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Lower Ordovician bivalves from southern Bolivia: paleobiogeographic affinities

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Abstract. Bivalves from the Sella Formation (middle Arenig, Tarija, Bolivia) are described and illustrated. The taxa recognized are *Hemiprionodonta lusitanica* (Sharpe), known from southern Europe (Spain, Armorican Massif, Montagne Noire), *Redonia riojana* Sánchez from the west-Argentina Famatina basin, and the new species *Coxiconchia sellaensis*. These species support the paleobiogeographic affinities between the south European (Armorica), Bolivian and west Argentine basins and corroborate the development of an extensive and continuous shelf throughout the northwest margin of Gondwana during the Arenig. Additionally, specimens at different stages of dental development of *Natasia boliviensis* (Babin and Branisa) are reported.

Resumen. BIVALVOS DEL ORDOVÍCICO TEMPRANO DEL SUR DE BOLIVIA: AFINIDADES PALEOBIOGEOGRÁFICAS. Se describen e ilustran bivalvos procedentes de la Formación Sella (Arenigiano medio, Tarija, Bolivia). Se identificaron las especies *Hemiprionodonta lusitanica* (Sharpe), conocida previamente en el sur de Europa (España, Macizo Armoricano, Montagne Noire) y *Redonia riojana* Sánchez, de la cuenca de Famatina, en el oeste de Argentina. Asimismo se define la nueva especie *Coxiconchia sellaensis*. La presencia de estas especies confirma las afinidades paleobiogeográficas entre el sur de Europa (Armorica), Bolivia y noroeste de Argentina y corrobora el desarrollo de una extensa y continua plataforma a lo largo del margen noroeste de Gondwana durante el Ordovícico temprano. Además se da a conocer la presencia de ejemplares en distintas etapas del desarrollo dentario de *Natasia boliviensis* (Babin y Branisa).

Key words. Bivalves. Arenig. Bolivia.

Palabras clave. Bivalvos. Arenigiano. Bolivia.

Introduction

Knowledge of Early Ordovician bivalves from Bolivia is limited to a few taxa. *Ctenodonta* cf. *C. laevigata* Harrington was illustrated by Branisa (1965) and the genera *Goniophora* and *Goniophorina* were mentioned by Havlíček y Branisa (1980). Babin and Branisa (1987) analyzed and described two species, *Ekaterodonta boliviensis*, later reassigned to the genus *Natasia* by Sánchez (1997a), and *Coxiconchia* sp. In the present work material referred to both species is included and a new species of *Coxiconchia* is proposed.

Since the bivalves described here are important elements to support the faunal affinities of southern Bolivia with other regions of western Gondwana, a brief paleobiogeographic discussion is included.

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Stratigraphy and age

The bivalves described below come from the Tarija area, southern Bolivia (figure 1.A). The lower Ordovician rocks are well exposed near the Sella village, about 16 km north of Tarija. The lithostratigraphic nomenclature of this area is rather confused because different formational names and subdivisions have been proposed (Rivas-Valenzuela *et al*., 1969; Suárez Soruco, 1976, 1992, and references therein). However, now there is consensus to nominate as Sella Formation the strata that conformably overlie the early Arenig Obispo Formation and in turn are unconformably overlain by the Late Ashgill-Llandovery Cancañiri Formation. This succession, about 500 m thick, has been divided into a lower fine-grained member and an upper predominantly sandy member (Suárez Soruco, 2000). The lower member is composed of gray to green bioturbated siltstones interbedded with thin sandstone layers bearing lenticular shell beds. Coquinas often fill gutter casts and include brachiopods, trilobites, bivalves and nautiloids. As a whole, the succession is clearly coarsening up. The upper member is composed of

