Geologica Acta, Vol.9, Nº 2, June 2011, 175-185
DOI: 10.1344/105.000001692
Available online at www.geologica-acta.com

geologica acta

Totoralia, a new conical-shaped mollusk from the middle Cambrian of western Argentina

M.F. TORTELLO and N.M. SABATTINI

CONICET-División Paleozoología Invertebrados, Museo de La Plata
Paseo del Bosque s/nª, 1900 La Plata, Argentina. Tortello E-mail: tortello@fcnym.unlp.edu.ar
Sabatini E-mail: nsabatti@fcnym.unlp.edu.ar

ABSTRACT

The new genus *Totoralia* from the late middle Cambrian of El Totoral (Mendoza Province, western Argentina) is described herein. It is a delicate, high, bilaterally symmetrical cone with a sub-central apex and five to seven prominent comarginal corrugations. In addition, its surface shows numerous fine comarginal lines, as well as thin, closely spaced radial lirae. *Totoralia* gen. nov., in most respects, resembles the Cambrian helcionellids *Scenella* BILLINGS and *Palaeacmaea* HALL and WHITFIELD. Although *Scenella* has been considered as a chondrophorine cnidarian by some authors in the past, now the predominant view is that it is a mollusk. Likewise, several aspects of *Totoralia* gen. nov. morphology indicate closer affinities with mollusks. The specimens studied constitute elevated cones that are rather consistent in height, implying that they were not flexible structures like those of the chondrophorines. The presence of a short concave slope immediately in front of the apex can also be interpreted as a mollusk feature. In addition, the numerous comarginal lines of the cone are uniform in prominence and constant in spacing, and are only represented on the dorsal surface of the shell; thus, they are most similar to the incremental growth lines of shells of mollusks. The morphology of *Totoralia* gen. nov. is regarded as primitive in the Helcionelloida because the ancestor of the class is likely to have had a minute, untorted limpet-shaped shell. Although the new genus herein described seems to be endemic to Argentina, the Cambrian occurrences of related scenellid genera suggest affinities with Laurentia.

KEYWORDS | **Mollusca. Helcionelloida. *Totoralia*. Middle Cambrian. Mendoza. Argentina.**

INTRODUCTION

Many Paleozoic biotas include conical-shaped fossils which are of uncertain taxonomic position. In some cases the suprageneric affinities of these fossils can be confidently established. For instance, well-preserved bilaterally symmetrical shells of patellacean gastropods show indications of an internal horseshoe-shaped muscle scar, which reflects torsion of the soft parts (Yochelson, 1984). In contrast, the presence of paired muscle scars is indicative of "monoplacophoran" affinities (e.g., Knight and Yochelson, 1960; Yochelson, 1984; Stinchcomb, 1986). Runnegar and Pojeta (1974), Runnegar and Jell (1976), Pojeta et al. (1987), and Runnegar (1987) described diagnostic features of early mollusks and discussed their phylogenetic

significance. Primitive taxa are characterized by having a minute, untorted shell with a small aperture, bilaterally symmetrical muscle insertions, and lacking an operculum. The fossil record showed that the "monoplacophorans" gave rise to the Gastropoda, Cephalopoda, and Rostroconchia.

Unfortunately it is not always possible to determine conclusively the affinities of "cap-shaped" fossils. Because of poor preservation many early Paleozoic genera were assigned either to Helcionellacea or "Monoplacophora" only on the basis of their external morphology. Debate continues about the affinities of many of these cones, in large part due to lack of muscle scars. *Palaelophacmaea* DONALDSON, 1962 was originally described as a patelliform gastropod (Donaldson, 1962) but was later reinterpreted as the pneumatophore of a chondrophorine cnidarian (Yochelson and Stanley, 1981; Stanley and Kanie, 1985; Bell et al., 2001). The late Cambrian genus *Palaeacmaea* HALL and WHITFIELD, 1872, originally placed in the Gastropoda and later transferred to the "Monoplacophora", was recently regarded by Webers and Yochelson (1999) as a medusiform fossil of uncertain affinities. *Marocella* GEYER (Geyer, 1986; Evans, 1992; Lin, 1999; see also Yochelson and Gil Cid, 1984) is another enigmatic (Incertae Sedis) conical fossil characterized by having a depressed, rigid shell with a peculiar internal structure, which also bears some similarities to both mollusks and chondrophorine cnidarians. Similarly, specimens of the Cambrian–Middle Ordovician *Scenella* BILLINGS, 1872 were first considered as mollusk shells (Billings, 1872; Knight, 1952; Knight and Yochelson, 1960; Runnegar and Jell, 1976; Berg-Madsen and Peel, 1986; Geyer, 1986; Landing, 1988; Landing and Narbonne, 1992) but have been reassigned by some authors to the Chondrophorina (Yochelson, 1984; Yochelson and Gil Cid, 1984; Stanley, 1986; Babcock and Robison, 1988). However, Pojeta et al. (1987) described bilaterally symmetrical pairs of muscle scars in a Cambrian specimen assigned to this genus, so that a relationship to helcionelloids is evident in this case. Recently, Martí Mus et al. (2008) described a helcionelloid protoconch on a *Scenella*-like mollusk, providing stronger evidence in favour of mollusk affinities.

Rusconi (1954, 1955) originally described *Pichynella* (type species *P. annulata* RUSCONI) near San Isidro in the Cambrian of Mendoza, Argentina, and assigned it to the Class Gastropoda. Subsequently, he described two other species (*P.*? *hornillensis* RUSCONI, 1956a and *P. striata* RUSCONI, 1958) from El Totoral, Mendoza. Rusconi's sketches of the three species of *Pichynella* depict similar cones strongly ornamented with comarginal corrugations. Nevertheless, the reexamination of the respective holotypes has demonstrated that the type species *Pichynella annulata* from San Isidro strongly differs from the material described from El Totoral. New specimens from the latter locality are studied herein. They include well-preserved individuals showing their original convexity and fine details of their ornamentation. The new genus *Totoralia* (type species *Pichynella*? *hornillensis* RUSCONI) is proposed in this work, and its biological affinities and paleobiogeographical implications are discussed.

GEOLOGICAL SETTING

Cambrian outcrops in the southern Precordillera in Mendoza Province, western Argentina, are predominantly isolated carbonate blocks chaotically mixed within Middle to Upper Ordovician siliciclastic sequences (Heredia and Beresi, 2004). These olistoliths range from centimeters to hundred of meters in thickness and represent shelf to upper slope environments containing diverse shelly faunas (e.g., Bordonaro, 1992, 2003b; Bordonaro et al., 1993; Bordonaro and Liñán, 1994; Heredia, 1994, 1996; Bordonaro and Banchig, 1996; Shergold et al., 1995; Tortello and Bordonaro, 1997; Keller, 1999; Heredia and Beresi, 2004). The most classic fossil localities are San Isidro, Cerro El Solitario, and El Totoral (Fig. 1).

