Mendoza, Argentina) has large rounded reticulate ornamentation, which at the antero-ventral margin has one areola occupying nearly the complete growth band width giving the appearance of radial lirae (see Fig. 5B).

The eosestheriid spinicaudatans from South America and Antarctica share many characters indicating close taxonomic and evolutionary relationships. From the 'euestheriid–loxomegaglyptid' ancestral forms, *menucoestheriid* type spinicaudatans probably evolved, and this latter group probably gave rise to the *Carapacestheria* and *C. (E.) taschi* types (that share reticulate ornamentation occupying nearly the whole surface of the carapace) as hypothesized by Gallego *et al.* (2005). An unpublished, new Upper Jurassic species from Cañadón Asfalto

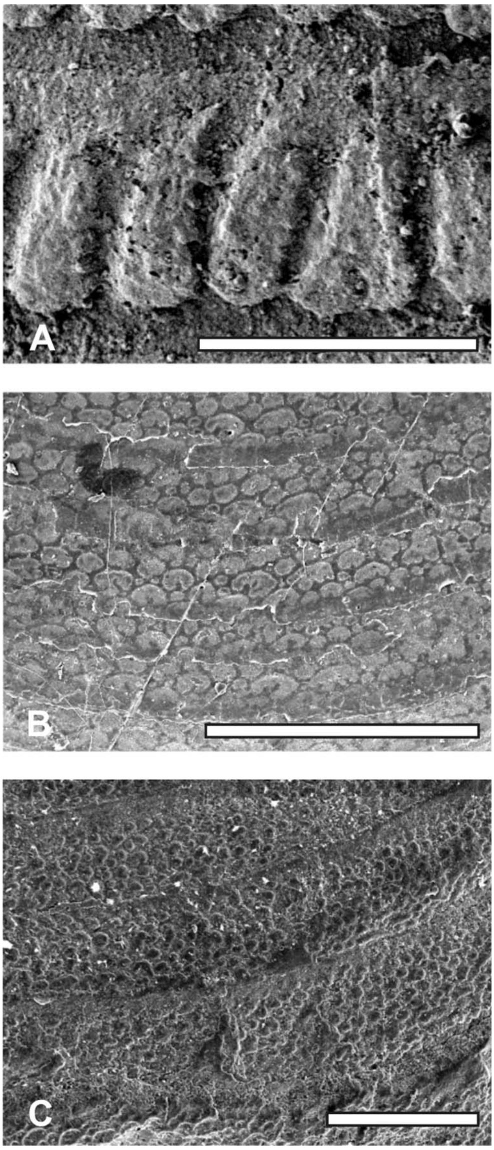

Fig. 5. **A**, *Menucoestheria wichmanni* sp. nov., CTES-PZ 7289, Puesto Visanelli-Bajo de Caltrauma (Río Negro Province, Argentina), ventral detail with the smooth space between radial lirate ornamentation. Scale bar = 0.05 mm. **B**, *Triasoglypta* sp. 3, CTES-PZ 7294, Agua de la Zorra locality (Uspallata, Mendoza Province), Cacheuta Fm (lower Upper Triassic), middle detail with large rounded areolae, locally occupying around half of the growth band. Scale bar = 0.5 mm. **C**, *Euestheria ?forbesi* Jones, 1862, CTES-PZ 7195, Qda. Ischichuca Chica (La Rioja Province), Ischichuca Fm (upper Middle Triassic to lower Upper Triassic), detail of middle region with small areolae. Scale bar = 0.25 mm.

Formation (Chubut province) supports the 'euestheriid' origin based on its ornamentation pattern with fine reticulation (0.01 mm areolae) occupying only the upper third of the carapace, mainly in the upper part of the transitional growth bands.

According to Martins-Neto *et al*. (2003) if such a proposal is accepted, the Jurassic eosestheriid forms subsequently migrated across southern South America through the Antarctic continent to Asia and ?Europe. However, the limited sampling for Mesozoic South American spinicaudatans means that their geographic and temporal ranges remain poorly constrained; hence determining palaeomigration or range-expansion patterns can only be provisional.

