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The first spinicaudatan (Crustacea: Diplostraca) from Permo-Triassic continental sequences of South America and its palaeoecological context

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Cornia martinsnetoi sp. nov., the first spinicaudatan from Permian–Triassic continental sequences of southern South America, is described. The new species has characters diagnostic of the typical late Palaeozoic–Early Triassic subfamily Vertexiinae from Gondwana. This new taxon was found in tuffaceous siltstones in the upper part of the Quebrada de los Fósiles Formation (Puesto Viejo Group), which may span the Permo-Triassic boundary in Argentina. The lower and coarser-grained interval of the Quebrada de los Fósiles Formation was deposited in distal alluvial fans and low- to high-sinuosity rivers. The upper fine-grained interval of this formation, which hosts the spinicaudatans and associated fossils (ostracods, megaspores, fish scales), was deposited in shallow floodplain lakes. Intense volcanic activity influenced the sedimentary evolution of this succession and was accompanied by aridification and some climatic seasonality that likely generated stressful conditions for the biota. Previous biostratigraphic studies support an Early Triassic age for the beds containing *Cornia martinsnetoi* sp. nov.

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Key words: Spinicaudata, Conchostraca, Permo-Triassic, Puesto Viejo Group, San Rafael Block, Argentina.

THE PERMIAN–TRIASSIC boundary is poorly documented in South America, being represented by only a few exposed sedimentary sections. In Argentina, this boundary may be positioned at the base of the continental sediments and volcanic rocks of the Puesto Viejo Group (Stipanicic *et al*. 2007), which represents the final stage of magmatism and sedimentation on the San Rafael Block (Criado Roque 1972), southern Mendoza province.

The Puesto Viejo Group comprises a continental volcaniclastic succession with intercalated ignimbrites and basalts. These were originally assigned to the Puesto Viejo Formation by González Díaz (1964, 1972) who considered the unit to be Triassic in age. This author had already distinguished two packages in the formation based on lithological criteria. Later, Stipanicic *et al.* (2007) raised this unit to the Puesto Viejo Group recognizing two subunits based on palaeontological and lithological characters. The lower unit (Quebrada de los Fósiles Formation) is characterized mainly by fine-grained, grey–greenish sedimentary rocks intercalated with ignimbrites and basalts. The upper unit (Río Seco de la Quebrada Formation) consists mainly of coarser red beds and acid volcanic rocks. The Puesto Viejo Group is significant because it contains one of the oldest and best-preserved Mesozoic tetrapod assemblages of South America (Abdala *et al*. 2009, Martinelli *et al*. 2009, Ezcurra *et al*. 2010, Martinelli 2010 and references mentioned therein).

Only vertebrates (dicynodonts and cynodonts) have been recorded from the coarser red beds of the Río Seco de la Quebrada Formation, and these faunas were correlated with South African assemblages (Bonaparte 1966a, b, 1969, Abdala 1996, Martinelli & De La Fuente 2008, Martinelli *et al*. 2009, Martinelli 2010). The fauna was originally correlated to the *Cynognathus* Assemblage Zone of South Africa (Bonaparte 1981) suggesting an Olenekian (e.g. Bonaparte 1969b, 1973, 1981, Lucas 1998) or Anisian age (Bonaparte 1966c, 1967). However, it was recently referred to the Middle Triassic based exclusively on its cynodont content (Martinelli *et al*. 2009).

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The palaeontological record of the lower unit (Quebrada de los Fósiles Formation) is more diverse. Dicynodonts and a basal archosauriform (Bonaparte 1981, Domnanovich & Marsicano 2009, Ezcurra *et al.* 2010) from this formation were correlated with the *Lystrosaurus* Assemblage Zone of South Africa and, therefore, considered Early Triassic in age. This unit has a sparse fossil flora including lycophytes (*Pleuromeia*) that favour an Early Triassic age (Morel & Artabe 1993, Stipanicic 1969, Stipanicic *et al.* 2007). More recently, articulated equisetalean remains, coniferalean trunks and leaves, lycopsid megaspores, unidentified seeds, ostracods and fish scales were recovered (Gallego *et al.* 2009) from the fluvial–lacustrine section of the Quebrada de los Fósiles Formation. Ottone & Garcia (1991) described a palynological assemblage from the *ex* Puesto Viejo Formation (González Díaz 1972) that indicated an Early to early Middle Triassic age. However, other palynological studies carried out on this unit suggest an earliest Triassic or even latest Permian age (Zavattieri *et al.* 2003, Sepúlveda *et al.* 2007, Stipanicic *et al.* 2007). Thus, an accurate age range for the Puesto Viejo Group remains unclear. Nevertheless, it likely corresponds to the oldest exposed Triassic succession in Argentina, with an age close to the Permian–Triassic boundary.

The present contribution describes the first Spinicaudata from the Permo-Triassic interval of South America based on material from the Quebrada de los Fósiles Formation (=*ex* Puesto Viejo Formation type locality). The new species has diagnostic morphological features of the typical late Palaeozoic–Early Triassic genus *Cornia* Lyutkevich, 1937 belonging to the subfamily Vertexiinae. According to Ghosh (2011), vertexiinids originated during the Carboniferous in Europe, being well represented in Russia and Germany at that time. Ghosh (2011) also noticed similarities in the carapace size between Indian and Russian forms, giving further support to the idea of Eastern Europe to India faunal interchange during the Early Triassic, as proposed by Novojilov (1970).

Geological setting

The continental volcaniclastic sequences of the Puesto Viejo Group crop out in the region called 'Sierra Pintada', approximately 35°S and 68°20′W, with a general NNW–SSE strike, southwest of San Rafael city, Mendoza Province, Argentina (Fig. 1). The Puesto Viejo Group (Stipanicic *et al.* 2002; = Puesto Viejo Formation, *sensu* González Díaz 1972) consists of synrift-continental successions of sedimentary deposits *ca* 300 m thick (Spalletti 1994, 1995; Spalletti *et al.* 1996) intercalated with intermediate to mafic volcanics (andesites and basalts) and acid ignimbrites that crop out in the San Rafael Block (Kleiman & Japas 2009, Valencio *et al.* 1975). They rest with erosional unconformity on the extrusive rocks of the Cerro Carrizalito Group (González Díaz 1972) of Middle Permian age (Valencio *et al.* 1975, Ottone & Ostera 2006; Fig. 2).