The San Isidro area is located 15km W of Mendoza city. There, the carbonate San Martín, San Isidro, and La Cruz Olistoliths, as well as other minor exotic blocks, are emplaced in the Ordovician green and black shales of the Estancia San Isidro and Empozada formations (see Beresi, 2003; Heredia and Beresi, 2004). These allochthonous units contain trilobites, sponge spicules, and chancellorid sclerites which are middle Cambrian (*Glossopleura* and *Oryctocephalus* Zones) and Furongian (*Crepicephalus*, *Glyptagnostus reticulatus*, *Elvinia* and *Saukia* Zones) in age (Bordonaro, 2003b; Beresi, 2003). The Cerro El Solitario locality is about 40km NNW of Mendoza city, and consists of a medium size olistolith (Solitario Olistolith) partially covered by alluvial material. It is composed of open-shelf dark limestones and black shales containing trilobites of latest middle Cambrian (*Lejopyge laevigata* Zone) age (Poulsen, 1960; Bordonaro and Liñán, 1994; Tortello and Bordonaro, 1997; Bordonaro, 2003b; Tortello, 2009 and references therein).

El Totoral is 25km NW of Mendoza city and 3.5km SE of Puesto El Totoral (Rusconi, 1956a, 1958; Castellaro, 1963; Borrello, 1965, 1971; Bordonaro and Banchig, 1996; Bordonaro, 2003b) (Fig. 1). The stratigraphy and paleontology of this area are still poorly known. Rusconi (1956a, 1958) provided a brief description of the outcrop and described trilobites, brachiopods, hyoliths, and "gastropods" (*P. hornillensis* RUSCONI, 1956a; *P. striata* RUSCONI,

1958) from a 20-m-thick succession of black limestones which were assigned to the middle Cambrian. These open-shelf limestones constitute an olistolith (assigned to "Olistoliths Totoral" in Bordonaro and Banchig, 1996) mixed within the late Darriwilian shales of the Estancia San Isidro Formation (Heredia and Beresi, 2004; Heredia, 2007) (Fig. 2). The El Totoral section is tectonically emplaced in the Silurian-Devonian shales of the Villavicencio Formation.

SAMPLING AND REPOSITORY

The specimens studied herein were collected in the Totoral Olistolith by Dr. Ángel V. Borrello and his associates (Universidad Nacional de La Plata) during the 1960s and housed in the Museo de Ciencias Naturales de La Plata (MLP), Argentina. In addition, Rusconi's collections are housed in the Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano" (PI-MCNAM), Mendoza, Argentina. The material is associated with *Tomagnostella* KOBAYASHI, 1939, *Clavagnostus calensis* RUSCONI, 1950 and other trilobites of the *Lejopyge laevigata* Zone, which indicate a late middle Cambrian age (Robison, 1984, 1988; Tortello and Bordonaro, 1997; Tortello, 2009).

SYSTEMATIC PALEONTOLOGY

Phylum: mollusca CUVIER, 1797
Class: helcionelloida PEEL, 1991

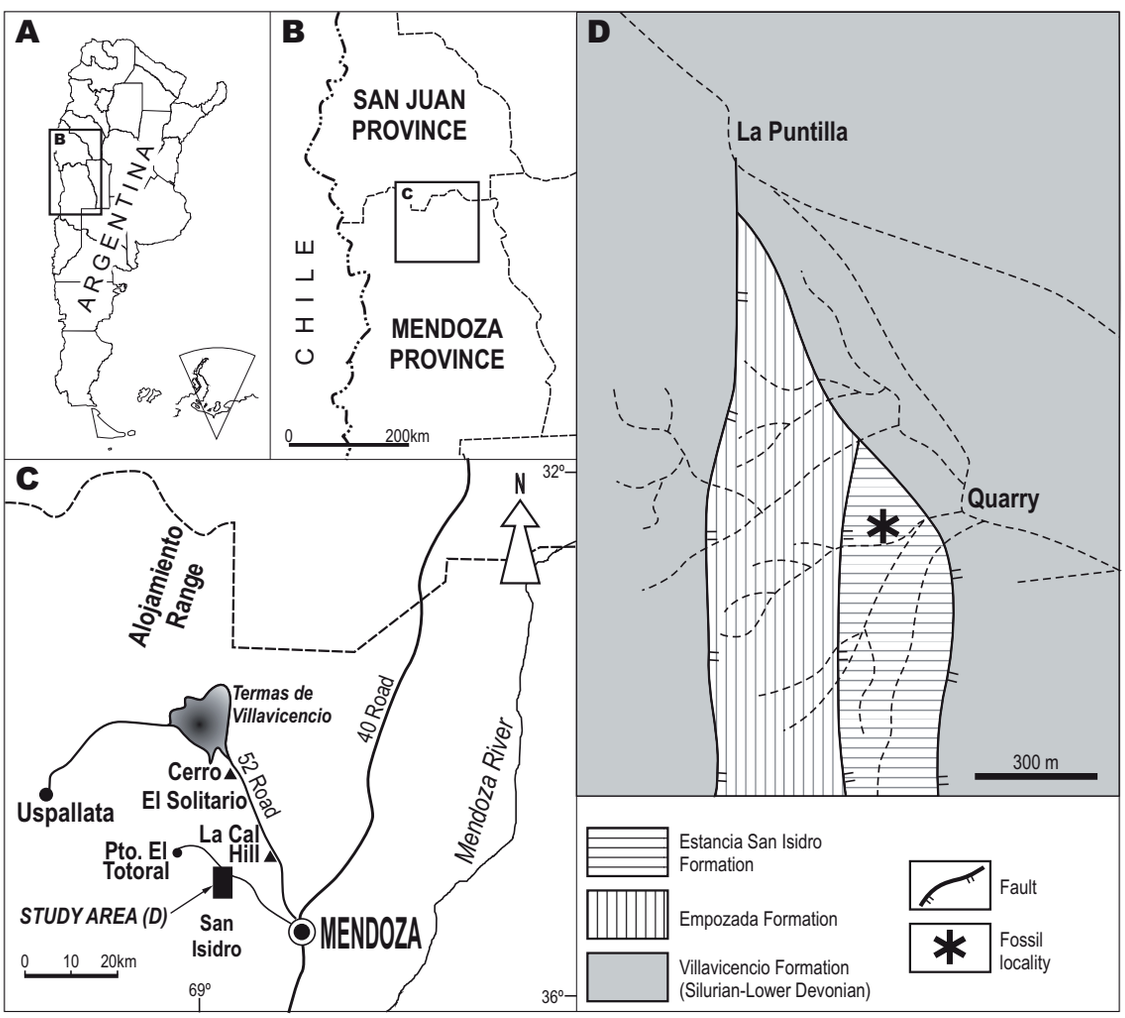

FIGURE 1 | **Location map of the fossiliferous locality. A) Map of Argentina showing San Juan and Mendoza Provinces in the western part of the country. B) Map of San Juan and Mendoza Provinces, indicating the area magnified in C. C) Map of northern Mendoza Province, showing the position of El Totoral area. D) Geological sketch of El Totoral area (based on Rolleri and De Giusto, 1950). The location of the fossiliferous locality (*) is based on Rusconi (1956a) and A.V. Borrello (unpublished data).**

Order: helcionellida GEYER, 1994
Family: scenellidae WENZ, 1938

GENUS ***Totoralia*** nov.

