

# UPPER ORDOVICIAN BRACHIOPODS FROM THE SAN BENITO FORMATION, CORDILLERA DEL TUNARI, BOLIVIA



JUAN L. BENEDETTO

Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), CONICET - Universidad Nacional de Córdoba, Facultad Ciencias Exactas, Físicas y Naturales, Av. Vélez Sarsfield 1611, Ciudad Universitaria, X5016GCA Córdoba, Argentina. [jbenedetto@efn.uncor.edu](mailto:jbenedetto@efn.uncor.edu)

**Abstract.** The brachiopod fauna from the San Benito Formation of Bolivia, of late Sandbian–Katian age, is re-studied on the basis of material collected in the Cordillera del Tunari. The new heterorthid genus *Tunaria* is erected to include the species *Orthis berthoisii?* var. *erratica* Davidson, 1869 (formerly attributed to *Drabovinella*) from England, France and Spain, and the new species *Tunaria cocksii* from Bolivia. The fauna also includes the first record in South America of *Rafinesquina pseudoloricata* (Barrande), and *Hirnantia* cf. *transgrediens* (Havlíček). Overall, the low diversity San Benito fauna corroborates the Mediterranean biogeographic signature of Central Andean brachiopod assemblages.

**Keywords.** Upper Ordovician. Bolivia. Brachiopods. Paleobiogeography.

**Resumen.** BRAQUIÓPODOS DEL ORDOVÍCICO SUPERIOR DE LA FORMACIÓN SAN BENITO, CORDILLERA DEL TUNARI, BOLIVIA. Se describe la fauna de braquiópodos de la Formación San Benito de Bolivia, de edad Sandbiano tardío–Katiano, en base a material coleccionado en la Cordillera del Tunari. Se erige el nuevo género *Tunaria* para incluir la especie *Orthis berthoisii?* var. *erratica* Davidson, 1869 (anteriormente atribuida a *Drabovinella*), registrada en Inglaterra, Francia y España, y la nueva especie de Bolivia *Tunaria cocksii*. La fauna también incluye *Hirnantia* cf. *transgrediens* (Havlíček) y el primer registro en América del Sur de *Rafinesquina pseudoloricata* (Barrande). En su conjunto, esta fauna de baja diversidad corrobora la signatura biogeográfica Mediterránea de las asociaciones de braquiópodos de la región Andina Central.

**Palabras clave.** Ordovícico Superior. Bolivia. Braquiópodos. Paleobiogeografía.

In spite of the widespread exposures of Upper Ordovician rocks in Bolivia, only few rhynchonelliformean brachiopods of that age have hitherto been published (Havlíček and Branisa, 1980; Havlíček, 1990). Most described specimens come from boulders within the Hirnantian/ lower Llandovery Cancañiri glaciogenic diamictite, but were collected from outcrops lacking stratigraphic references, and some of them come from loose blocks of uncertain stratigraphic provenance. In 1989 I had the opportunity to study some material from the San Benito Formation in the Cordillera del Tunari, north of Cochabamba City, housed in the Natural History Museum of Cochabamba that had been collected by Dr. Ramiro Suárez Soruco (Suárez Soruco and Benedetto, 1996). New information on additional specimens sampled from this locality elicits reassessment of the previous systematic identifications. The main goals of this paper are to describe the new material collected from the San Benito Formation at the Río Titiri syncline, and to discuss the systematic position of *Drabovinella erratica* (Davidson, 1869), to which the Tunari material was compared in a previous paper by Suárez Soruco and Benedetto (1996). The paleobiogeographical relationships of the Central Andean faunas of northwestern Argentina and Bolivia are also briefly analyzed in the light of this and other recent discoveries.