The spinicaudatan assemblage described herein derives from the type section of the Quebrada de los Fósiles Formation, at Agua de los Burros (Fig. 2). Spalletti (1994) described the lithological and sedimentological characteristics of the type section in detail and noted that this unit locally rests unconformably on Upper Choiyoi volcanics and corresponds to the final stage of Gondwanan magmatism in the San Rafael Massif (Kleiman & Salvarredi 2001, Kleiman & Japas 2009). In the Agua de los Burros section (Fig. 3) the sedimentary succession starts with thick multi-storey lenticular conglomerates, conglomeratic sandstones and coarse-grained sandstones in trough cross-stratified sets and/or massive or plane bedded beds. This unit grades upwards into massive mudstones intercalated with massive and/or wavy parallel laminated sandstones. This basal facies association was interpreted by Spalletti (1994) to correspond to a low-sinuosity gravely river deposit. The succession is truncated by an intrusive thick basalt mantle. Further upwards, the fluvial cycles were deposited under largely high-sinuosity meandering channels and floodplain conditions. The channels are represented by thick trough cross-stratified conglomeratic sandstones and sandstones that fine progressively upwards to facies representative of a lower flow-regime. Floodplain facies are thick intervals dominated by massive and laminated greenish–grey mudstones, siltstones and tuffaceous mudstones with well-developed palaeosols, evidenced by fine and dense root cast systems. Minor and scattered sandy lenticular bodies and wedge-shaped coarsening-up siltstones and medium-grained sandstones are interpreted to represent crevasse channel and crevasse splay deposits. The fossil levels identified in the type locality of the Quebrada de los Fósiles Formation are located in the floodplain facies of the lowermost high-sinuosity fluvial system that pass laterally into shallow lacustrine deposits characterized by greenish to whitish shale banks, in which thin limestone levels with biological (stromatolite-like) structures are interbedded. The package of interest (Fig. 3) consists of tuffaceous, whitish, laminated siltstones interbedded with light yellow-orange laminated carbonate layers and light grey to whitish mudstones having fine, densely distributed, root casts (palaeosols). This spinicaudatan-bearing interval also yields abundant silicified megaspores, ostracod impressions and a few fish scales. The upper part of the Agua de Los Burros section is composed of thick amalgamated felsic pyroclastic flow deposits, ranging from lapilli to massive tuffaceous siltstones. The sequence terminates with overlapping sheets of dark pink ignimbrite *ca* 12–15 m thick (Fig. 3).

Material and methods

For morphometric measurements (41 specimens in total), we used a Leitz-Wetzlar binocular microscope

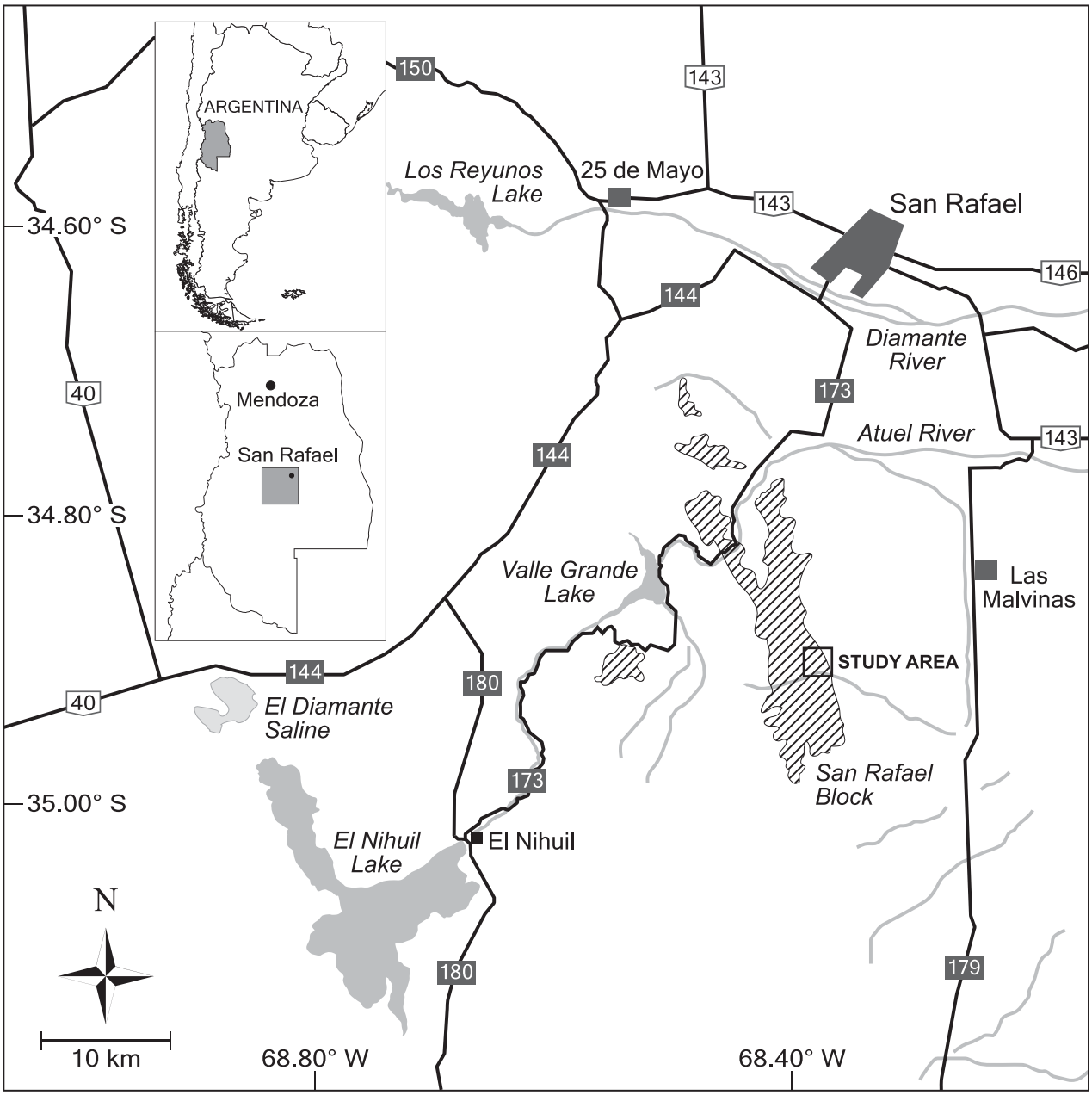

Fig. 1.. Location map of the studied exposures of the Puesto Viejo Group, San Rafael Block, South of Mendoza, Argentina.