Derivation of the name: After El Totoral locality.

Type species: *Pichynella? hornillensis* RUSCONI, 1956a (see below).

Diagnosis of the genus (nov.). Elongate, bilaterally symmetrical, moderately high patelliform organism having a sub-central, erect apex, and five to seven comarginal rugosities separated by wide troughs. Surface with fine radial lirae closely spaced, forming a reticulate pattern by intersection with comarginal growth lines.

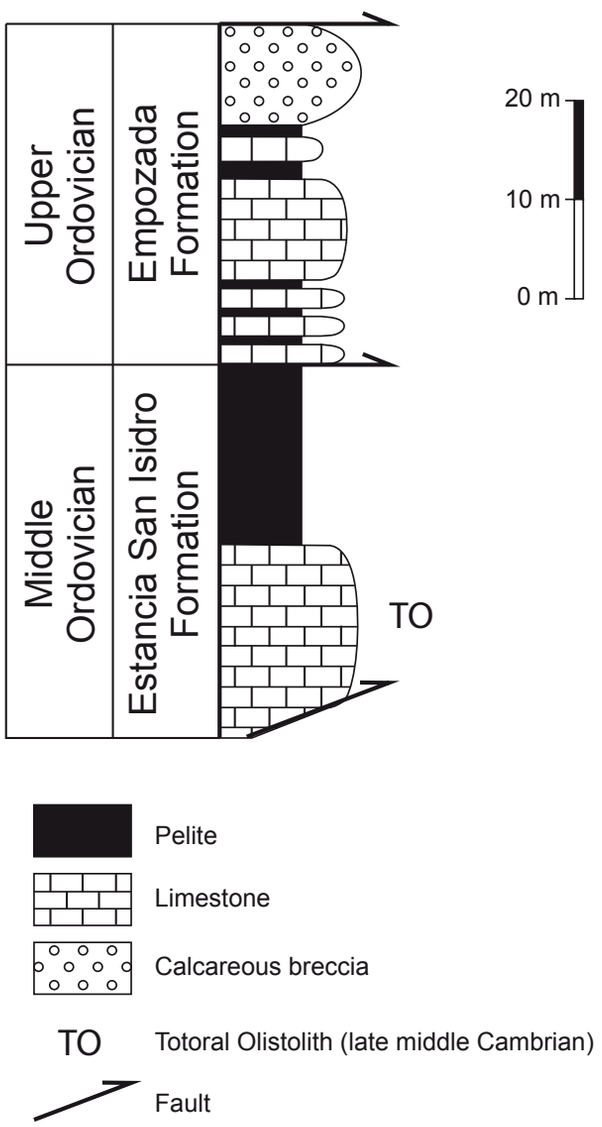

FIGURE 2 | **Generalized stratigraphic section of El Totoral (based on Rusconi, 1956a, and S. Heredia and M. Beresi, unpublished information). The specimens studied come from the Totoral Olistolith (TO).**

Discussion. "*Pichynella*?" *hornillensis* from El Totoral was tentatively assigned to *Pichynella* RUSCONI, 1954 by Rusconi (1956a, 1958). However, the type species *Pichynella annulata*, from the Cambrian of San Isidro, Mendoza (Rusconi, 1954; Rusconi, 1955, pl. 4, fig. 2), is characterized by a very small shell that has a curved marginal apex, and an ornamentation consisting of inflated, smooth rings separated by deep, narrow furrows (Fig. 3). Based on "*P.*?" *hornillensis* the new genus *Totoralia* is erected herein (Fig. 4), which clearly differs from *Pichynella* in its larger size, a sub-central apex, and an ornamentation comprising an alternation of prominent rugosities and wide troughs, as well as fine radial lirae.

Totoralia gen. nov. superficially resembles *Palaeacmaea* from the upper Cambrian of North America (see Webers and Yochelson, 1999), in its sub-central apex, elliptical shape and presence of comarginal undulations. However, the former is much smaller and proportionately higher, its surface shows radial lirae, and the slopes are steeper near the margin. It also resembles *Scenella*, from the Cambrian–Ordovician of North America, Europe and Asia (Yochelson, 1984; Babcock and Robison, 1988), in its elliptical basal outline, sub-central apex, and co-occurrence of comarginally arranged rugosities and fine radial ribs forming a reticulate pattern. *Totoralia* gen. nov. is mainly distinguished from the *Scenella* type material (Knight, 1941, pl. 2, figs. 5.a-b) by its steeper slopes and its more prominent corrugations. *Totoralia* gen. nov. and *Palaelophacmaea*, from the Lower Ordovician of North America (Donaldson, 1962; Yochelson and Stanley, 1981), share a thin shell, subcentral apex, comarginal rugosities, and fine growth lines between coarser corrugations. However, the latter further differs by its lower conical form and the presence of one prominent radial ridge extending from near the apical region to the margin, and a circular basal outline.

The new genus is distinguished from *Protoconchoides* SHAW, 1962a (see also Shaw, 1962b) and *Kirengella* ROZOV, 1968 mainly by having stronger comarginal undulations, and from *Palaeoscurria* PERNER, 1903 by having uniform, steeply inclined slopes. *Irondalia* STINCHCOMB and ANGELI, 2002 shows a medusiform morphology with a subcentral apex and pronounced growth lines, but mainly differs from *Totoralia* gen. nov. because the former possesses a low shell. *Calloconus* PERNER, 1903 is further distinguished by its larger, thicker shell, which shows an ornamentation consisting of numerous imbricating lamellae.

Totoralia gen. nov. and the helcionellids *Ginella* MISSARZHEVSKY in ROZANOV et al., 1969 and *Mellopegma* RUNNEGAR and JELL, 1976, as well as some species of *Stenotheca* SALTER in HICKS, 1872

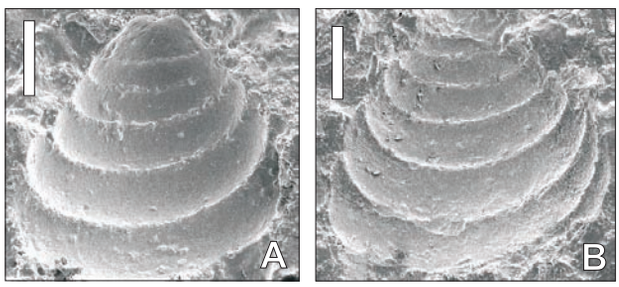

FIGURE 3 | ***Pichinella annulata*** **RUSCONI, 1954, Cambrian, San Isidro, Mendoza. A) Latex mould of the holotype PI-MCNAM 18075. B) Latex mould of the paratype PI-MCNAM 18076. Scale bars 0.2mm.**

(Runnegar in Bengtson et al., 1990; Skovsted and Peel, 2007), have similar comarginal rugae, but the latter differ by having a cyrtoconic, strongly laterally compressed shell. *Helcionella* GRABAU and SHIMER, 1909 (e.g., Knight, 1941; Gubanov et al., 2004a) is distinguished from the new genus mainly because it shows the apex closer to the posterior end of the shell.