## LOCALITY, STRATIGRAPHY AND AGE

One hundred years ago the German geologist Gustav Steinmann—with the collaboration of H. Höek in paleontological aspects—divided the Upper Ordovician succession in the Cochabamba region of Bolivia into three units named, from bottom to top, “*Bilobites* Sandstein”, “*Lingula* Sandstein”, and “Oberer Quarzit” (Steinmann and Höek, 1912). The Oberer Quarzit was formally named San Benito Formation by Ahlfeld and Branisa (1960), the type locality being designated at Cerro San Benito, about 10 km east of the Cochabamba–Chapare road. It is overlain paraconformably by the uppermost Ordovician–Llandovery Cancañiri glaciogenic diamictite (Schönian *et al.*, 1999; Díaz-Martínez and Grahn, 2007). The San Benito Formation is a *c.* 500 m thick succession of shallow-water quartzitic sandstones with minor interbeds of dark gray micaeous siltstones. Shelly fossils have been found at few horizons and consist mainly of linguliformean brachiopods, bivalves (Suárez Soruco, 1976; Sánchez and Suárez Soruco, 1996), and a few homalonotid trilobite remains. Poorly preserved graptolites occur occasionally in the shaly beds.

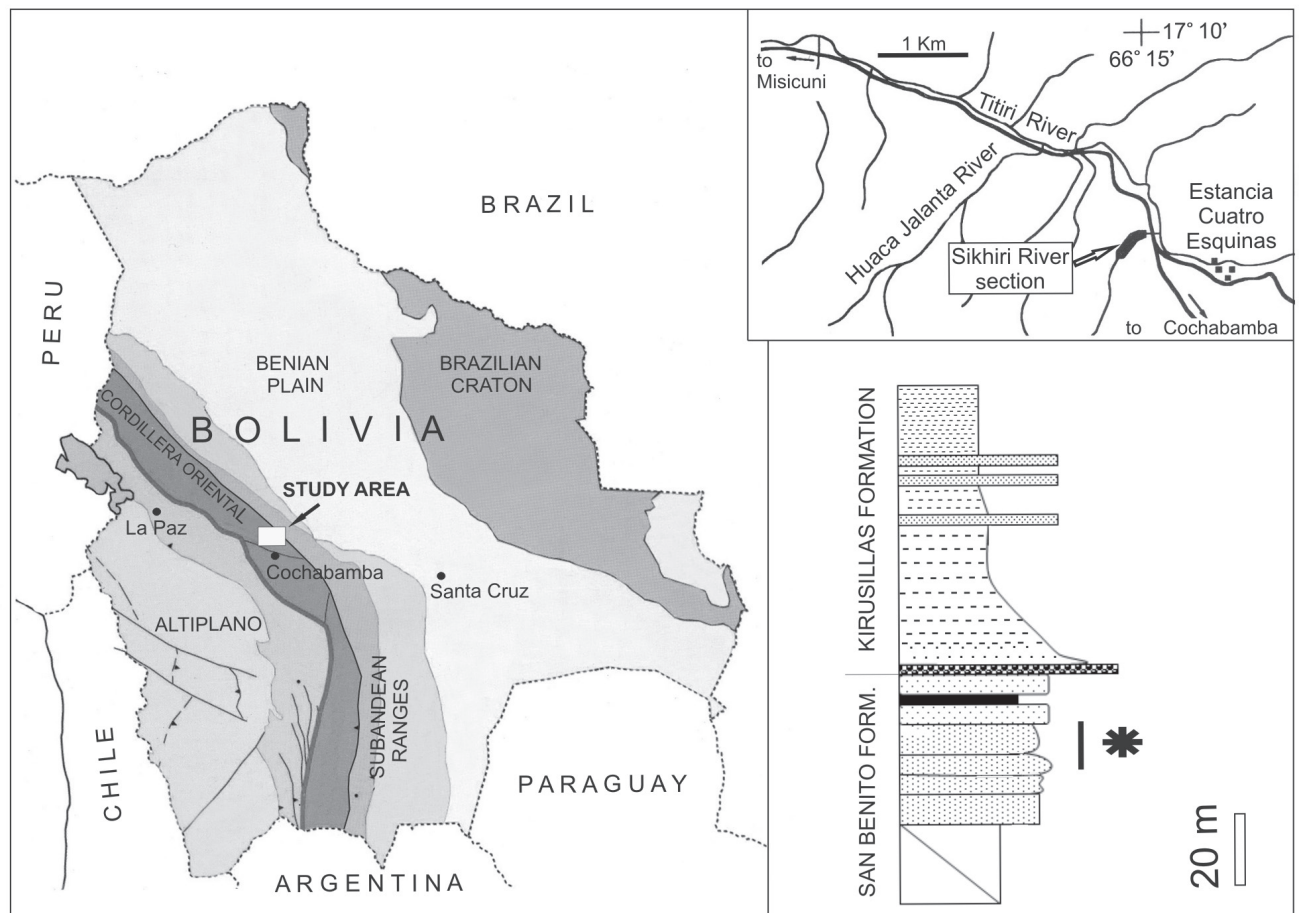
The brachiopods described in this paper are from the upper part of the San Benito Formation in the Cordillera del Tunari, an approximately 3900 m high mountain range