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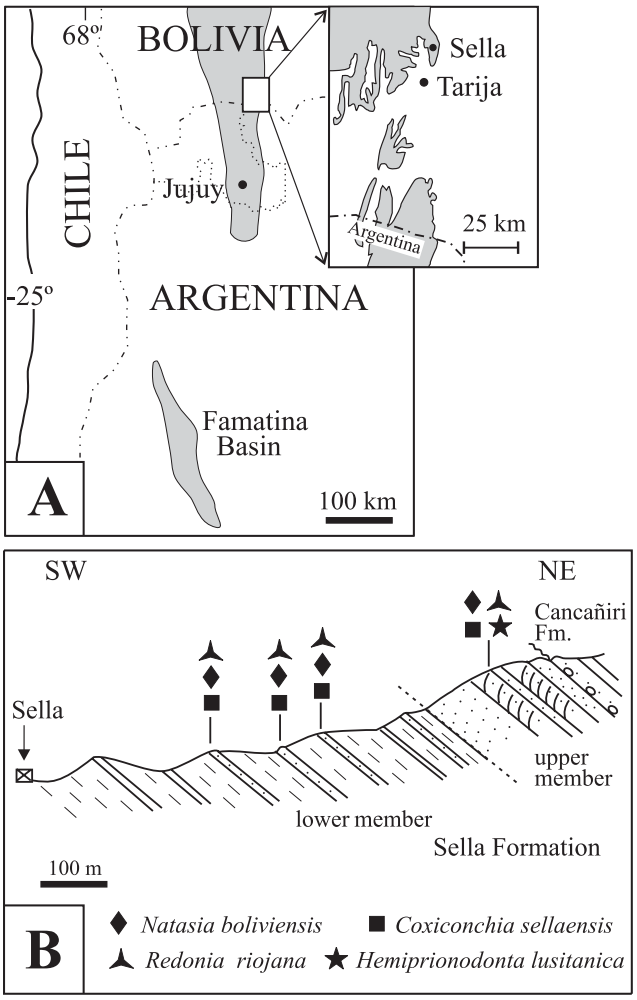

Figure 1. A, Location map of the Sella locality. Grey area: Early Ordovician outcrops in the Cordillera Oriental and Sierras Subandinas/*Mapa de ubicación. Áreas en gris: afloramientos del Ordovícico Temprano de Cordillera Oriental y Sierras Subandinas.* **B,** Stratigraphic section in the Sella locality showing location of fossiliferous horizons/*Sección estratigráfica de la localidad de Sella indicando la ubicación de los horizontes fosilíferos.*

amalgamated quartzitic sandstone beds displaying low-angle cross stratification and abundant *Cruziana* traces.

Although this upper sandy succession has long been correlated with the quartzitic San Benito Formation of Caradoc age, graptolite samples from this member and equivalent units of the Tarija area indicate the mid-Arenig *Baltograptus minutus* Zone (Maletz *et al*., 1995). Moreover, shelly faunas from the lower member, including the brachiopods *Desmorthis segnis* Havlíček and Branisa, 1980, and *Glyptorthis imbrex* Havlíček and Branisa, 1980, are almost identical to those from the upper part of the Acoite Formation (Benedetto, 1998), of well-constrained mid-Arenig age (*Baltograptus deflexus* Zone, Toro, 1997; Brussa *et al*., 2003).

The bivalves described in this paper occur in the sandy beds of the lower and upper members of the unit, with exception of *Hemiprionodonta lusitanica* (Sharpe) that is confined to the uppermost sandy levels, 35 meters below the contact with the Cancañiri Formation (figure 1.B).

Comments on paleobiogeographic affinities

Affinities between the Sella fauna and those of the Armorican Massif, Montagne Noire, and Spain were discussed by Babin and Branisa (1987), on the basis of the record of *Coxiconchia* and the rostroconch *Ribeiria* in the Sella locality. The presence of *Hemiprionodonta* and *Redonia* in the Sella Formation supports the strong relationships of the Early Ordovician faunas throughout the west Gondwanan shelves, and reinforces the suggestion by Benedetto and Sánchez (1996) that the early to middle Ordovician brachiopod and mollusc assemblages from the autochthonous South American basins are closely related to those of the Mediterranean Province defined on the basis of brachiopod faunas (Havlíček, 1989, and references therein) (figure 2). Notably *Hemiprionodonta* is represented in Bolivia and southern Europe (Armorica) by the same species, suggesting a strong link between both areas. Other genera capable to migrate around the Gondwanan margins during the early Ordovician are *Xestoconcha* Pojeta and Gilbert-Tomlinson, recorded from the Amadeus Basin of Australia and South Wales (Cope and Babin, 1999),