Leptostega GEYER, 1986 resembles *Totoralia* gen. nov. by bearing a similar quantity of prominent comarginal thickenings that continue around the shell. However, the former differs by possessing a smaller, cyrtoconically curved shell, as well as wider corrugations. *Mackinnonia* RUNNEGAR in BENGTSON et al., 1990 also differs by having a shell with a smooth exterior.

Latouchella COBBOLD, 1921 and *Oelandia* WESTERGÅRD, 1936 are distinguished from *Totoralia* gen. nov. by bearing an apex that is curved backwards. *Anabarella* VOSTOKOVA, 1962 (Gubanov and Peel, 2003; Gubanov et al., 2004b) clearly differs by its smooth, laterally compressed shell which is coiled through about a whorl. Similarly, *Bemella* MISSARZHEVSKY in ROZANOV et al., 1969 is distinguished by having an excentric apex, whereas *Bestashella* MISSARZHEVSKY in MISSARZHEVSKY and MAMBETOV, 1981 and *Kistasella* MISSARZHEVSKY, 1989 have a laterally compressed shell, which is strongly asymmetrically coiled.

Stratigraphic and geographic range: Upper middle Cambrian, El Totoral, Mendoza, Argentina.

Totoralia hornillensis (RUSCONI, 1956a)
Figures 4A–L

1956a *Pichynella*? *hornillensis,* Rusconi, fig. 1.
1958 *Pichynella striata* Rusconi, fig. 13.

Material. Holotype (PI-MCNAM 19959; Fig. 4E) and paratype (PI-MCNAM 19960) of *Pichynella hornillensis* RUSCONI, 1956a; holotype (PI-MCNAM 22015; Fig. 4L) of *Pichynella striata* RUSCONI, 1958. Five additional individuals (MLP 31850–31853; Figs. 4A–D, F–K). All specimens from the El Totoral locality.

Diagnosis: As for the genus, which is monotypic.

Emended Rusconi (1956a) description: Elongate, moderately high, bilaterally symmetrical cone with a blunt, sub-central apex. Outline of margin sub-elliptical; length about 1.3 times width, ranging up to 5mm. Apex located 45% sagittal length from anterior margin. Lateral slopes uniform, steeply inclined. Anterior slope slightly concave near the apex. Specimens ornamented with five to seven prominent comarginal corrugations, interspaces being wider than rugosities; in addition, a narrow belt occurs at the margin. Shell thin. Surface showing regular comarginal growth lines running parallel to the basal margin of the cone, commonly eight to ten between coarser corrugations, and fine, closely spaced radial lirae. Comarginal lines and radial lirae form a reticulate pattern of nearly square blocks, which show faint nodes at the vertices. Evidence of apical pore, snorkel and muscle scars lacking.

Discussion. Characters that have taxonomic significance in patelliform organisms include relative size, length/width ratio, position of the apex, apical and slope morphology, and presence or absence of radial ribs and ornamentation. Some of these features can be variable within collections, a fact that is partially attributed to taphonomic factors (Babcock and Robison, 1988). The degree of expression of the corrugations of *Totoralia hornillensis* gen. nov. varies between specimens. Some well-preserved individuals (Figs. 4A–E, K) show conspicuous comarginal ridges, whereas others (Figs. 4F–H, L) exhibit moderately-developed undulations. On the other hand, a specimen interpreted as a composite mould (Figs. 4I–J) shows only three faint rugosities near the margin, lacking any traces thereof towards the apical zone.

The distinctness of radial lirae also fluctuates, since they are clearly seen in some materials (Figs. 4D, G, L) but are weaker in the holotype (Fig. 4E) and other individuals (Figs. 4I–K). Similarly, the variability of *T. hornillensis* involves the steepness of slopes of the cones. Although the collections studied suggest a uniform slope from apex to margin, the inclination in specimens MLP 31850, 31851 (Figs. 4A–D, F–H) is greater than that of MLP 31852 (Figs. 4I–J).

Pichynella striata RUSCONI (1958, fig. 13) was erected on the basis of material from El Totoral, found in association with *T. hornillensis*. A mould of the holotype, which shows the apical zone imperfectly preserved, is re-illustrated herein (Fig. 4L). According to Rusconi (1958), this taxon is characterized by a

conical shell having an ovoid outline, six comarginal rings, and numerous and conspicuous radial ridges. Taking into account the variability described above, these characters correspond with those of *Totoralia hornillensis*, so we suppress *P. striata* as a subjective junior synonym.