More recently, Gallego & Shen (2006) proposed a model of parallel evolution (following origination from a common ancestor) for the similarities between conchostracan faunas from the Northern and Southern hemispheres. The evolutionary relationships between the South American and European Triassic menucoestheriids and eosestheriids remain unresolved.

Conclusions

(1) *Menucoestheria wichmanni* sp. nov. represents the first record of the Eosestheriidae from the Triassic of Argentina and the southernmost occurrence of South American Triassic spinicaudatans. It supports previous findings that the oldest-known members of the Eosestheriidae occur in the Triassic of southern South America. It shows close affinities with Middle Jurassic forms from Antarctica (Tasch 1987, Shen 1994) and possibly constitutes the ancestral stock of Gondwanan eosestheriids.

(2) These specimens further elucidate spinicaudatan architecture, clarify the importance of certain characters (e.g. ornamentation) in spinicaudatan taxonomy and help assess the use of the recent taxon, *Cyzicus* for forms otherwise referable to the subgenera *Euestheria* and *Lioestheria*.

(3) These findings enhance the importance of the *Menucoestheria* species as local stratigraphic indices for Upper Triassic non-marine successions of southern South America (Gallego & Martins-Neto 2005, Gallego *et al*. 2005). *Menucoestheria* spp. and *Polygrapta troncosoi* Gallego characterize Upper Triassic (Carnian) units: the La Ternera and Santa Juana formations (Chile) and Potrerillos, Cacheuta and Vera formations (Argentina).

(4) This record is compatible with the proposal of Martins-Neto *et al*. (2003) that suggests Triassic–Jurassic eosestheriids migrated across southern South America through Antarctica to Asia. It is also consistent with the model of parallel evolution based on the similarities between Chinese and South American spinicaudatan faunas (Gallego & Shen 2006). The evolutionary relationships between the South American and European Triassic menucoestheriids and eosestheriids remain uncertain.

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References

Artabe, A.E., Morel, E.M. & Spalletti, L.A., 2001. Paleoecología de las floras triásicas argentinas. In *El Sistema Triásico en la Argentina*, A.E. Artabe, E.M. Morel & A.B. Zamuner, eds, Fundación Museo de La Plata ‘Francisco Pascasio Moreno,’ La Plata, 99–225.

Audouin, M., 1837. Séance du I-er Février 1837. *Annales de la Société Entomologique de France 6*, 9–11.

Baird, W., 1849. Monograph of the Family Limnadiidae, a family of Entomostracans Crustacea. *Proceedings of the Zoological Society 17*, 84–90.

Brea, M., Artabe, A. & Spalletti, L.A., 2008. Ecological reconstruction of a mixed Middle Triassic forest from Argentina. *Alcheringa 32*, 365–393.

Camacho, H.H., 1995. Los Crustáceos Branquiópodos. In *Contribuciones a la Palaeophytologia Argentina (Partes I a VII)*, P.N. Stipanicic & M.A. Hünicken, eds, Actas de la Academia Nacional de Ciencias 11, Córdoba, 233–234.

Casamiquela, R.M., 1964. *Estudios icnológicos*, Ministerio Asuntos Sociales, Provincia de Río Negro, Buenos Aires, 229 pp.

Casamiquela, R.M., 1975. Nuevo material y reinterpretación de las icnitas mesozoicas (Neotriásicas) de Los Menucos, provincia de Río Negro (Patagonia). *Actas 1° Congreso Argentino de Paleontología y Bioestratigrafía*, San Miguel de Tucumán, 555–580.

Casamiquela, R.M., 1984. Los vertebrados mesozoicos. In *Geología y Recursos Naturales de la Provincia de Río Negro*, V.A. Ramos, ed., *Relatorio 9° Congreso Geológico Argentino 2*, Buenos Aires, 527–538.