(Centro de Ecología Aplicada del Litoral—Centro Científico Tecnológico Nordeste—Consejo Nacional de Investigaciones Científicas y Técnicas) and follow the Defretin Le-Franc measurement system (Tasch 1987). SEM studies and photomicrographs were undertaken using a JEOL JSM-5800LV scanning electron microscope at the Secretaría General de Ciencia y Técnica—Universidad Nacional del Nordeste, Corrientes, Argentina. The holotype and paratypes are deposited in the palaeoinvertebrate repository at the Natural History Museum of San Rafael, Mendoza Province, Argentina (MHNSR-PI). Additional studied materials referred to in this contribution and the SEM samples are deposited in the repository of the Colección Paleontológica de la Universidad Nacional del Nordeste (UNNE), Corrientes, Corrientes Province, Argentina (CTES-PZ). The samples were collected during a field trip conducted by the authors in 2010.

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

Systematic palaeontology

Class CRUSTACEA Pennant, 1777

Order DIPLOSTRACA Gerstaecker, 1866

Remarks. Recent studies (Martin & Davis 2001) based on molecular and morphological analyses, indicate a non-monophyletic status for 'Conchostraca', hence this group is no longer considered a strict taxonomic unit (Fryer 1987, Olesen 1998, Stenderup *et al*. 2006, Li *et al*.

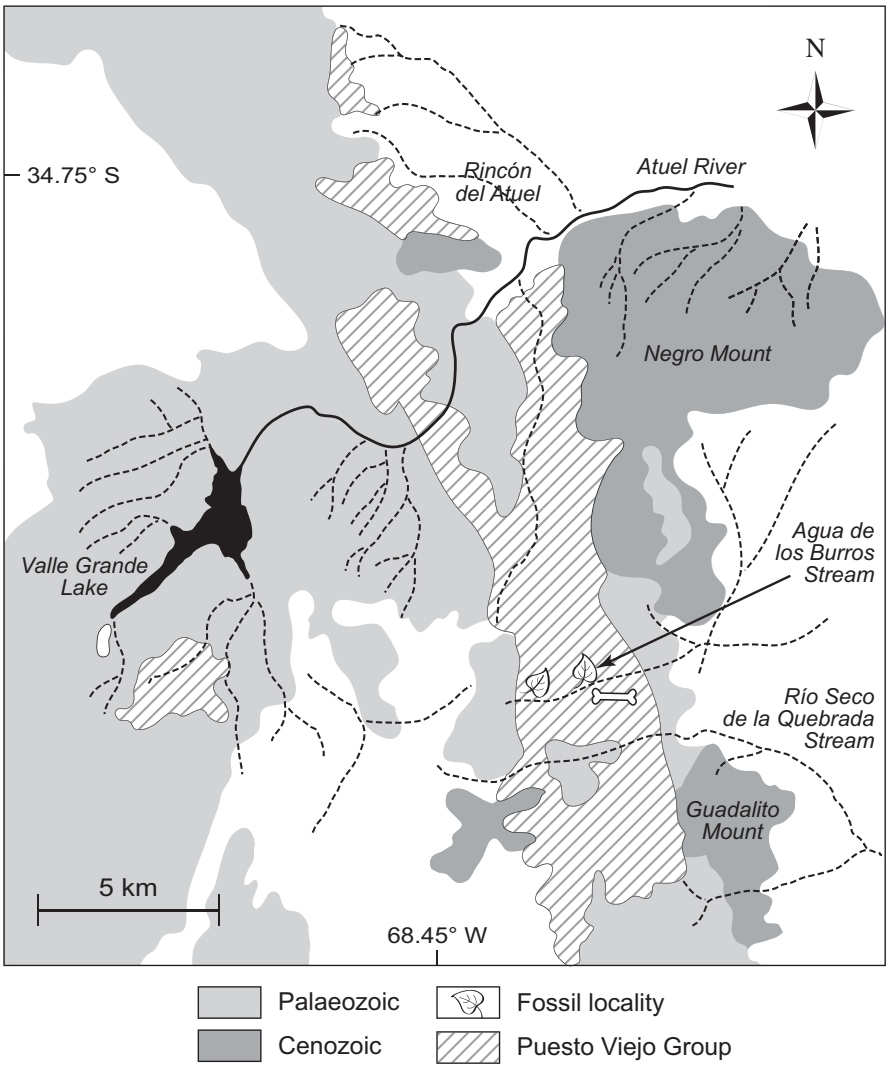

Fig. 2.. Schematic geologic map of the study area showing the distribution of the Quebrada de Los Fósiles Formation, Puesto Viejo Group, with the fossiliferous localities indicated.

2009a, b, c). According to Martin & Davis (2001), Diplostraca is now divided into four extant suborders (Laevicaudata, Spinicaudata, Cyclestherida and Cladocera); however, Shen (2003, 2011), Shen *et al*. (2006), and Shen & Huang (2008) proposed the incorporation of two extinct suborders (Leaiina and Estheriellina). The terms 'clam-shrimp' and 'conchostraca' are still useful to make reference to laevicaudatans, spinicaudatans, leaiids, estherielliids and cyclestherids in non-technical publications.

Suborder SPINICAUDATA Linder, 1945
Superfamily LIOESTHERIOIDEA Raymond, 1946
Family LIOESTHERIIDAE Raymond, 1946
Subfamily VERTEXIINAE Kobayashi, 1954

Cornia Lyutkevich, 1937

Type species. *Cornia papillaria* Lyutkevich, 1937, Upper Permian (Changhsingian), Kuznetsk Basin, Siberia, Russia.

Remarks. The original diagnosis of *Cornia* Lyutkevich, 1937 (in Tasch 1969, 1987) briefly described the umbo and ornamentation morphologies, mentioning the presence of a spine or tubercle in the umbonal area and a punctate ornamentation. More recent studies by Ghosh (2011) and new investigations of *Cornia* show that a greater range of morphological variation is present such as a granulate ornamentation (*C. sonensis*, *C. spinosus* and *C. martinsnetoi* sp. nov.) and a rib-like node (*C. panchetella* and *C. martinsnetoi*). These features suggest that more detailed studies and an emended diagnosis are necessary for this genus.