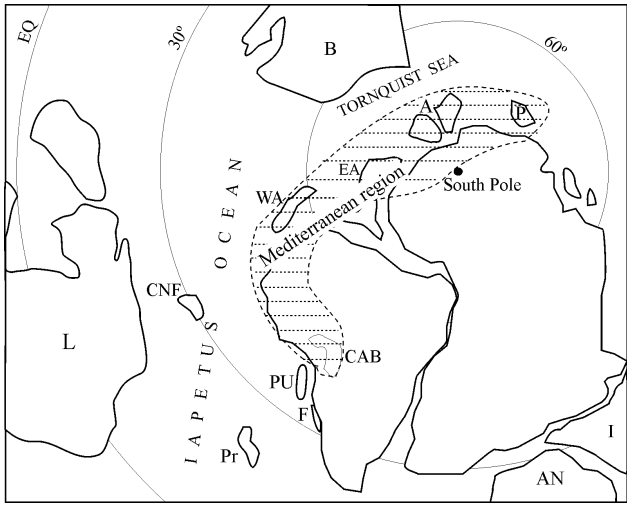

Figure 2. Middle Arenig paleogeographic reconstruction/*Reconstrucción paleogeográfica del Arenigiano medio.* **A,** Armorica; **AN,** Antarctica; **B,** Baltica; **CAB,** Central Andean basin; **CNF,** Central New Foundland; **EA,** east Avalonia; **F,** Famatina basin; **I,** India; **L,** Laurentia; **P,** Perunica; **Pr,** Precordillera basin; **PU,** Western Puna; **WA,** west Avalonia. Simplified from Benedetto and Sánchez (1996) and Benedetto (2003)/*Simplificado de Benedetto y Sánchez (1996) y Benedetto (2003).*

and *Noradonta* Pojeta and Gilbert-Tomlinson, from Australia and the Montagne Noire (Sánchez and Babin, 2003). However, they represent a minor percentage of the 62 genera documented from Gondwanan and peri-Gondwanan localities (see a complete list of data in Sánchez and Babin, 2003). Consequently, the restricted distribution of these species confirms the statement of Sánchez and Babin (2003) that the Ordovician bivalves could have been stenotopic forms lacking planctotrophic larvae, and consequently had limited dispersal capabilities.

The bivalve fauna of the Sella Formation shares with the Acoite Formation fauna the species *Natasia boliviensis* (Babin and Branisa). The Argentine Acoite Formation has yielded abundant specimens of *N. boliviensis* showing different stages of dental development, leading to the recognition of a succession of dental changes through growth in this species. On the other hand, the Sella region and the Famatina Range have in common *Redonia riojana* Sánchez, suggesting close relationships between the two areas. The volcaniclastic setting and climatic conditions in the Famatina Range resulted in the development of peculiar type assemblages, different to those of the coeval successions of the northwest Argentina and Precordillera basin (Waisfeld *et al*., 2003). The fact that this species has been able to colonize both areas with different environmental conditions suggests that it was an eurytopic form.

Systematic paleontology

Material described in this paper is deposited in the paleontological collections of the Museo de Historia Natural de Cochabamba, Bolivia, under the prefix MHNC, and in the Centro de Investigaciones Paleobiológicas, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, prefix CEGH-UNC. Systematic arrangement follows Carter *et al*. (2000).

Superorder NUCULIFORMII Gray, 1824
Order NUCULOIDA Dall, 1889
Family TIRONUCULIDAE Babin, 1982
Subfamily NATASIINAE Sánchez, 1997a

Genus ***Natasia*** Sánchez, 1995

Type species. *Ekaterodonta boliviensis* Babin and Branisa, 1987. Original designation.

Natasia boliviensis (Babin and Branisa, 1987)
Figures 3.K-L

1987. *Ekaterodonta boliviensis* Babin and Branisa, p. 122, fig. 2, lám. 1, figs.9-12.
1995. *Natasia boliviensis* (Babin and Branisa), Sánchez, p. 684, Lam. 86, fig. 2.
1997a. *Natasia boliviensis* (Babin and Branisa), Sánchez, p. 473, fig. 4.
2002. *Natasia boliviensis* (Babin and Branisa), Sánchez, pl. 1, fig. 1.
2003. *Natasia boliviensis* (Babin and Branisa), Sánchez, p. 279, pl. 3, figs.19-20.