Chen, P.J. & Hudson, J.D., 1991. The conchostracan fauna of the Great Estuarine Group, Middle Jurassic, Scotland. *Palaeontology 15*, 515–545.

Chen, P.J. & Shen, Y.B., 1985. *An Introduction to Fossil Conchostraca*, Science Press, Beijing, 241 pp. (in Chinese).

Cucchi, R., Busteros, A. & Lema, H., 2001. Hoja Geológica 4169—II, Los Menucos. *Boletin de IGRM-SEGEMAR 265*, 1–105.

Defretin, S., 1958. Remarques à propos de la Note de N.I. Novojilov sur quelques conchostracés Chinois et Africains. *Société Géologique du Nord Annales 67*, 244–260.

Defretin, S., Joulia, F. & Lapparent, A.F., 1956. Les *Estheria* de la region d'Agadès (Niger). *Bulletim de la Société Geologique de France 7*, 679–690.

Domnanovich, N., Tomassini, R., Manera de Bianco, T. & Dalponte, M., 2008. Nuevos aportes al conocimiento de la icnofauna de tetrápodos del Triásico Superior de Los Menucos (Complejo Los Menucos), provincia de Río Negro, Argentina. *Ameghiniana 45*, 211–224.

Feruglio, E., 1949. Complejo Porfírico de la Patagonia Extra-Andina. In *Descripción Geológica de la Patagonia*, E. Feruglio, ed., Dirección General Yacimientos Petrolíferos Fiscales (YPF), Buenos Aires, 118–139.

Frank, P.W., 1988. Conchostraca. *Palaeogeography, Palaeoclimatology, Palaeoecology 62*, 399–403.

Fryer, G., 1987. A new classification of the branchiopod Crustacea. *Zoological Journal of the Linnean Society 91*, 357–383.

Gallego, O.F., 1992. Conchostracos Triásicos de Mendoza y San Juan, Argentina. *Ameghiniana 29*, 159–175.

Gallego, O.F., 1999a. Estudio Sistemático de las Faunas de Conchostracos Triásicos de la República Argentina. PhD thesis, Facultad de Ciencias Exáctas Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, 210 pp. (unpublished).

Gallego, O.F., 1999b. *Triasoglypta santamariensis* Gallego nov. comb. (Conchostraca) de la Formación Santa María (Tríasico Medio a Superior) Rio Grande do Sul, Brasil. *Revista Universidade Guarulhos, Serie Geociências 4*, 61–66.

Gallego, O.F., 2001a. Conchostracofauna Sudamericana del Paleozoico y Mesozoico: Estado actual del conocimiento. Parte 1: Argentina y Chile. *Acta Geologica Leopoldensia 24*, 311–328.

Gallego, O.F., 2001b. Conchostracofauna Sudamericana del Paleozoico y Mesozoico: Estado actual del conocimiento. Parte 2: Sur de Brasil y Uruguay. *Acta Geologica Leopoldensia 24*, 329–337.

Gallego, O.F., 2005. First record of the family Palaeolimnadiopseidae (Defretin-LeFranc, 1965) from the Triassic of Argentina. *Journal of South American Earth Science 18*, 223–231.

Gallego, O.F. & Covacevich, V., 1998. Conchostracos Triásicos de las Regiones de Antofagasta, Atacama y Coquimbo, Chile. *Revista Geológica de Chile 25*, 115–137.

Gallego, O.F. & Martins-Neto, R.G., 2005. A preliminary approach to stratigraphical distribution of the Triassic insect and conchostracan faunas from southern South America. In R.J. Pankhurst & G.D. Veiga, eds, *Gondwana 12*, Academia Nacional de Ciencias, Mendoza, 164.

Gallego, O.F. & Melchor, R.N., 2000. La Familia Ulugkemiidae Novozhilov, 1958 (Conchostraca) en el Triásico de Argentina: Implicancias Paleobiogeográficas. *Ameghiniana 37*, 47–58.