Cornia martinsnetoi sp. nov. (Figs 4A–H, 5A–H)

Holotype. MHNSR-PI 1128.

Paratypes. MHNSR-PI 1129–1134; CTES-PZ 7550–7551.

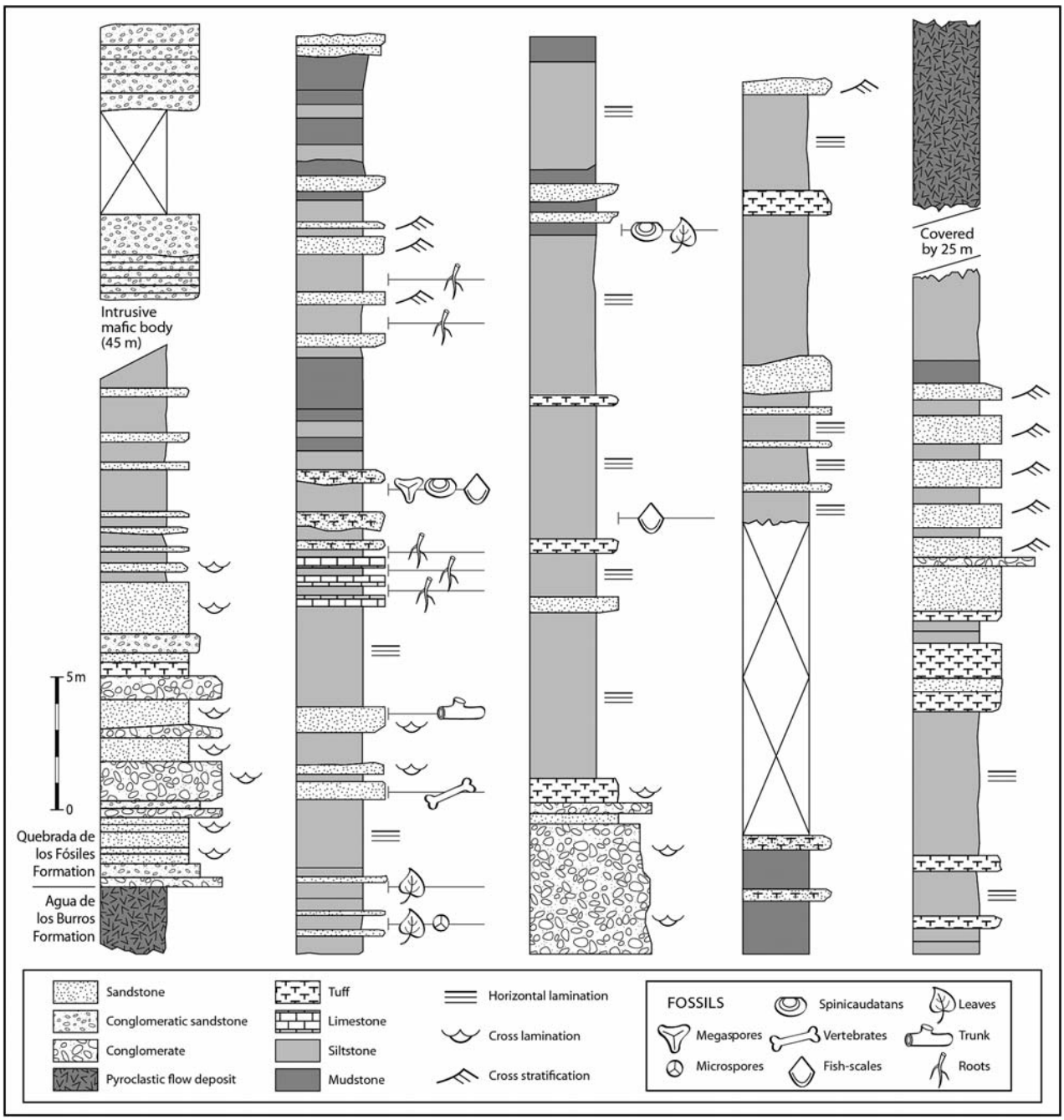

Fig. 3.. Geological section at Agua de Los Burros (Quebrada de Los Fósiles); modified from Spalletti (1994).

Type locality, unit and age. Quebrada de los Fósiles Formation, Puesto Viejo Group, Permo-Triassic interval, San Rafael Block, Mendoza Province, Argentina.

Etymology. In memorium of the Brazilian palaeoentomologist Rafael Gioia Martins-Neto.

Diagnosis. Small carapace valve sub-trapeziform, subquadrate to subovate in outline; convex prominent central to sub-central umbo, occupying around one-fifth of the valve and bearing a vertical rib-like node; straight to slightly curved dorsal margin with short anterior and posterior branches forming obtuse angles at both ends, posterior margin slightly elongated relative to the slightly convex anterior one, growth bands ornamented by small grana providing a granulate texture.

Description. Small spinicaudatan carapace valve subtrapeziform (?female, Fig. 4A, B), subquadrate (?juvenile female, Fig. 4C) to subovate (?male, Fig. 4D) in outline; multilamellar shell structure reaching *ca* 30 μm thick in the middle of the valve (Fig. 5E, F). Smooth convex umbo placed central to subcentrally, raised above the dorsal margin and occupying around one-fifth of the valve surface. Umbo bears a short central rib-like node, which is vertically aligned and approximately 164