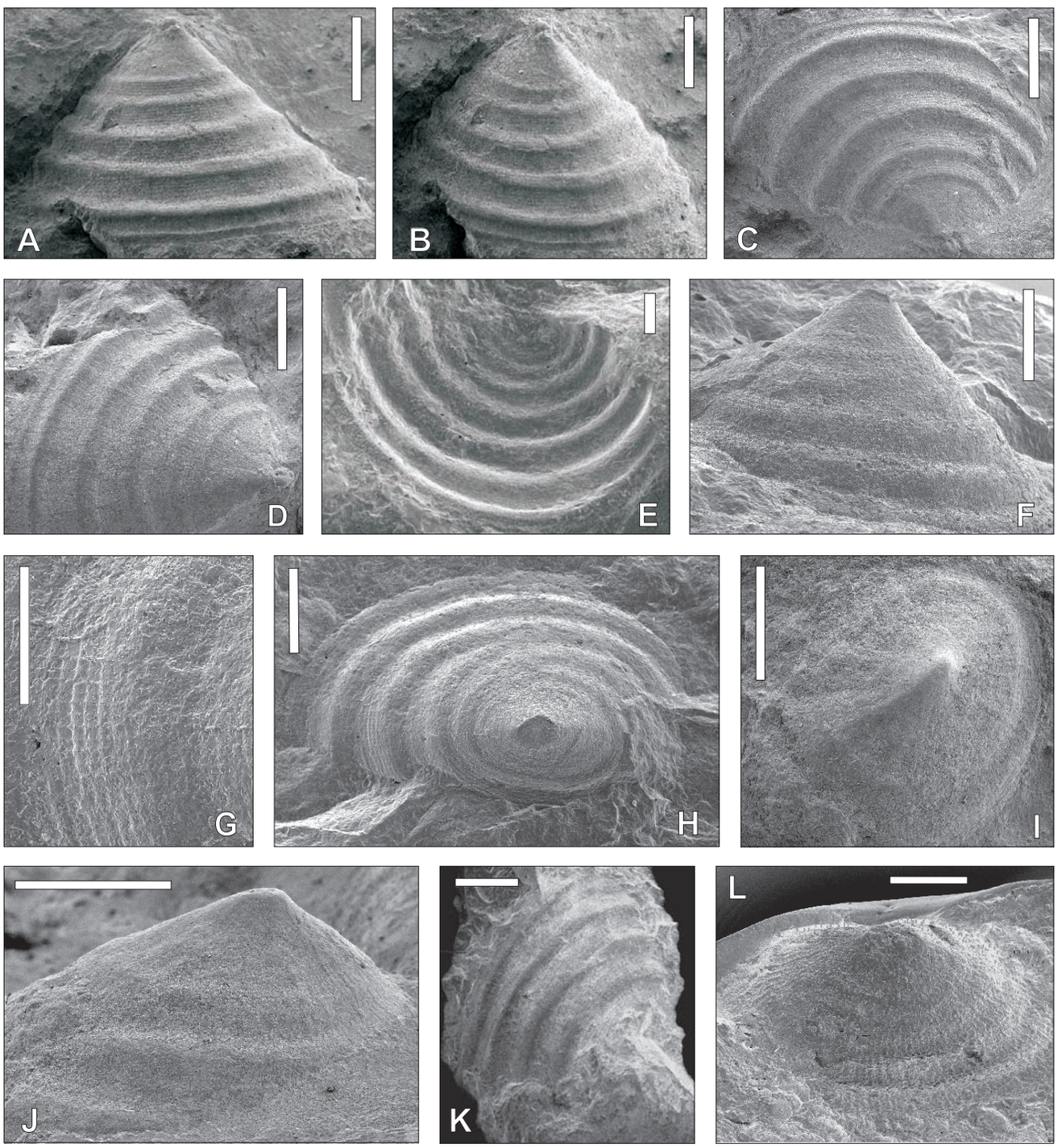

FIGURE 4 | ***Totoralia hornillensis*** **(RUSCONI, 1956a), late middle Cambrian, El Totoral, Mendoza, Argentina. A–D) MLP 31850; A) Lateral view; B–D) Dorsolateral view. E) Latex mould of the holotype PI-MCNAM 19959, dorsolateral view. F–H) MLP 31851, latex mould; F) Lateral view; G) Detail of the ornamentation; H) Dorsal view. I–J) MLP 31852, partially preserved composite mould; I) Dorsal view; J) Lateral view. K) MLP 31853, fragment, lateral view. L) PI-MCNAM 22015 (latex mould of the holotype of *Pichynella striata* RUSCONI, 1958), dorsolateral view. Scale bars 1mm (excepting G, 0.5mm).**

Stratigraphic and geographic range: Upper middle Cambrian, El Totoral, Mendoza, Argentina.

TAXONOMIC AFFINITY

The presence of a delicate cone having a sub-central apex and strong comarginal corrugations invites us to compare *Totoralia* gen. nov. especially with *Palaeacmaea* HALL and WHITFIELD, 1872, *Scenella* BILLINGS, 1872, and *Palaelophacmaea* DONALDSON, 1962 (see above). These taxa were originally described as mollusk shells and later reinterpreted by some authors as medusiform organisms, with possible affinities with the chondrophorines (e.g., Yochelson and Stanley, 1981; Yochelson, 1984; Stanley and Kanie, 1985; Stanley, 1986; Babcock and Robison, 1988; Webers and Yochelson, 1999). Yochelson et al. (1983), Yochelson (1984), and Stanley and Kanie (1985) provided criteria for distinguishing superficially similar chondrophorines and low-conical molluscan shells, including analyses of features such as wall thickness, apical position, profile, growth lines and ornamentation. Typical chondrophorines are characterized by having a fine, low conical float which shows a circular or elliptical aperture, pneumatocysts slightly variably in width, and surface irregularities, whereas cap-shaped mollusks have a more rigid, smooth shell with an oval apertural outline, and growth lines that are uniform in strength and constant in spacing (Yochelson, 1984).

Since no muscle scars are preserved in the specimens studied herein, the criteria cited above are useful in discussing the biological affinities of *Totoralia* gen. nov. A partially exfoliated specimen (Figs. 4A–D) shows indications of a thin shell. Although such a delicate covering may allude chondrophorine affinities, it is important to note that many Cambrian mollusks are represented by fine skeletons (e.g., *Irondalia* STINCHCOMB and ANGELI; *Anabarella* VOSTOKOVA; *Stenotheca* SALTER in HICKS; *Latouchella* COBBOLD). All the specimens from El Totoral constitute elevated cones that are rather consistent in height, implying that they were not flexible structures like those of the chondrophorines. Therefore, the lack of flexibility, as well as the low rates of deformation in the material studied, are consistent with mollusk affinity. Some individuals of *Totoralia* gen. nov. exhibit both external and internal features on the same surface (Figs. 4I–J), and thus can be interpreted as composite moulds, which could have been generated by dissolution of an aragonitic shell during early diagenesis.

In addition, the general shape and ornamentation of the shell are vital to determine the taxonomic affinities of *Totoralia* gen. nov. The disposition of the comarginal lines and the contour close to the apex provide valuable elements for discussion. The numerous comarginal lines of *Totoralia* gen. nov. are uniform in strength and constant in spacing, being only represented on the dorsal surface of the shell; thus, they are most similar to the incremental growth lines of shells of mollusks (see e.g., Kase, 1988). The new genus possesses a short concave slope immediately in front of the apex (Figs. 4F, J). According to Yochelson (1984), specimens that have a minute concave slope on one side of the apex and a long convex slope on the other may be mollusks. Following Yochelson's (1984) criteria (see also Yochelson and Stanley, 1981) the absence of both a ridge from the apex and a slight marginal sinus also suggests affinities with mollusks rather than with chondrophorines.

PALEOBIOGEOGRAPHIC ASPECTS

The Cambrian faunas of western Argentina share close affinities with those of North America. Based on Harrington and Leanza (1943), Leanza (1947), Rusconi (e.g., Rusconi, 1956b, c), Poulsen (1960), and Borrello (1965, and references therein), Borrello (1971) pointed out the strong Laurentian aspect of the Cambrian trilobites from the Precordillera, a fact that was corroborated in subsequent papers (e.g., Bordonaro, 2003b). The biostratigraphic implications of these faunas are mostly compatible with the classic scheme of biozones of the middle Cambrian and Furongian of North America (e.g., Bordonaro, 2003a, and references therein).

Although *Totoralia* gen. nov. seems to be endemic to Argentina, the middle Cambrian occurrences of the most closely related scenellid genera suggest affinities with Laurentia. Since the material studied herein represents a *Scenella*-like fossil characterized by having visible concentric corrugations, it is rather similar to the type species *Scenella reticulata* BILLINGS, a taxon that was described from the lower Cambrian of Newfoundland, Massachusetts (USA), and northern Mexico (Billings, 1872; Knight, 1941; Landing, 1988). Besides, it is important to note that the middle Cambrian species of *Scenella* are especially abundant in western North America. *Scenella amii* (MATTHEW), *S. radians* BABCOCK and ROBISON, and *S. hermitensis* RESSER were described from the middle Cambrian of the British Columbia, Utah and Arizona, respectively (Babcock and Robison, 1988), whereas *Scenella* sp. and *Scenella barrandei* (LINNARSSON) was also punctually reported from central North Greenland (Peel, 1988) and Baltoscandia (Berg-Madsen and Peel, 1986) (Fig. 5).