which belongs to the Cordillera Oriental geological province. The San Benito Formation is widely exposed along the Titiri River where it forms the flanks of a syncline the nucleus of which is constituted by the Silurian Kirusillas Formation (Benedetto and Suárez Soruco, 1998). The sampled section crops out along Río Sikhiri, a small tributary of the Titiri River (Fig. 1). The fossiliferous interval is located between 15–20 m below the top of the San Benito Formation.

The age of the San Benito Formation has been considered largely as Late Ordovician on the basis of its stratigraphic position below the Hirnantian/ Early Silurian Cancañiri Formation and above the Anzaldo Formation, which is significant because it yielded numerous articulated specimens of the pteraspidomorph agnathan *Sacabambaspis janvieri* Gagnier, Blicke and Rodrigo, 1986. Although the precise age of the Anzaldo Formation remains unclear, a late Darriwillian to early Sandbian age is accepted on the basis of its palynomorph content (Gagnier *et al.*, 1986; Suárez Soruco, 2000; Davies *et al.*, 2007) as well as its correlation with conodont-dated stratigraphic

units of Argentina bearing microremains of *Sacabambaspis* (Albanesi *et al.*, 1995; Albanesi and Astini, 2002). Unpublished palynomorphs and chitinozoans from the beds yielding the brachiopods described in this paper include *Villosacapsula setosapellicula* (Loeblich), *Rhabdochitina cf. magna* Eisenack, *Ancyrochitina cf. ancyrea* Eisenack and *Desmochitina minor cocca* Eisenack suggesting a Katian age (Pérez-Leyton, 1996).

The brachiopods described here are also indicative of a late Sandbian–Katian age. The species *Hirnantia transgrediens* Havlíček is confined to the upper Sandbian–lower Katian Zahořany Formation of Bohemia. *Rafinesquina pseudoloricata* (Barrande, 1884) is present in the Zahořany Formation but has also been recorded in the overlying Bohdalec Formation of lower-middle Katian age. Outside the Prague basin, this species occurs in the lower part of the Fombuena Formation of the Iberian Chains of northeastern Spain (Villas, 1985), and a comparable species was described from the late Sandbian “Shales with *Onnia*” of the Central Iberian Zone (Villas, 1995). Havlíček (1971) reported a few specimens of



**Figure 1.** Geological provinces of Bolivia (simplified from Suárez Soruco, 2000) showing location of the study area, map of the Titiri River area, and stratigraphic column at the Sikhiri River showing fossil levels (asterisk).