Gallego, O.F. & Rinaldi, S., 2001. Conchostracofauna Jurásica de la Argentina: antecedentes, perspectivas y su importancia paleontológica y paleobiogeográfica. *Reunión de Comunicaciones Científicas y Tecnológicas*, Secretaría General de Ciencia y Técnica, Universidad Nacional del Nordeste, CD-ROM-Ciencias Biológicas, Corrientes, 58.

Gallego, O.F. & Shen, Y.B., 2006. Jurassic–Cretaceous conchostracan faunas from Asia and South America: relationship, paleogeography and probable evolution-dispersion pattern. *Resúmenes IX Congreso Argentino de Paleontología y Bioestratigrafía*, Academia Nacional de Ciencias, Córdoba, 66.

Gallego, O.F., Zavattieri, A.M. & Lopez Arbarello, A., 2004. Conchóstracos y restos de peces de la Formación Río Mendoza (Mesotriásico) en su localidad tipo, provincia de Mendoza, Argentina. *Ameghiniana 41*, 289–301.

Gallego, O.F., Martins-Neto, R.G. & Nielsen, S.N., 2005. Conchostracans and insects from the Upper Triassic of the Biobío River ('Santa Juana Formation') from Chile. *Revista Geológica de Chile 31*, 293–311.

Geinitz, H.G., 1876. Contribuciones a la Paleontología de la República Argentina. Sobre plantas y animales réticos en las provincias argentinas de La Rioja, San Juan y Mendoza. *Actas Academia Nacional de Ciencias (Traduct. 1925) 8*(3–4), 337–344.

Gerstaecker, A., 1866. Crustacea (Erste Halfe). In *Die Klassen und Ordungen der Thier-Reichs 5 (Arthropoda), 1*, H.G. Bronn, ed., C.F. Winter, Leipzig, 1–1320, Taf.1–49.

Jones, R.T., 1862. A monograph of the fossil Estheriae. *Monographs of the Palaeontographical Society 14*, 1–134.

Jones, R.T., 1897. On some fossil Entomostraca from South America. *Geological Magazine, New Series IV*, *4*, 259–265.

Kobayashi, T., 1954. Fossil estherians and allied fossils. *Journal of the Faculty of Science, University of Tokyo, Section 2*, *9*(1), 1–192.

Kobayashi, T., 1972. On the two discontinuities in the history of the Order Conchostraca. *Proceedings of the Japan Academy 48*, 725–729.

Kokogian, D., Spalletti, L.A., Morel, E.M., Artabe, A.E., Martínez, R.N., Alcober, O.A., Milana, J.P. & Zavattieri, A.M., 2001. Estratigrafía del Triásico argentino. In *El Sistema Triásico en la Argentina*, A.E. Artabe, E.M. Morel & A.B. Zamuner, eds, Fundación Museo de La Plata 'Francisco Pascasio Moreno,' La Plata, 23–54.

Kozur, H.W., 1982. Beiträge zur Taxonomie und Stratigraphischen Auswertung der Untertriassischen Conchostracen. *Geologische und Paläontologische Mitteilungen 11*, 355–398.

Kozur, H.W. & Weems, R.E., 2007. Upper Triassic conchostracan biostratigraphy of the continental rift basin of eastern North America: its importance for correlating Newark Supergroup events with the Germanic Basin and the International Geologic Time Scale. In *The Global Triassic*, S.G. Lucas & J.A. Spielmann, eds, *New Mexico Museum of Natural History and Science Bulletin 41*, 137–187.

Kurtz, F., 1921. Atlas de las Plantas Fósiles de la Rep. Argentina. *Actas Academia Nacional Ciencias 7*, 129–153.

Labudía, C.H. & Bjerg, E.A., 2001. El Grupo Los Menucos: redefinición estratigráfica del Triásico Superior del Macizo Nordpatagónico. *Revista de la Asociación Geológica Argentina 56*, 404–407.