Material. 20 specimens of articulated and isolated left and right valves, all preserved as internal molds, MHNC 13031, 13032 and CEGH-UNC 21715, 21716, and 21720-21722.

Geographic and stratigraphic provenance. Sandy beds of the lower and upper members of the Sella Formation, Sella locality, Tarija.
Occurrence. Acoite Formation, northwestern Argentina, middle Arenig.
Discussion. The abundant material from several levels of the unit includes specimens displaying different stages of dentition development. Modifications from the taxodont type to the actinodont-like pattern coincide with those described by Sánchez (1997a) on the basis of the Acoite Formation collection. In figures 3.K and L the juvenile and intermediate stages are illustrated.

Superorder PTERIOMORPHIA Beurlen, 1944
Order ARCOIDA Stoliczka, 1871
Superfamily GLYPTARCOIDEA Cope, 1996
Family GLYPTARCIDAE Cope, 1996

Genus ***Hemiprionodonta*** Cope, 1996

Type species. *Dolabra* ? *lusitanica* Sharpe, 1853.

Hemiprionodonta lusitanica (Sharpe, 1853)
Figures 3.J, 3.M, 4

1853. *Dolabra* ? *lusitanica* Sharpe, p. 151, pl- 9, fig. 3.
1853. *Cypricardia* ? *beirensis* Sharpe, p. 152, fig. 16.
1856. *Arca naranjoana* de Verneuil and Barrande, p. 989, pl. 26, fig. 12
1912. *Actinodonta acuta* Barrois, Douvillé, p. 440, fig. 12.
1918. *Modiolopsis* ? *lusitanica* (Sharpe), Born, p. 342.
1966. *Actinodonta naranjoana* (de Verneuil and Barrande), Babin, p. 233, pl. 10, figs. 5, 7, 11.
1970. *Actinodonta naranjoana* (de Verneuil and Barrande), Bradshaw, p. 636, text-figs. 13-15.
1978. *Glyptarca naranjoana* (de Verneuil and Barrande), Morris, pl. 1, fig. 2.
1984. *Glyptarca naranjoana* (de Verneuil and Barrande), Gutiérrez-Marco *et al*., p. 302.
1985. *Glyptarca naranjoana* (de Verneuil and Barrande), Babin and Gutiérrez-Marco, fig. 4. Synonymy from Babin and Gutiérrez-Marco, 1991. Add:
1991. *Glyptarca* ? *lusitanica* (Sharpe), Babin and Gutiérrez-Marco, p. 126, text-fig. 6.
1996. *Hemiprionodonta lusitanica* (Sharpe), Cope, p. 991.

Material. A single right and a single left valves preserved as internal molds, MHNC 13027 and CEGH-UNC 21705.