*R. pseudoloricata* from the middle part of the Lower Ktaoua Formation of the Moroccan Anti-Atlas where it occurs in association with *Aegiromena aquila aquila* Havlíček (1971), like in Spain and Bohemia. In their revision of the biostratigraphy of the Upper Ordovician succession exposed at Alnif, in the eastern Anti-Atlas, Villas *et al.* (2006) and Álvaro *et al.* (2007) reported *Rafinesquina? pomoides* Havlíček (a senior synonym of *R. lignani* Villas) and *Rafinesquina* sp. from the highest beds of the Lower Ktaoua Formation, immediately below the occurrence of *A. aquila aquila*. They considered these beds as Katian (Pusgillian of the British Ordovician chronostratigraphic scale) and age-equivalent of the “Bancos Mixtos” of central Spain. However, the relationships between the levels yielding the Havlíček’s specimens of *R. pseudoloricata* and the Alnif stratigraphic section of eastern Anti-Atlas remain unclear.

#### PALEOBIOGEOGRAPHY

*Rafinesquina pseudoloricata* (Barrande), previously thought to be endemic to Bohemia, Spain, and Morocco, is recorded here from outside the Mediterranean region for the first time. Its presence in the San Benito Formation is consistent with the occurrence in other Bolivian localities of the typical Mediterranean Realm species *Heterorthis alternata* (Sowerby, 1839) (Havlíček, 1990) and different species of the genera *Eorhipidomella* Hints, 1971 *Destombesium* Havlíček, 1971, and *Drabovinella* Havlíček, 1951 (Havlíček and Branisa, 1980). The finding in the San Benito Formation of a form comparable to *Hirnantia transgrediens* (Havlíček, 1950), which is a distinctive species of the Berounian of Perunica, reinforces the Bohemian affinities of the Central Andean brachiopod assemblages. The new genus *Tunaria*, as conceived in this paper, occurs in England (Cocks and Lockley, 1981), in the Armorican Massif of France (Mélou, 1985), and in the Central Iberian Zone of Spain (Villas, 1995). These European peri-Gondwanan terranes (a part of the ‘Western European Platform’ as redefined by Hamman, 1992), together Perunica (Havlíček *et al.*, 1994, but see discussions in Servais and Sintubin, 2009, and Fatka and Mergl, 2009), North Africa, and the Central Andean region form a well defined cluster denoting a relatively high degree of faunal affinity (Benedetto *et al.*, 2009). The almost ‘pure’ Mediterranean signature of the Bolivian-NW Argentina faunas, not only of brachiopods (Benedetto, 1998, 1999) but also of bivalves (Sánchez and Astini, 2011) and trilobites (Waisfeld and Henry, 2003), indicates a free migration of the inshore benthic biota along the shallow-water clastic platforms marginal to the Amazonian and NW Africa cratons,

the same route followed by a number brachiopods and bivalves since the Lower Ordovician (Benedetto *et al.*, 2009 and references therein). The record of the high-latitude Gondwanan genus *Tissintia* Havlíček, 1971 in late Darriwilian–early Sandbian strata of Bolivia (Havlíček and Branisa, 1980) and eastern Perú (Hughes *et al.*, 1980) is especially significant, as well as the report of *Heterorthis* sp. in the lower Sandbian Caparo Formation of the Venezuelan Andes (Hughes, 1978; Gutiérrez-Marco *et al.*, 2011), which constitutes an intermediate step between the north African and the peri-Amazonian faunas. Pre-Hirnantian marine deposits are absent in the intracratonic basins of Brazil (Paraná, Paranaíba, Amazonas) (Milani *et al.*, 2007), whereas in the West Africa basins the Hirnantian glacial tillites are underlain by fluviodeltaic cross-bedded sandstones with *Skolithos* and fragments of inarticulate brachiopods (Villeneuve, 2005). This evidence makes the existence of such an intra-Gondwanan dispersion route prior to the latest Ordovician postglacial sea-level high stand rather unlikely (Benedetto *et al.*, 2013).

The Sandbian–early Katian faunas from the Precordillera of western Argentina, characterized by a mixture of pandemic, Scoto-Appalachian, Baltic and Mediterranean forms, are quite different from those of the Central Andes. The arrival of *Tissintia*, *Aegiromena*, and *Destombesium* into this basin has been interpreted as reflecting the approximation of the Cuyania terrane to the Gondwana margin (Benedetto and Sánchez, 1996; Benedetto, 2004; Benedetto *et al.*, 2009).