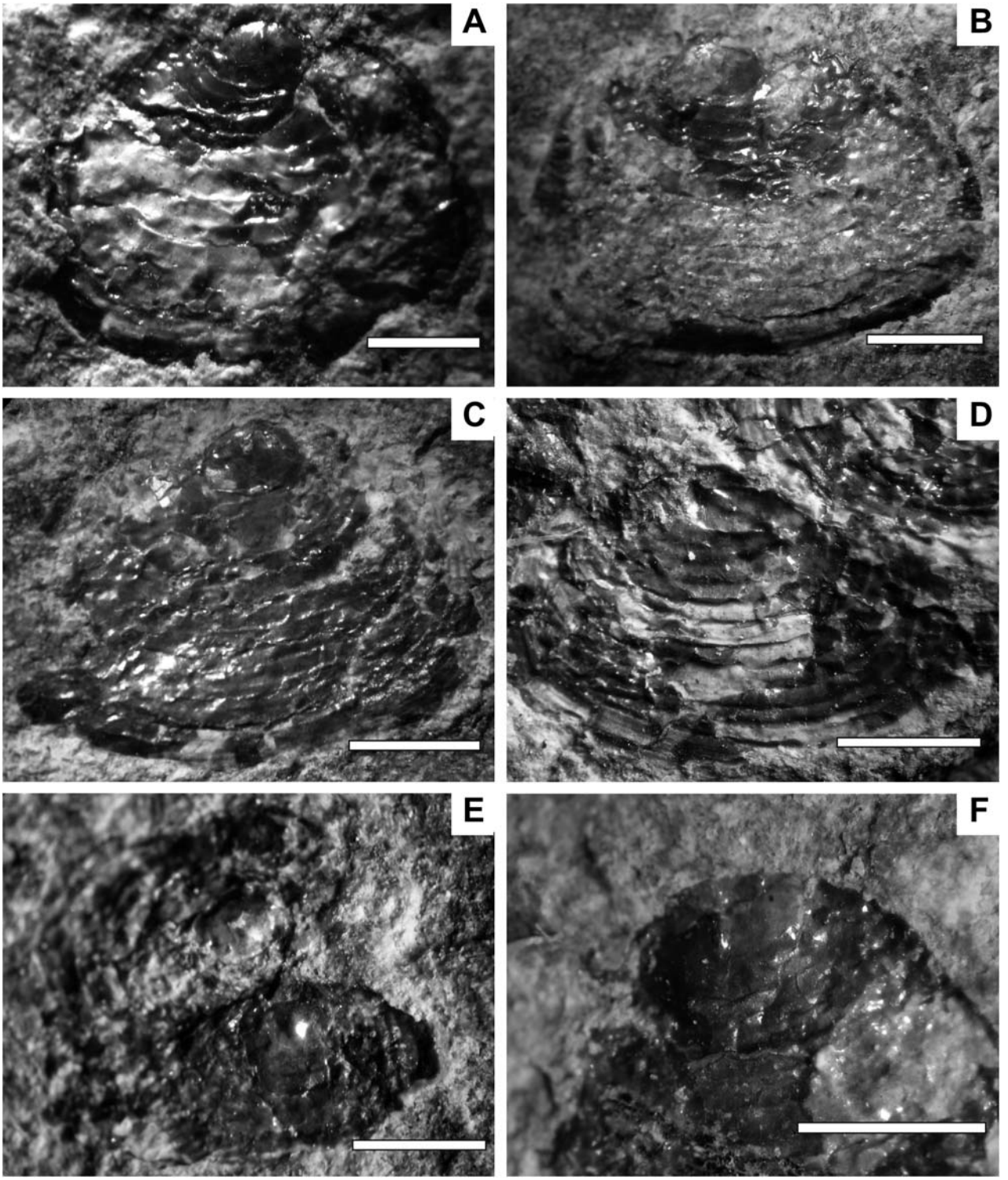

Fig. 4.. Cornia martinsnetoi sp. nov., Quebrada de los Fósiles Formation, Puesto Viejo Group (Mendoza Province, Argentina). **A**, MHNSR-PI 1128A holotype, right female? valve, subtrapeziform outline; vertical rib-like node indicated by the shaft. **B**, MHNSR-PI 1128B, paratype, left female? valve, sub-trapezoidal outline. **C**, CTES-PZ 7551, paratype, right female? valve, sub-trapezoidal outline, prominent central umbo as indicated by the shaft. **D**, MHNSR-PI 1133, paratype, left female? juvenile valve, subquadrate outline. **E**, MHNSR-PI 1130, paratype, right and left juvenile male? valves in opened 'butterfly' position indicating decomposition before burial. **F**, CTES-PZ 7551, paratype, detail of the rib-like node. Scale bar = 1 mm.

μm long (Fig. 5A, B). The maximum height is in the middle of the carapace. Straight to slightly curved dorsal margin with two portions separated by the umbo, the posterior part being slightly longer than the anterior part. Both portions join abruptly with the anterior and posterior margins, at obtuse angles. Subtrapeziform carapaces have a larger ventrally elongated posterior margin compared with the slightly convex anterior one.