Geographic and stratigraphic provenance. Upper-

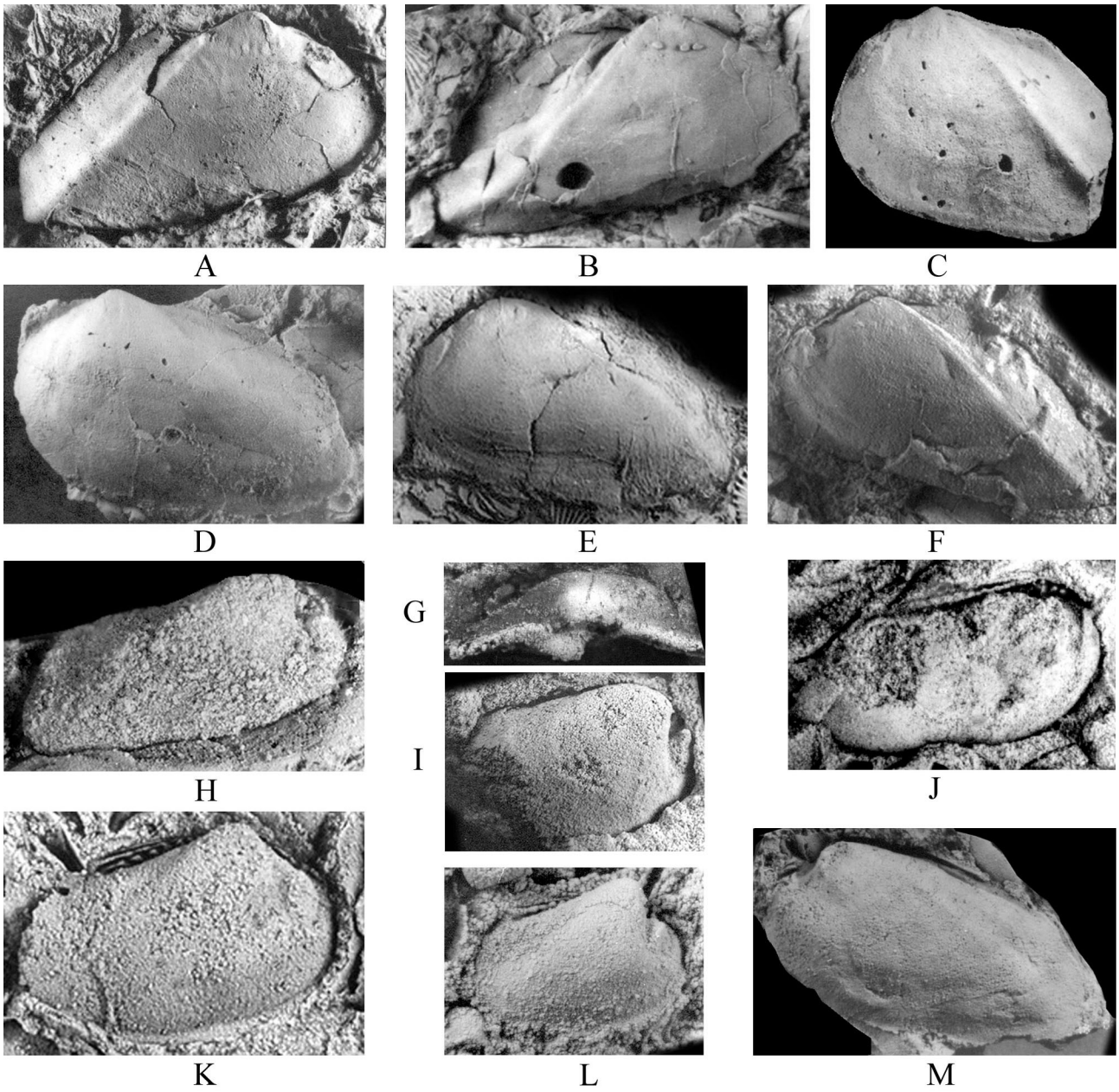

Figure 3. A-G. ***Coxiconchia sellaensis*** sp.n. A, right valve/*valva derecha*, CEGH-UNC 21711(x 2); **B,** right valve/*valva derecha*, CEGH-UNC 21709 (x 2); **C,** left valve, holotype/*valva izquierda, holotipo*, MHNC 13023 (x 2); **D,** left valve/*valva izquierda*, CEGH-UNC 21706 (x 2,5); **E,** left valve/*valva izquierda*, CEGH-UNC 21708 (x 2); **F,** left valve/*valva izquierda*, MHNC 13026 (x 2,5); **G,** anterior view showing cardinal tooth, latex cast of specimen/*vista anterior mostrando el diente cardinal, molde de caucho* CEGH-UNC 21714 (x 1,5); **H, I,** *Redonia riojana* Sánchez. **H,** right valve/*valva derecha,* MHNC 13029 (x 3); **I,** right valve/*valva derecha*, MHNC 13028 (x 3); **J, M,** ***Hemiprionodonta lusitanica*** (Sharpe); **J,** right valve/*valva derecha*, CEGH-UNC 21705 (x 3); **M,** left valve/*valva izquierda*, MHNC 13027 (x 2,5); **K, L,** ***Natasia boliviensis*** (Babin and Branisa); **K,** right valve/*valva derecha*, CEGH-UNC 21715 (x 6,5); **L,** right valve/*valva derecha*, MHNC13031 (x 7).

most sandy beds of the Sella Formation, 35 m below the contact with the Cancañiri Formation, Sella locality, Tarija.

Occurrence. Llanvirn and Llandeilo strata of the Hesperian Massif, Iberian Cordillera, and Arenig of the Armorican Massif.