#### SYSTEMATIC PALEONTOLOGY

Studied specimens are deposited in the paleontological collection of the Centro de Investigaciones Paleobiológicas (CIPAL), Universidad Nacional de Córdoba, Argentina (CE-GH-UNC). Other material examined is housed at Museo de Historia Natural of Cochabamba, Bolivia (MHNC).

Order ORTHIDA Schuchert and Cooper, 1932

Suborder DALMANELLIDINA Moore, 1952

Superfamily DALMANELLOIDEA Schuchert, 1913

Family HETERORTHIDAE Schuchert and Cooper, 1932

Genus *Tunaria* gen. nov.

**Type species.** *Tunaria cocksi* sp. nov. from the Upper Ordovician San Benito Formation, Cordillera del Tunari, Cochabamba Department, Bolivia.

**Etymology.** From the Cordillera del Tunari.

**Species assigned.** *Orthis berthoisii?* var. *erratica* Davidson, 1869, from the Triassic Budleigh Salterton Pebble Bed of Devon, England.

**Diagnosis.** Convexiplane to strongly dorsibiconvex profile. Ventral interarea moderately high, strongly apsacline to catacline. Large subflabellate to flabellate ventral muscle field. Pedicle callist present. Cardinal process differentiated into a long shaft and a bulbous, bi- or trilobed myophore. Brachiophore bases long, subparallel, converging towards low notothyrial platform continuous with broad median ridge. Fulcral plates absent

**Discussion.** In the preliminary report by Suárez Soruco and Benedetto (1996), this very abundant orthide from the San Benito Formation was attributed to *Drabovinella* and compared with *D. erratica* (Davidson, 1869), with which it shares several external and internal features, in particular its almost convexiplane shell, large flabellate diductor scars, long subparallel brachiophore supporting plates, and lobate myophore. However, a survey of specimens referred to Davidson's species, including the type material from the Budleigh Salterton Pebble Bed (Cocks and Lockley, 1981), the Saint Germain-sur-Ille Formation of the Armorican Massif, France (Mélou, 1985), and the 'Quartzite with *Calymenella*' of the Central Iberian Zone of Spain (Villas, 1995) revealed that *erratica* does not belong to the genus *Drabovinella* Havlíček, as Mélou (1985) proposed.