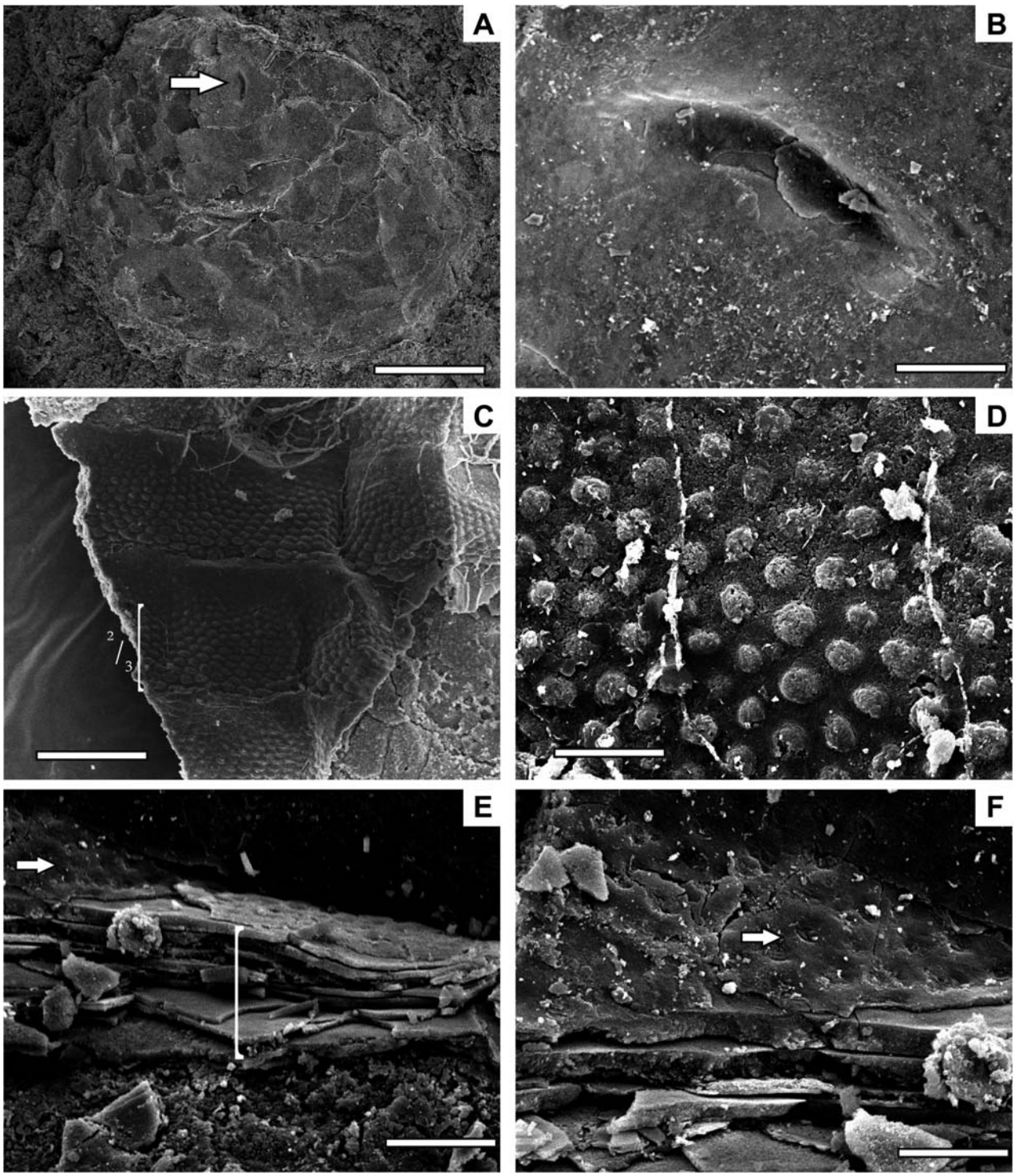

Fig. 5.. Cornia martinsnetoi sp. nov., Quebrada de los Fósiles Formation, Puesto Viejo Group (Mendoza Province, Argentina). **A, B**, CTES-PZ 7551A, general view (**A**) of the valve (scale bar = 600 μm) and dorsal detail (**B**) showing the smooth umbonal zone with the rib-like node vertically aligned and around 164 μm long (scale bar = 66.5 μm). **C**, CTES-PZ 7550, detail of the ornamentation occupying the lower two-thirds of the growth band and showing that grana dimensions increase in size ventrally (scale bar = 100 μm). **D**, CTES-PZ 7550, granulate ornamentation, with diameter ranging from 1.87 μm to 5.36 μm (scale bar = 53 μm). **E**, Multilamellar shell structure reaching *ca* 30 μm thick in the middle of the valve (scale bar = 16.5 μm); and **F**, Detail of Fig. 1E showing shell structure with multiple layers of cuticle and the upper (outer?) layer with depressions of the ornamentation (scale bar = 30 μm).

Nine to 16 wide growth bands are uniformly spaced in the middle part of the valve and closely spaced near the ventral margin, and bear small rounded granulate ornamentation. This ornamentation creates a granulate texture when preserved in positive relief (where the outer surface of the valve is preserved) in around 50% of the studied specimens. In negative impressions, the ornamentation appears as small holes forming a sieve-like

pattern (Fig. 5E, F). The holes or grana are filled with five to six minute dots (Fig. 5D). In some cases, the ornamentation occupies the lower two-thirds of the growth band, in which the granule diameter ranges from 1.87 μm to 5.36 μm and increases in size ventrally (Fig. 5C, D). The umbonal area does not bear ornamentation, or it has not been preserved in the studied specimens (Fig. 5A, B).

Measurements of the valve (in mm). L, 2.16–3.86; H, 1.44–2.83; H/L, 0.54–0.96; Ch, 1.28–2.57; Cr, 0.77–1.8; Av, 0.1–0.77; Arr, 0.12–1.03; a, 0.51–1.54; b, 0.51–1.54; c, 1.03–1.8. Abbreviations are according to Tasch (1987); see Gallego *et al*. (2005).

Discussion. *Cornia martinsnetoi* sp. nov. has morphological characters typical of the subfamily Vertexiinae and especially of *Cornia* as evidenced by a rib-like node in the umbonal area and punctate? (granulate) ornamentation. The diagnostic features considered in the comparative analysis are mainly: the outline, carapace size, umbonal position and morphology of the node/rib. The new species was compared with Permo-Carboniferous and Triassic species from the Northern Hemisphere, especially those from Russia. Additionally, *Cornia martinsnetoi* sp. nov. was compared with species from Gondwanan strata of Permian to Late Jurassic age (Table 1).

The ornamentation of *C. martinsnetoi* resembles *Euestheria trotternishensis* Chen & Hudson, 1991 in having many small grana on the surface, especially in distal parts of the growth bands but differs in having its ornamentation represented by punctae on the external mould (Chen & Hudson 1991). Orlova & Sadovnikov (2009) also illustrated similar sculpture on *Eulimnadia shorokhovi* Novojilov and *Loxomicroglypta subcircularis* (Chernyshev) using scanning micrography. Gallego & Breitkreuz (1994) mentioned a punctate ornamentation between the growth lines of *Cornia* sp. (Late Permian, northern Chile) but the description lacks illustration of its microsculpture. Further microscopic comparisons with *Cornia* species are not possible due to the lack of SEM studies.