Labudía, C.H., Llambías, E.J., Rapela, C.W. & Artabe, A.E., 1995. El Triásico de Los Menucos: Procesos volcánicos y sedimentarios. *Actas 2° Reunión sobre el Triásico del Cono Sur*, Univerdidad Nacional del Sur, Bahía Blanca, 17–21.

Labudía, C.H., Llambías, E.J. & Stipanicic, P.N., 2002a. Grupo Los Menucos. In *Léxico Estratigráfico de la Argentina, Volúmen VIII, Triásico*, P.N. Stipanicic & C.A. Marsicano, eds, Asociación Geológica Argentina, Serie 'B' (Didáctica y Complementaria) 26, Buenos Aires, 182–183.

Labudía, C.H., Bjerg, E.A., Stipanicic, P.N. & Llambías, E.J., 2002b. Formación Sierra Colorada. In *Léxico Estratigráfico de la Argentina, Volúmen VIII, Triásico*, P.N. Stipanicic & C.A. Marsicano, eds, Serie 'B' (Didáctica y Complementaria) 26, Asociación Geológica Argentina, Buenos Aires, 265.

Labudía, C.H., Llambías, E.J., Bjerg, E.A. & Stipanicic, P.N., 2002c. Formación Vera. In *Léxico Estratigráfico de la Argentina, Volúmen VIII, Triásico*, P.N. Stipanicic & C.A. Marsicano, eds, Serie 'B' (Didáctica y Complementaria) 26, Asociación Geológica Argentina, Buenos Aires, 295–296.

LEMA, H., BUSTEROS, A., GIACOSA, R., DALPONTE, M., GODEAS, M. & ZUBIA, M., 2005. Geología del Macizo Nordpatagónico, Provincia de Río Negro. *Actas 16° Congreso Geológico Argentino, La Plata, 1*, 27–32.

LI, G., CHEN, P., WANG, D. & BATTEN, D.J., 2009a. The spinicaudatan *Tylestheria* and biostratigraphic significance for the age of dinosaur eggs in the Upper Cretaceous Majiacun Formation, Xixia Basin, Henan Province, China. *Cretaceous Research 30*, 477–482.

LI, G., SHEN, Y., LIU, Y., BENGTSON, P., WILLEMS, H. & HIRANO, H., 2009b. Revision of the clam shrimp genus *Magumbonia* from the Upper Jurassic of the Luanping Basin, Hebei, Northern China. *Acta Geologica Sinica 83*, 46–51.

LI, G., WAN, X., BATTEN, D., BENGTSON, P., XI, D. & WANG, P., 2009c. Spinicaudatans from the Upper Cretaceous Nenjiang Formation of the Songliao Basin, northeast China: taxonomy and biostratigraphy. *Cretaceous Research 30*, 687–698.

LINDER, F., 1945. Affinities within the Branchiopoda with notes on some dubious fossils. *Arkiv för Zoologi 37A*, 1–28.

MANCEÑIDO, M.O. & DAMBORENEA, S.E., 1984. Megafauna de invertebrados Paleozoicos y Mesozoicos. In *Geología y Recursos Naturales de la Provincia de Río Negro*, V.A. RAMOS, ed., Relatorio 9° Congreso Geológico Argentino 2, Buenos Aires, 413–465.

MARTIN, J.W. & DAVIS, G.E., 2001. An updated classification of the recent Crustacea. *Natural History Museum of Los Angeles County Contributions in Science 39*, 1–124.

MARTINS-NETO, R.G., GALLEGO, O.F. & MELCHOR, R.N., 2003. The Triassic insect fauna from South America (Brazil, Argentina and Chile): a checklist (except Blattoptera and Coleoptera) and descriptions of new taxa. *Acta Zoologica Cracoviensia 46*, 229–256.

MATTOX, N.T., 1957. A new estheriid conchostracan with a review of other North American forms. *American Midland Naturalist 58*, 367–377.

MELCHOR, R.N., GENISE, J.F. & POIRÉ, D.G., 2001. Icnología de los depósitos continentales triásicos. In A.E. ARTABE, E.M. MOREL & A.B. ZAMUNER, eds, *El Sistema Triásico en la Argentina*, Fundación Museo de La Plata 'Francisco Pascasio Moreno,' La Plata, 185–198.