The lower and middle Cambrian genus *Protoconchoides* SHAW from western North America represents another group of small *Scenella*-like cones with an oval aperture and a sub-central apex. Although most of its species show

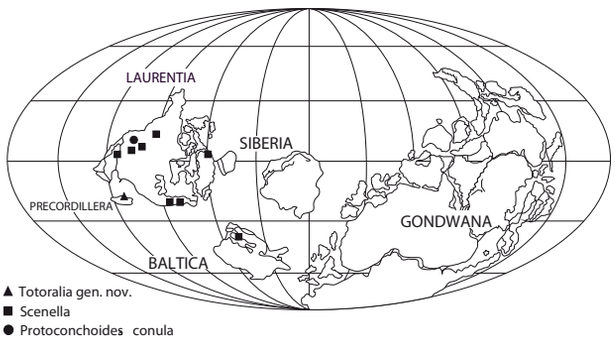

FIGURE 5 | **Paleogeographic reconstruction of the middle Cambrian (modified from Gozalo et al., 2003) and the distribution of *Totoralia* gen. nov., *Scenella reticulata*, and closely allied middle Cambrian taxa.**

very faint indications of concentric ornamentation, the middle Cambrian *Protoconchoides conula* WALCOTT is characterized by the retention of slight comarginal corrugations and, therefore, exhibits a close morphologic affinity with *Totoralia* gen. nov. *Protoconchoides conula* was described from the Eldorado Limestone in the Eureka District, Nevada, USA (Shaw, 1962a).

CONCLUSIONS

Totoralia gen. nov. represents a late middle Cambrian helcionellid from northern Mendoza, Argentina. It is a delicate, high, bilaterally symmetrical cone with a sub-central apex, five to seven comarginal corrugations, and fine radial lirae. Although it resembles taxa that were originally described as mollusk shells and later reinterpreted by some authors as medusiform organisms, most aspects of its morphology indicate closer affinities with scenellid mollusks. *Totoralia* gen. nov. appears to be restricted to the Precordillera; however, the Cambrian occurrences of comparable *Scenella*-like fossils suggest affinities with North America.

ACKNOWLEDGMENTS

We are grateful to Carlos Cingolani, Marta Alfaro (Museo de Ciencias Naturales de La Plata, Argentina), Susana Devincenzi, Héctor Ahumada, Esperanza Cerdeño and Clara Abal (Museo de Ciencias Naturales y Antropológicas “Juan Cornelio Moyano”, Mendoza, Argentina) for offering assistance and permitting access to the collections studied. Susana Heredia (Universidad de San Juan, Argentina) kindly shared unpublished geologic information on the El Totoral locality. John Pojeta (Smithsonian, National Museum of Natural History, USA), Bruce Runnegar (University of California, USA) and an anonymous referee are thanked for detailed reviews of the manuscript. We extend our thanks to Euan Clarkson (University of Edinburgh, UK) for reviewing the final presentation of the paper. Rafael Urrejola assisted with photography and Mario Campaña prepared the Figs. 1, 2 and 5. This work has been possible thanks to financial support from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), the Instituto Superior de Correlación Geológica and the Universidad Nacional de La Plata, Argentina.

REFERENCES

Babcock, L.E., Robison, R.A., 1988. Taxonomy and paleobiology of some middle Cambrian *Scenella* (Cnidaria) and Hyolithids (Mollusca) from western North America. University of Kansas, Paleontological Contributions, 121, 1-22.

Bell, C.M., Angseesing, J.P.A., Townsend, M.J., 2001. A chondrophorine (medusoid hydrozoan) from the Lower Cretaceous of Chile. Palaeontology, 44, 1011-1023.

Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A., Runnegar, B.N., 1990. Early Cambrian fossils from South Australia. Memoirs of the Association of Australasian Palaeontologists, 9, 1-364.

Beresi, M.S., 2003. Cambrian sponge spicules and Chancelloriid sclerites from the Argentine Precordillera: A review. Geologica Acta, 1(1), 73-84.

Berg-Madsen, V., Peel, J.S., 1986. *Scenella barrandei* (Mollusca) from the Middle Cambrian of Baltoscandia. Norsk Geologisk Tidsskrift, 66, 81-86.

Billings, E., 1872. On some fossils from the primordial rocks of Newfoundland. Canadian Naturalist and Quarterly Journal of Science, new series, 6, 465-479.

Bordonaro, O.L., 1992. El Cámbrico de Sudamérica. In: Gutiérrez Marco, J.C., Saavedra, J., Rábano, I. (eds.). Paleozoico Inferior de Ibero-América. España, Universidad de Extremadura, 69-84.

Bordonaro, O.L., 2003a. Review of the Cambrian Stratigraphy of the Argentine Precordillera. Geologica Acta, 1(1), 11-21.

Bordonaro, O.L., 2003b. Evolución paleoambiental y paleogeográfica de la cuenca cámbrica de la Precordillera argentina. Revista de la Asociación Geológica Argentina, 58, 329-346.

Bordonaro, O.L., Banchig, A.L., 1996. Estratigrafía de los olistolitos Cámbricos de la Precordillera argentina. Mendoza, Actas 13º Congreso Geológico Argentino y 3º Congreso de Exploración de Hidrocarburos, 5, 471-479.

Bordonaro, O.L., Liñán, E., 1994. Some Middle Cambrian agnostoids from the Precordillera argentina. Revista Española de Paleontología, 9, 105-114.

Bordonaro, O.L., Beresi, M., Keller, M., 1993. Reinterpretación estratigráfica del Cámbrico del área de San Isidro, Precordillera de Mendoza. Mendoza, Actas 12º Congreso Geológico Argentino y 2º Congreso de Exploración de Hidrocarburos, 2, 12-19.

Borrello, A.V., 1965. Sobre el desarrollo bioestratigráfico del Cámbrico de la Precordillera. Acta Geológica Lilloana, 7, 39-46.

Borrello, A.V., 1971. The Cambrian of South America. In: Holland, C.H. (ed.). Cambrian of the New World. Cardiff, Wiley Intersciences, 1, 385-438.

Castellaro, H.A., 1963. Faunas cámbricas. In: Amos, A.J., Camacho, H.H., Castellaro, H.A., Menéndez, C.A. (eds.). Guía Paleontológica Argentina. Buenos Aires, Publicación del Consejo Nacional de Investigaciones Científicas y Técnicas, 13-37.

Cobbold, E.S., 1921. The Cambrian horizons of Comley (Shropshire) and their Brachiopoda, Pteropoda, Gastropoda. Quarterly Journal of the Geological Society of London, 76, 325-386.