The genus Cornia and related forms from the Southern Hemisphere

According to Tasch (1987), *Cornia* and three other genera (*Estheriina*, *Palaeolimnadia* and *Cyclestheriopsis*) dispersed to all five Southern Hemisphere continents during Palaeozoic/Mesozoic times. *Cornia panchetella* Tasch, 1987 was recorded in India from the East Bokaro Coal Field (west Bengal), above the Permian (Raniganj Formation)/Triassic (Panchet Formation) boundary. This species was also reported in coeval beds above the *Glossopteris/Schizoneura*-bearing Mangli horizon in the Raniganj Basin, Mangli village (Tasch 1987). Three other species of the genus were reported by Ghosh (2011) from the Lower Triassic of India (*Cornia spinosus* Ghosh, *C. sonensis* Ghosh and *C. shahi* Ghosh, see Discussion). Its record from South America includes the doubtful *Cornia semigibosa* (Cardoso) Tasch, 1987 from the Upper Triassic Motuca Formation (Brazil) formerly attributed to *Echinestheria* and later ascribed to *Echinopalma* Cardoso. The South American records are completed by species from the Upper Permian Rio do Rasto Formation (Brazil: Rohn 1987) and the Peine Formation (Chile: Gallego & Breitkreuz 1994). The first was recently re-assigned by Ferreira-Oliveira (2007) to *Megasitum* (Novojilov). The African records incorporate *Cornia angolata* Tasch from the Upper Triassic Cassanje I Series (Oesterlen northern Angola, Africa) and *Cornia haughtoni* Tasch recovered from the Upper Triassic Cave Sandstone of Lesotho (Tasch 1987). Australian Permian and Triassic strata (Tasch 1987) have yielded several corniid records: *Cornia* sp. from Upper Permian strata at Sirius Creek (Queensland) and *Cornia coghlani* Etheridge from the Lower Triassic of the Sydney Basin. Jurassic corniid records include only *Cornia* sp. 1 and *Cornia* sp. 2 from Blizzard Heights (Antarctica: Tasch 1987).

Palaeoecology and palaeoenvironments

Spalletti (1994) studied the evolution of fluvial systems in the Sierra Pintada suggesting that the clastic sediments of the Quebrada de los Fósiles Formation (=*ex* Puesto Viejo Formation) were deposited in medium to distal alluvial fan deposits, channels, bars and floodplains (eolian and aqueous facies) together with low- and high-sinuosity rivers. According to Spalletti (1994, 1995) and Spalletti *et al*. (1996), acyclic factors including explosive felsic volcanic activity, tectonism and increasing aridity controlled the evolution of these deposits. González Díaz (1972) had already alluded to some seasonality (with at least one wet season) in the palaeoclimate. Furthermore, Robinson (1973) and Dubiel *et al*. (1991) also suggested that the Triassic climate in the southwestern basins of the Pangea supercontinent was monsoonal.

The spinicaudatan-bearing layers from the Quebrada de los Fósiles Formation (Puesto Viejo Group) were probably part of a series of alternating high and low flow regimes, marked by the intercalation of sandy and silty beds formed during the flooding of the river systems. In addition, the presence of palaeosols (dense root casts) indicates probable shallow-water sub-environments (small lakes, ponds) under a seasonal regime.

González Díaz (1967) mentioned the presence of limestones formed by chemical (organic?) precipitation in small and closed basins, saturated with salt-rich waters due to nearby volcanic activity. The presence of these limestones in the profile, approximately 20 cm below the spinicaudatan level indicates the development of stagnant water bodies (Fig. 3).

The fine-grained interval in the type section of the Quebrada de los Fósiles Formation is composed mainly of grey siltstones, deposited as fine laminae

Species name, stratigraphic source, age	Shape/size	Umbo/rib	Dorsal margin	Ornamentation	Other features
***C. panchetella* Tasch, 1987 (Panchet/Raniganj Formations contact, Permo-Triassic boundary, India)**	Subovate rounded to subcircular outline; /L: 1.6–1.9, H: 1.3–1.4	Small sub-central rib perpendicular to the dorsal margin	–	Punctate	–
***C. spinosus* Ghosh, 2011 (Panchet Formation, Early Triassic, India)**	Ovate outline	Umbo sub-elliptical, large globose with a small sub-central spine/node	Short and slightly curved	Shell structure punctate in umbonal region	Spines in median and ventral parts of the valve
***C. sonensis* Ghosh, 2011(Pachmarhi Formation, ?Early Triassic, India)**	Subovate outline	Triangular umbo sub-central, raised, flat, below dorsal margin with an elongated spine	Straight dorsal margin in adults	Granulate structure	–
***C. shahi* Ghosh, 2011 (Mangli bed, Maharashtra, Early Triassic, India)**	Elliptical outline	Large smooth and rounded umbo, without any growth bands near it, with an upright spine	Arched?	–	–
***C. angolata* Tasch, 1987 (Cassanje I Series, Phyllopod beds, Upper Triassic, Angola)**	Ovate to subovate outline	Large umbo, slightly or markedly anterior with a prominent node in dorsal position	–	–	–
***C. haughtoni* Tasch, 1984 (Cave Sandstone, Upper Triassic, Lesotho)**	Subovate outline	Small tappered to blunt node on a slightly inflated, smooth, subterminal umbo that occupies the antero-subdorsal sector of the valve	Straight	–	–
***C. dunaevae* Novojilov, 1970 (Carboniferous, Russia)**	Subtrapezoidal outline	Anterior node and the umbo does not rise above the markedly straight dorsal margin	Straight	–	–
***C. votchiana* Novojilov, 1970 (Triassic, Russia)**	Subtrapezoidal outline	Subterminal to terminal umbo, rib slightly oblique and markedly anterior	Straight to slightly curved	–	–
***C. jugensis* Novojilov, 1966 (Triassic, Russia)**	Subtrapezoidal to elliptical outline	Umbo subterminal, node more anterior	Straight to slightly curved	–	Numerous growth bands
***C. portenta* Novojilov, 1970 (Jurassic, Russia)**	Subtrapezoidal shape and similar size	Larger umbonal area, with more anterior and larger rib	Straight	–	Few growth lines

Table 1. Diagnostic features considered in the comparative analysis of *Cornia martinsnetoi*.

from suspension, and probably corresponds to shallow lacustrine floodplain deposits, with crevasse-splay channels. This interval bears the spinicaudatans and associated fossils (ostracods, megaspores, fish scales and fragmentary plant remains) and includes a significant volcanigenic fraction. The pyroclastic sediments indicate coeval nearby volcanic activity, which implies an environment under stressful conditions.

The fossil flora of the lower unit of the Puesto Viejo Group consists mainly of the lycopsid *Pleuromeia* (Stipanicic 1969, Morel & Artabe 1993, 1994) and indeterminate Equisetales. The root cast systems of these opportunistic plant groups reflect the formation of shallow (swampy) soils in stressed environments (Retallack 1975). Moreover, the presence of these plants suggests that the vegetation had some physiological tolerance to stressful conditions (Retallack 1975). The monsoonal climate suggested by González Díaz (1972), Robinson (1973) and Dubiel *et al*. (1991) suggests the maintenance of seasonal water bodies (ponds, swamps and/or small shallow lakes) inhabited by the spinicaudatans. The presence of sparse dispersed fish scales in this context might reflect allochthonous material transported from fluvial channels to the floodplain.