NOVOZHILOV, N.I., 1954. Crustacés phyllopodes du Jurassique supérieur et du Crétacé de la Mongolie. *Travaux Institut Páleontologique Academie des Sciences de l'URRS 48*, 7–124.

NOVOZHILOV, N.I., 1958a. Crustacés bivalves de l'ordre des Conchostracés du Crétacé inférieur Chinois et Africain. *Société Géologique du Nord, Extrait des Annales 67*, 235–243.

NOVOZHILOV, N.I., 1958b. Recueil d'articles sur les phyllopodes conchostracés. *Service de Information Géologique, Annales, Bureau de Recherches Géologique, Géophysiques et Miniéres 26*, 1–135.

OLEMPSKA, E., 2004. Late Triassic spinicaudatan crustaceans from southwestern Poland. *Acta Palaeontologica Polonica 49*, 429–442.

OLESEN, J., 1998. A phylogenetic analysis of the Conchostraca and Cladocera (Crustacea, Branchiopoda, Diplostraca). *Zoological Journal of Linnean Society*, *122*, 491–536.

PAGE, R., ARDOLINO, A., DE BARRIO, R.E., FRANCHI, M., LIZUAIN, A., PAGE, S. & SILVA NIETO, D., 1999. Estratigrafía del Jurásico y Cretácico del Macizo de Somún Curá, Provincias de Río Negro y Chubut, In *Geología de la República Argentina*, R. CAMINOS, ed., Instituto de Geología y Recursos Minerales 29(17), Buenos Aires, 460–488.

PHILLIPI, R.A., 1887. *Die Tertiären und Quartären Versteinerungen Chiles*, F.A. Brockhaus, Leipzig, 266 pp.

ROHN, R., 1986. Caracteres diagnósticos dos conchostráceos fósseis—exemplos da Formaçâo Rio do Rasto (Permiano Superior, Bacia do Paraná). *Anais da Academia Brasileira de Ciências 58*, 596.

RUSCONI, C., 1948a. Algunas especies de Estherias del Triásico en Mendoza. *Revista del Museo de Historia Natural 2*, 199–202.

RUSCONI, C., 1948b. Apuntes sobre el Triásico y el Ordovícico de El Challao, Mendoza. *Revista del Museo de Historia Natural 2*, 165–198.

SHEN, Y.B., 1994. Jurassic conchostracans from Carapace Nunatak, southern Victoria Land, Antarctica. *Antarctic Science 6*, 105–113.

SHEN, Y.B., 2003. Review of the classification of the Family Afrograptidae (Crustacea: Conchostraca). *Acta Palaeontologica Sinica 42*, 590–597.

SHEN, Y.B. & HUANG, D., 2008. Extant clam shrimp egg morphology: taxonomy and comparison with other fossil branchiopod eggs. *Journal of Crustacean Biology 28*, 342–350.

SHEN, Y.B., GALLEGO, O.F. & ZAVATTIERI, A.M., 2001. A new conchostracan genus from the Triassic Potrerillos Formation, Argentina. *Acta Geologica Leopoldensia 24*, 227–236.

SHEN, Y.B, GALLEGO, O.F., BUCHHEIM, H.P. & BIAGGI, R.E., 2006. Eocene conchostracans from the Laney Member of the Green River Formation, Wyoming, USA. *Journal of Paleontology 80*, 447–454.

SPALLETTI, L.A., ARTABE, A.E., MOREL, E.M. & BREA, M., 1999. Biozonación paleoflorística y cronoestratigráfica del Triásico Argentino. *Ameghiniana 36*, 419–451.

STENDERUP, J.T., OLESEN, J. & GLENNER, H., 2006. Molecular phylogeny of the Branchiopoda (Crustacea)—Multiple approaches suggest a 'diplostracan' ancestry of the Notostraca. *Molecular Phylogenetics and Evolution 41*, 182–194.