Cuvier, G., 1797. Tableau élementaire de l'histoire naturelle des animaux. Paris, Baudouin, 700pp.

Donaldson, A.C., 1962. A patelliform gastropod, *Palaelophacmaea criola*: a new genus and species from the Lower Ordovician of central Pennsylvania. Proceedings of the West Virginia Academy of Science, 34, 143-149.

Evans, K.R., 1992. *Marocella*: Antarctic specimens of an enigmatic Cambrian animal. Journal of Paleontology, 66, 558-562.

Geyer, G., 1986. Mittelkambrische Mollusken aus Marokko und Spanien. Senckenbergiana Lethaea, 67, 55-118.

Geyer, G., 1994. Middle Cambrian mollusks from Idaho and early conchiferan evolution. In: Landing, E. (ed.). Studies in Stratigraphy and Paleontology in Honour of Donald W. Fisher. New York State Museum Bulletin, 481, 69-86.

Gozalo, R., Mayoral, E., Gámez-Vintaned, J.A., Dies, M.E., Muñiz, F., 2003. A new occurrence of the genus *Tonkinella* in northern Spain and the Middle Cambrian intercontinental correlation. Geologica Acta, 1(1), 121-126.

Grabau, A.W., Shimer, H.W., 1909. North American Index Fossils–Invertebrates, volume 1. New York, A.G. Seiler & Co., 853pp.

Gubanov, A.P, Fernández Remolar, D.C., Peel, J.S., 2004a. Early Cambrian molluscs from sierra de Córdoba (Spain). Geobios, 37, 199-215.

Gubanov, A.P, Skovsted, C.B., Peel, J.S., 2004b. *Anabarella australis* (Mollusca, Helcionelloida) from the lower Cambrian of Greenland. Geobios, 37, 719-724.

Gubanov, A.P, Peel, J.S., 2003. The Early Cambrian helcionelloid mollusc *Anabarella* Vostokova. Palaeontology, 46, 1073-1087.

Hall, J., Whitfield, R.P., 1872. Notice of two new species of fossil shells from the Potsdam sandstone of New York. New York State Cabinet Natural History Annual Report, 23, 241-242.

Harrington, H.J., Leanza, A.F., 1943. Paleontología del Paleozoico inferior de la Argentina. 1. Las faunas del Cámbrico Medio de San Juan. Revista del Museo de La Plata, 2(11), 207-223.

Heredia, S., 1994. Conodontes y Bioestratigrafía del Cámbrico Superior de Cerro Pelado y San Isidro, Provincia de Mendoza, Argentina. Doctoral Thesis. Argentina, Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, unpublished, 285pp.

Heredia, S., 1996. El Paleozoico Inferior del Cerro Pelado, Precordillera de Mendoza, Argentina. Buenos Aires, Actas 13º Congreso Geológico Argentino y 3º Congreso de Exploración de Hidrocarburos, 1, 591-600.

Heredia, S., 2007. Personal communication.

Heredia, S., Beresi, M.S., 2004. La Formación Empozada y su relación estratigráfica con la Formación Estancia San Isidro (nom. nov.), Ordovícico de la Precordillera de Mendoza. Revista de la Asociación Geológica Argentina, 59, 178-192.

Hicks, H., 1872. On some undescribed fossils from the Mendevian Group. Quarterly Journal of the Geological Society of London, 28, 173-185.

Jaekel, O., 1909. Über die Agnostiden. Zeitschrift der Deutschen Geologischen Gesellschaft, 61, 380-401.

Kase, T., 1988. Reinterpretation of *Brunonia annulata* (Yokoyama) as an Early Cretaceous carinariid mesogastropod (Mollusca). Journal of Paleontology, 62, 766-771.

Keller, M., 1999. Argentine Precordillera. Sedimentary and Plate Tectonic History of a Laurentian Crustal Fragment in South America. The Geological Society of America, 341(Special Paper), 1-131.

Knight, J.B., 1941. Paleozoic gastropod genotypes. The Geological Society of America, 32(Special Paper), 1-510.

Knight, J.B., 1952. Primitive fossil gastropods and their bearing on gastropod classification. Smithsonian Miscellaneous Collections, 117(13), 1-56.

Knight, J.B., Yochelson, E.L., 1960. Monoplacophora. In: Moore, R.C. (ed.). Treatise on Invertebrate Paleontology, Part I, Mollusca 1. Lawrence, Geological Society of America and University of Kansas Press, 177-184.

Kobayashi, T., 1939. On the agnostids. Part 1. Imperial University of Tokyo, Journal of the Faculty of Science, Section II (Geology, Mineralogy, Geography, Seismology), 5, 69-198.

Landing, E., 1988. Lower Cambrian of eastern Massachusetts: stratigraphy and small shelly fossils. Journal of Paleontology, 62, 661-695.

Landing, E., Narbonne, G.M., 1992. *Scenella* and "a chondrophorine (medusoid hydrozoan) from the basal Cambrian (Placentian) of Newfoundland". Journal of Paleontology, 66, 338.

Leanza, A.F., 1947. El Cámbrico Medio de Mendoza. Revista del Museo de La Plata (Nueva Serie), Sección Paleontología, 3, 223-235.

Lin, Tian-Rui, 1999. Discovery of middle Cambrian *Marocella* from Yaxian County, Hainan Province, China. Acta Palaeontologica Sinica, 38(1), 102-105.

Linnarsson, J.G.O., 1869. Om Vestergötlands Cambriska och Siluriska aflagringar. Kongliga Svenska Vetenskaps-Akademiens Handlingar, 8(2), 1-89.

Martí Mus, M., Palacios, T., Jensen, S., 2008. Size of the earliest mollusks: Did small helcionellids grow to become large adults? Geology, 36(2), 175-178.

Missarzhevsky, V.V., 1989. Oldest skeletal fossils and stratigraphy of Precambrian and Cambrian boundary beds (In Russian). Moscow, Nauka, 237pp.

Missarzhevsky, V.V., Mambetov, A.M., 1981. Stratigraphy and fauna of Cambrian and Precambrian boundary beds of Maly Karatau (In Russian). Moscow, Nauka, 87pp.

Peel, J.S., 1988. Molluscs of the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddelelser om Grønland, Geoscience, 20, 145-168.

Peel, J.S., 1991. Functional morphology of the Class Helcionelloida nov., and the early evolution of the Mollusca. In: Simonetta, A., Conway Morris, S. (eds.). The Early Evolution of Metazoa and the Significance of Problematic Taxa. Camerino, 27-31 March 1989, Proceedings International Symposium held at the University of Camerino, 157-177.

Perner, J., 1903. Patellidae et Bellerophontidae. In: Barrande, J.. (ed.). Système silurien du centre de la Boheme, 4 Gastéropoden, tome 1. Praha, 1-164.