Climatic factors such as temperature, humidity and salinity can induce physiological responses in living spinicaudatan morphology, as noted by Tiwari (1965), Chen & Hudson (1991) and Ghosh (2011), resulting in different types of shell ultrasculpture between the growth bands. Consequently, the spinicaudatan faunas would respond to the particular climatic conditions that prevailed during Permo-Triassic times (see Ghosh 2011, pp. 116–124).

Taphonomy and palaeobiology

The valves of *Cornia martinsnetoi* sp. nov. are yellow to brownish and have a multilamellar aspect. According to a classification proposed by Tasch (1982) based on colour variation of fossil spinicaudatan valves in relation to temperature, the studied valves belong to the Br (brown crust) class. This class indicates burial temperatures reached 450–600°C as demonstrated by laboratory experimentation. As stated by Tasch (1982), the chemical composition of the valve varies during the heating process.

The studied specimens are preserved as either articulated (perfectly conjoined, opened or displaced; Fig. 4F) or disarticulated single valves (Fig. 4A–E). This indicates a mix of essentially autochthonous to at least slightly allochthonous or decayed specimens (*sensu* Orr & Briggs 1999; Fig. 4E).

Adult and juvenile specimens were identified based on the relative size of the valves and number of growth bands (Tasch 1969, pp. 144, 145; 1987, p. 94). They are also represented by different morphotypes (Fig. 4A–E). Among the studied specimens, we observed a height/length (H/L) ratio of 0.54–0.96, which may imply the presence of males and females in the population (see Tasch 1969). Tasch (1987) noted dimorphism in corniids via the presence of a spine (male) or node (female). We observed only nodes in the umbonal area of the Argentinean specimens and dimorphism could be identified only via the presence of different shapes and the height/length ratio. The density of the corniid population found in the Quebrada de los Fósiles Formation is relatively low when compared with Middle and Upper Triassic spinicaudatan faunas from Argentina, suggesting that the organisms lived in unfavorable environments.

Biostratigraphy

Some species of *Cornia* Lyutkevich have been used as biostratigraphic indices to define and calibrate biozones in the Lower Triassic sequences of Germany (Kozur & Seidel 1983a, b, Kozur 1993, Bachmann & Kozur 2004, Kozur & Weems 2007, 2010) and India (Ghosh *et al*. 1987a, b, Ghosh 2011). Kozur & Weems (2010) defined the *Cornia germari-Magniestheria subcircularis* zone for the late Induan (widely distributed in the Germanic Basin in central and northern Germany, Poland and Hungary).

Cornia germari Beyrich is recorded mainly in monospecific associations from the Early Triassic (late Induan) of the Northern Hemisphere, particularly in brackish water deposits of Greenland and the Krasnobakovskij Formation of Russia (no stratigraphic source available). In Hungary, this species occurs in *Claraia aurita*-bearing beds of late Induan age (Kozur 1993, Kozur & Mock 1993). Late Induan conchostracans also occur in Africa (Cassange III Formation and equivalents, Angola and Zaire) including a species very similar to *C. germari*. *Cornia marimbensis* Marliere (formely *Echinestheria*) has also been recorded in the upper Assagno Formation of Gabon. Similar forms occur in the Panchet Formation (*Cornia panchetella* Tasch), India. *Cornia coghlani* Etheridge is present in the Early Triassic (Narrabeen Group, Sydney Basin) of Australia. Other species of *Cornia* derive from different regions and older stratigraphic levels [eg., Carboniferous–Permian of Russia (Novojilov 1970), Late Permian of Chile (Gallego & Breitkreuz 1994) and Late Permian of Brazil (Rohn 1987)].

Ghosh (2011) characterized the Early Triassic 'conchostracan' fauna of India as containing *Cornia*, *Gabonestheria*, *Curvacornutus, Protomonocarina*, *Macrolimnadiopsis*, *Palaeolimnadiopsis*, *Estheriella*, *Cornutestheriella* and *Vertexia*. Ghosh (2011) also defined nine conchostracan biozones, two of them, biozones 7 (East Bokaro Coalfield, close to the P/T boundary) and 8 (upper Panchet of East Bokaro Basin and Eastern part of Raniganj Basin, Pachmari Formation, Madhya Pradesh), are of particular note in the context of this study as they include *Cornia* species.

Gabonestheria, *Cornia* and *Estheriella* are found in the Mangli beds and Maharashtra and Panchet forma-

tions, Andal area, Raniganj Coalfield, West Bengal. A similar assemblage (with the notable absence of *Estheriella*) was found in the Triassic succession of Africa (Lesotho) and South America (Brazil). The distribution of these taxa between what were then contiguous landmasses has resulted in broadly similar pan-gondwanan Triassic spinicaudatan faunas (Ghosh 2011).

The appearance of *Cornia martinsnetoi* sp. nov. likely reflects similar palaeoenvironmental conditions and age between the Quebrada de los Fósiles Formation (Puesto Viejo Group, Argentina) and Indian Gondwanan strata (Raniganj and Panchet formation transitional package; Ghosh 2011). The new record adds support for the proposed Early Triassic age of the *Cornia martinsnetoi*-bearing interval in the Puesto Viejo Group.

Conclusions

Cornia martinsnetoi sp. nov. has morphological features diagnostic of the late Palaeozoic–Early Triassic genus *Cornia* Lyutkevich, 1937, recorded widely in Gondwanan sequences. From the fine siliciclastic sediments and palaeontological data we conclude that the depositional environment was probably a small low-energy pond. Ash beds and reworked pyroclastic grains indicate coeval volcanic activity nearby, which implies an environment under stressful conditions. The presence of *Cornia*, together with the sedimentological and palaeoclimatical data, reflect a similar palaeoenvironmental setting to that of the coeval Indian sequences (see Ghosh 2011, pp. 116–124). Biostratigraphically, the new taxon favours an Early Triassic (Induan–Olenekian) age for the host strata.

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