Description. Ovate, posteriorly elongate shell with umbo placed in the anterior third of valve. Shell convexity moderate, with a gently subumbonal carina. Dentition includes anterior, posterior pseudolateral, and pseudocardinal teeth. Right valve with two short, anterior pseudolateral teeth radiating towards the dorsal margin; two short pseudocardinal, the anterior curved and the posterior right, oblique from

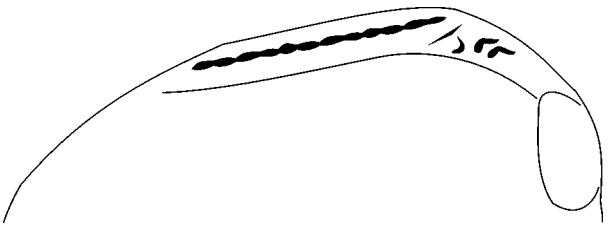

Figure 4. Hinge details of *Hemiprionodonta lusitanica* (Sharpe). Camera lucida drawing of specimen CEGH-UNC 21705/*Detalle de la charnela de* Hemiprionodonta lusitanica *(Sharpe). Dibujo en cámara clara del ejemplar CEGH-UNC 21705.*

the umbo towards the posterior margin; the latter is overlapped by an elongate, crenulated, posterior pseudolateral (figure 4). Left valve with a single posterior pseudolateral socket, and two anterior pseudolateral short teeth; pseudocardinals not preserved. Anterior adductor muscle deeply impressed, posterior ovate, weakly impressed, and larger than the anterior one. Other muscle scars not preserved. Ornamentation not preserved.

Discussion. The specimens are very close to those assigned to *Glyptarca* ? *lusitanica* Sharpe described and illustrated by Babin and Gutiérrez-Marco (1991). The material described by Babin and Gutiérrez-Marco was subsequently assigned by Cope (1996) to the genus *Hemiprionodonta* Cope. However, this author did not include a diagnosis of the new genus but only a brief description of the dentition. Consequently, comparisons are based on the description of *H. lusitanica* by Babin and Gutiérrez-Marco. Cope (1996, p. 991) stated that "the latter (the pseudocardinal) do not overlap the posterior lateral tooth to any significant degree". However, in the description of *H. lusitanica* Babin and Gutiérrez-Marco noted the overlaping of the posterior pseudolateral over the pseudocardinal posterior. This feature is also evident in the text-figures 6d and 7d by Babin and Gutiérrez-Marco (1991).

Superorder HETEROCONCHIA Hertwig, 1895
Superfamily CYCLOCONCHOIDEA Ulrich, 1893
Family REDONIIDAE Babin, 1966
Genus ***Redonia*** Rouault, 1851

Type species. *Redonia deshayesiana* Rouault, 1851.

Redonia riojana Sánchez, 1997b
Figures 3.H-I

2003. *Redonia riojana* Sánchez. Sánchez, p. 278, pl. 2, figs. 5-6.

Material. Twelve articulated and isolated left and right valves, all preserved as internal molds, MHNC 13028, 13029, and CEGH-UNC 21717-21719.

Geographic and stratigraphic provenance. Sandy beds of the lower and upper members of the Sella Formation, Sella locality, Tarija.

Occurrence. Middle Arenig beds of the Suri Formation, Gualcamayo River, Famatina Range, Argentina.

Description. Ovate, subtrapezoidal, posteriorly elongated shells. Periumbonal region wide; prominent, prosogyrate umbo, gently incurved toward the hinge line, with a marked constriction in the apical area. Anterior adductor muscle scar strongly impressed, limited by an anterior buttress; posterior adductor scar wide, gently impressed. Two anterior teeth running parallel to the hinge line. Size of specimens is about 15 mm long and 10 mm high.

Discussion. No significant differences between the Bolivian sample described here and the type material from Famatina Range have been found. The shell outline, the gently projection of the umbo over the cardinal margin, and the terminal protuberance in the beak in the internal molds are all diagnostic features of *R. riojana* (Sánchez, 1997b) and indicate that the Sella material is conspecific with the Argentine species.

Superorder ?ANOMALODESMATA
Family uncertain
Subfamily COXICONCHIINAE Babin, 1977

Genus ***Coxiconchia*** Babin, 1966

Type species. *Lyonsia britannica* Rouault, 1851.