STIGALL, A.L. & HARTMAN, J.H., 2008. A new spinicaudatan genus (Crustacea: 'Conchostraca') from the Late Cretaceous of Madagascar. *Palaeontology 51*, 1053–1067.

Stigall Rode, A.L., Leslie, S.A. & Babcock, L.E., 2005. Ontogenetic change in the microstructure of Jurassic conchostracans (Crustacea, Spinicaudata, Cyzicidae) from Antarctica: implications for conchostracan phylogeny and taxonomy. *PaleoBios 25*, 112–113.

Stipanicic, P.N., 1967. Consideraciones sobre las edades de algunas fases magmáticas del Neopaleozoico y Mesozoico. *Revista de la Asociación Geológica Argentina 22*, 101–133.

Stipanicic, P.N. & Archangelsky, S., 2002. Megafloras. In *Léxico Estratigráfico de la Argentina, Volúmen VIII, Triásico*, P.N. Stipanicic & C.A. Marsicano, eds, Serie 'B' (Didáctica y Complementaria) 26, Asociación Geológica Argentina, Buenos Aires, 309–313.

Stipanicic, P.N., Rodrigo, F., Baulies, O. & Martinez, C., 1968. Las formaciones presenonianas en el denominado Macizo Nordpatagónico y regiones adyacentes. *Revista de la Asociación Geológica Argentina 23*, 67–98.

Tasch, P., 1969. Branchiopoda. In *Treatise on Invertebrate Paleontology. Part R, Arthropoda 4(1)*, R.C. Moore, ed., University of Kansas, Lawrence, R141–R163.

Tasch, P., 1987. Fossil Conchostraca of the Southern Hemisphere and continental drift. Paleontology, biostratigraphy and dispersal. *The Geological Society of America, Memoir 165*, 1–290.

Tasch, P. & Volkheimer, W., 1970. Jurassic conchostracans from Patagonia. *The University of Kansas Paleontological Contributions 50*, 1–23.

Vallati, P., 1986. Conchostracos Jurásicos de la Provincia de Chubut, Argentina. *Actas 4° Congreso Argentino de Paleontología y Bioestratigrafía 4*, Mendoza, 29–38.

Wang, S., 1981. On Upper Jurassic phyllopods (Conchostraca) from northern Hebei and Daxinganling and their significance. *Bulletin of the Institute of Geology, Chinese Academy of Geological Sciences 3*, 97–118, pls 1–4 (in Chinese, English abstract).

Wang, S.E., 1983. Some Jurassic conchostracans from Quinghai. *Acta Paleontologica Sinica 22*, 460–466.

Webb, J.A., 1979. A reappraisal of the palaeoecology of conchostracans (Crustacea: Branchiopoda). *Neues Jahrbuch fur Geologie und Palaontologie Abhandlungen 158*, 259–275.

Webb, J.A., 1980. Aspects of the Palaeontology of Triassic Continental Sediments in South-East, Queensland. Section 2, Vol. 2. PhD thesis, Department of Geology and Mineralogy. University of Queensland, 69 pp. (unpublished).

Weeks, S.C., Marcus, V. & Alvarez, S., 1997. Notes on the life history of the clam shrimp *Eulimnadia texana*. *Hydrobiologia 359*, 191–197.

Wichmann, B., 1927. Resultados de un viaje de estudios geológicos en los territorios de Río Negro y del Chubut efectuado durante los meses de enero hasta junio del año 1923. *Publicaciones Dirección General de Minas, Geología e Hidrogeología 33*, 1–59.

Zhang, W.T., Chen, P.J. & Shen, Y.B., 1976. *Fossil Conchostraca of China*. Science Press, Beijing, 325 pp. (in Chinese).

Zhang, W.T., Shen, Y.B. & Niu, S., 1990. Discovery of Jurassic conchostracans with well-preserved soft parts and notes on its biological significance. *Palaeontologia Cathayana 5*, 311–352.