Pojeta, A.Jr., Runnegar, B., Peel, J.S., Gordon, M.Jr., 1987. Phylum Mollusca. In: Boardman, R.S., Cheetham, A.H., Rowell, A.J. (eds.). Fossil Invertebrates. Palo Alto (California), Blackwell Scientific Publications, 270-435.

Poulsen, C., 1960. Fossils from the late Middle Cambrian *Bolaspidella* Zone of Mendoza, Argentina. Matematisk-fysiske Meddelelser, Det Kongelige Danske Videnskabernes Selskab, 32(11), 1-42.

Robison, R.A., 1984. Cambrian Agnostida of North America and Greenland, Part I, Ptychagnostidae. The University of Kansas Paleontological Contributions, 109, 1-59.

Robison, R.A., 1988. Trilobites of the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddelelser om Grønland, Geoscience, 20, 23-103.

Rolleri, E., De Giusto, J.M., 1950. Descripción Geológica de la Hoja 23 C, Mendoza. Argentina, Gerencia de Exploración YPF, unpublished.

Rozanov, A.Yu., Missarzhevsky, V.V., Volkova, N.A., Voronova, L.C., Krylov, I.N., Keller, B.M., Korolyuc, I.K., Lendzion, K., Michniak, R., Pykhova, N.G., Sidarov, A.D., 1969. The Tommotian Stage and the Cambrian Lower Boundary Problem. New Delhi, Amerind Publishing Co., 1-359.

Rozov, S.N., 1968. New genus of Late Cambrian mollusca from the class of Monoplacophora, southern part of Siberian platform (In Russian). Doklady, U.S.S.R. Academy of Sciences, 183(6), 1527-1430.

Runnegar, B., 1987. Class Monoplacophora. In: Boardman, R.S., Cheetham, A.H., Rowell, A.J. (eds.). Fossil Invertebrates. Palo Alto (California), Blackwell Scientific Publications, 297-304.

Runnegar, B., Jell, P.A., 1976. Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. Alcheringa, 1, 109-138.

Runnegar, B., Pojeta, A.Jr., 1974. Molluscan phylogeny: the paleontological viewpoint. Science, 186, 311-317.

Rusconi, C., 1950. Trilobitas y otros organismos del Cámbrico de Canota. Revista del Museo de Historia Natural de Mendoza, 4, 71-84.

Rusconi, C., 1954. Fósiles cámbricos y ordovícicos de San Isidro. Boletín Paleontológico de Buenos Aires, 30, 1-4.

Rusconi, C., 1955. Fósiles cámbricos y ordovícicos al oeste de San Isidro, Mendoza. Revista del Museo de Historia Natural de Mendoza, 8, 3-64.

Rusconi, C., 1956a. Fósiles cámbricos al sud del Totoral, Mendoza. Revista del Museo de Historia Natural de Mendoza, 9, 115-120.

Rusconi, C., 1956b. Lista de los géneros y especies fundadas por Carlos Rusconi. Revista del Museo de Historia Natural de Mendoza, 9, 121-156.

Rusconi, C., 1956c. Correlaciones Cambro-Ordovícicas entre Mendoza y Norteamérica. México, 20º Congreso Geológico Internacional, Simposio Cámbrico, 2, 751-762.

Rusconi, C., 1958. Nuevos fósiles cámbricos de El Totoral, Mendoza. Revista del Museo de Historia Natural de Mendoza, 11, 93-107.

Shaw, A.B., 1962a. Paleontology of northwestern Vermont. IX. Fauna of the Monkton Quartzite. Journal of Paleontology, 36, 322-345.

Shaw, A.B., 1962b. Paleontology of northwestern Vermont. VIII. Fauna of the Hungerford Slate. Journal of Paleontology, 36, 314-321.

Shergold, J.H., Bordonaro, O.L., Liñán, E., 1995. Late Cambrian agnostoid trilobites from Argentina. Palaeontology, 38, 241-257.

Skovsted, C.B., Peel, J.S., 2007. Small shelly fossils from the argillaceous facies of the Lower Cambrian Forteau Formation of western Newfoundland. Acta Palaeontologica Polonica, 52, 729-748.

Stanley, G.D.Jr., 1986. Chondrophorine hydrozoans as problematic fossils. In: Hoffman, A., Nitecki, M.H. (eds.). Problematic Fossil Taxa. New York and Oxford, Oxford University Press, Oxford Monographs on Geology and Geophysics, 5, 68-86.

Stanley, G.D.Jr., Kanie, Y., 1985. The first Mesozoic chondrophorine (medusoid hidrozoan), from the Lower Cretaceous of Japan. Palaeontology, 28, 101-109.

Stinchcomb, B.L., 1986. New monoplacophora (Mollusca) from Late Cambrian and Early Ordovician of Missouri. Journal of Paleontology, 60, 606-626.

Stinchcomb, B.L., Angeli, N.A., 2002. New Cambrian and Lower Ordovician monoplacophorans from the Ozark Uplift, Missouri. Journal of Paleontology, 76, 965-974.

Tortello, M.F., 2009. Systematic revision of the latest Middle Cambrian trilobites from Cerro El Solitario, Mendoza, Argentina. Memoirs of the Association of Australasian Palaeontologists, 37, 247-272.

Tortello, M.F., Bordonaro, O.L., 1997. Cambrian agnostoid trilobites from Mendoza, Argentina: a systematic revision and biostratigraphic implications. Journal of Paleontology, 71, 74-86.

Vostokova, V.A., 1962. The Cambrian gastropods from Siberia and Taimyr (In Russian). Trudy Nauchno Issledovatel'skogo Instituta Geologii Arktiki, 28, 51-74.

Webers, G.F., Yochelson, E.L., 1999. A revision of *Palaeacmaea* (Upper Cambrian) (?Cnidaria). Journal of Paleontology, 73, 598-607.

Wenz, W., 1938. Gastropoda. Allgemeiner Teil und Prosobranchia. In: O.H. Schindewolf (ed.). Handbuch der Paläozoologie, Band 6. Berlin, Borntrager, 1-720.

Westergård, A.H., 1936. Paradoxides oelandicus beds of Őland. Sveriges Geologiska Undersökning, Series C, 394, 1-66.

Yochelson, E.L., 1984. North American Middle Ordovician S*cenella* and *Macroscenella* as possible chondrophorid coelenterates. Palaeontographica Americana, 54, 148-153.

Yochelson, E.L., Gil Cid, D., 1984. Reevaluation of the systematic position of *Scenella*. Lethaia, 17, 331-340.

Yochelson, E.L., Stanley, G.D.Jr., 1981. An early Ordovician patelliform gastropod, *Palaelophacmaea,* reinterpreted as a coelenterate. Lethaia, 15, 323-330.

Yochelson, E.L., Stürmer, W., Stanley, G.D.Jr., 1983. *Plectodiscus discoideus* (Rauff): a redescription of a chondrophorine from the early Devonian Hunsrück Slate, West Germany. Palaeontologische Zeitschrift, 57, 39-68.

Manuscript received July 2009;
revision accepted November 2010;
published Online May 2011.