Discussion. The placement of Coxiconchiinae into a major taxonomic group is unclear. As was discussed by Sánchez (2005), the new arrangement of modiomorphids by Fang and Morris (1997) removes *Coxiconchia* from its previous location into the Family Modiomorphidae (Babin, 1977). Fang and Morris (1997) suggested that this genus could be placed into the Anomalodesmata. However, it lacks the diagnostic surface spicules. Consequently, the relationships of *Coxiconchia* with Anomalodesmatans remain doubtful.

Coxiconchia sellaensis nov. sp.
Figures 3.A-G, 5

Holotype. An internal mold of left valve (MHNC 13023, figure 5, C).

Paratypes. 18 left and right valves, all preserved as internal molds, MHNC 13024, 13025, 13026, 13032b, and CEGH-UNC 21706-21714.

Diagnosis. *Coxiconchia* with subumbonal carina, usually strongly marked and well-developed, wide posteroventral slope.

Derivation of name. After the Sella locality.

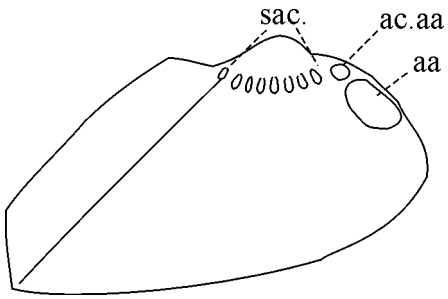

Figure 5. Schematic drawing of *Coxiconchia sellaensis* sp. n. showing muscle scars (based on specimens CEGH-UNC 21711 and MHNC 13023)/*Esquema de las impresiones musculares de* Coxiconchia sellaensis *sp. n. (basado en los ejemplares CEGH-UNC 21711 y MHNC 13023).*

Horizon and locality. Sandy beds of the lower and upper members of the Sella Formation, middle Arenig, Sella locality, Tarija.

Description. Subtrapezoidal, posteroventrally elongated shells; not protruding umbo placed in the anterior third of the valve; hinge line short and straight; anterior margin broadly convex, ventral margin gently rounded, posterior margin oblique and straight; ventral and posterior margins forming an acute angle. Subumbonal carina usually strongly marked limiting a posteroventral slope; in some specimens an additional subumbonal carina developed on the slope; in few specimens the carina is ill defined and the slope is developed by a broad inflexion of the valve (see figure 3.D). Anterior adductor muscle scar deep, ovate, with maximum length parallel to the anterior margin. An additional small, rounded muscle scar is placed ahead the anterior adductor scar. Seven subumbonal accessory muscle scars extend between the anterior adductor muscle and the carina. Some specimens possess an additional accessory muscle scar on the carina (figure 5). Posterior adductor muscle scar ill-defined, ovate, placed on the slope. A single elongated subumbonal tooth runs parallel to the hinge line. Ornament not preserved, with the exception of some irregularly disposed concentric rugae. Radial ornament lacking.

Discussion. In the original diagnosis of *Coxiconchia*, Babin (1966) did not mention the presence or absence of a carina. Later, in the revision of the genus this author stated "*le talus postéro-umbonal se raccorde sans discontinuité flagrante (pas de carène) avec la convexité latérale de la valve...quoiqu'une dépression extrêmement discrète soit parfois soupçonnable en avant du talus sur certains individus*" (Babin, 1977, p. 55). His figures 2a and 2c of Plate 1 show two specimens with a gently inflexion of the valve which marks the limit of the posterior talus. This gently inflexion is similar to those of some specimens of the Sella material. Consequently, the Bolivian collection displays an inverse pattern with regard to those of *C. brittannica* described by Babin: most specimens of the Sella Formation have a strong carina and in some isolated individuals it is absent or gently marked. The definition of the carina points out a clear difference with the European species of *Coxiconchia*. This fact was recognized by Babin and Branisa (1987) but in view of the inadequate sample (a single specimen) they did not erect a new species. The current abundant collection we have now allows us to propose a new species for the Bolivian material.

Previous mentions of *Goniophorina* Isberg in the Sella Formation (Havlíček and Branisa, 1980) could be attributed to the similarities in shell outline and subumbonal carina between this genus and *Coxiconchia sellaensis* n.sp. However, *Goniophorina* is edentulous and lacks the typical subumbonal accessory muscles, as was verified in the abundant collections of this genus from the Acoite Formation (northwest Argentina, Sánchez, 1997b).

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