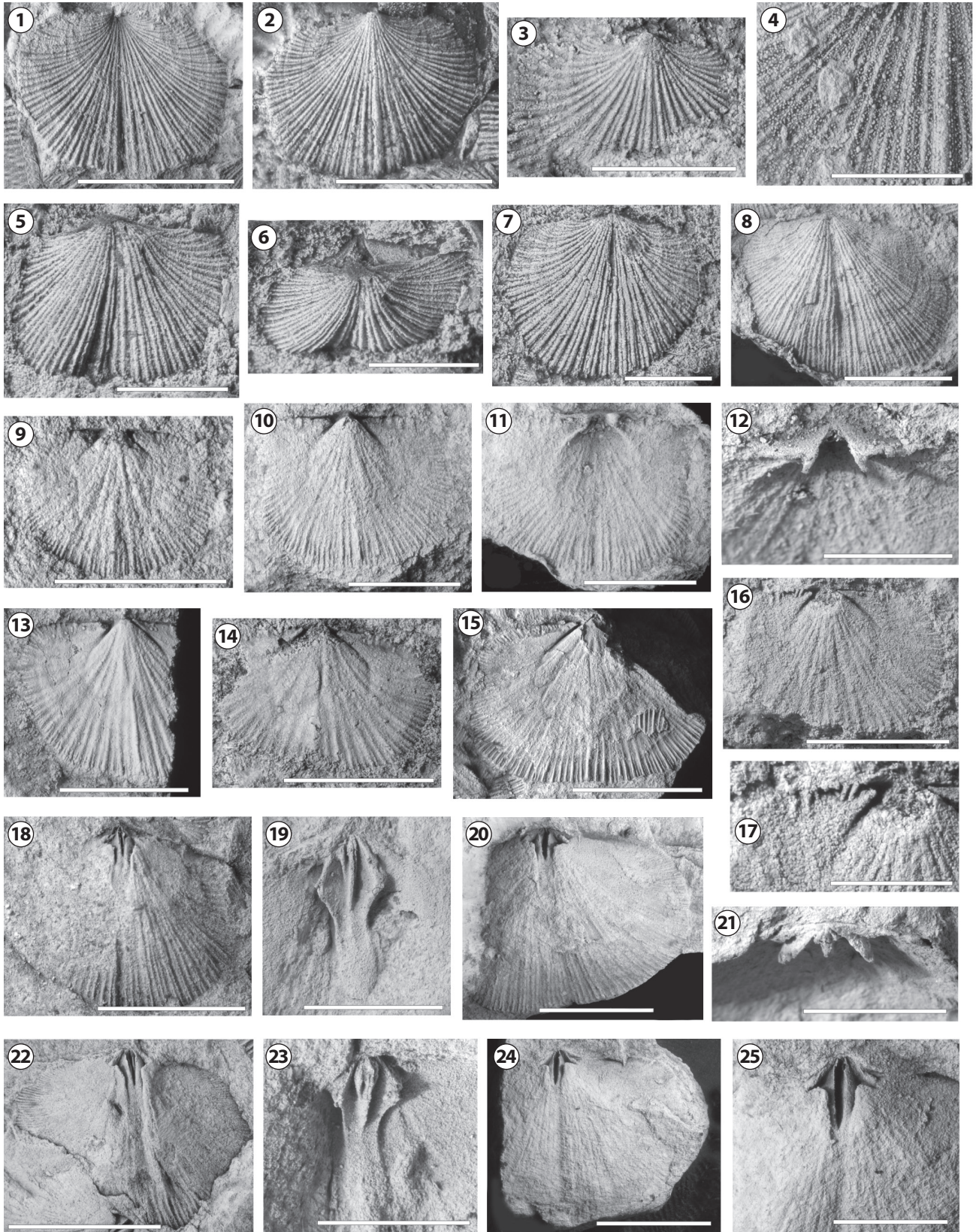
The European specimens formerly referred to as *Drabovinella erratica* (Davidson) differ from the genus *Drabovinella* (type species: *D. drabovens* Havlíček, 1951), as characterized by Havlíček (1950, 1971; see also diagnosis by Harper, 2000 in the *Treatise revised*), in the following features: (1) shells in *erratica* are dorsibiconvex to convexiplane whereas in *Drabovinella* are always biconvex; (2) the pedicle callist is fully developed in *erratica* but it is absent in *Drabovinella*; instead, there is a short transverse plate; (3) in *erratica* the dorsal valve is sulcate and the ventral one bears a carina; the dorsal valve of *Drabovinella* lacks sulcus; (4) in *erratica* the ventral muscle field is large and widely splayed whilst in *Drabovinella* it is narrow and suboval in outline; (5) in *erratica* the cardinal process expanded into a posteriorly bilobed or trilobed myophopre, whilst in *Drabovinella* the myophore is simple; (6) fulcral plates are absent in *erratica* but they are well developed in all species of *Drabovinella*. This feature was previously noted by Villas (1995, p. 70) but

he considered it as having specific value; (7) brachiophore plates in *erratica* are strongly convergent towards valve floor and are fused onto a broad notothyrial platform, while in *Drabovinella* they are high and less convergent, and the notothyrial platform is undifferentiated. In *Drabovinella maxima* Mergl, 1983, the brachiophore plates rest nearly vertical respect to the valve floor (Mergl, 1983, pl. 2, fig. 4); (8) lateral ribs in *erratica* are strongly incurved posterolaterally to intersect the posterior margin. In addition, in the Bolivian material the cardinal canals (or follicular embayments *sensu* Williams, 1974) are always present, a feature not described in *Drabovinella* but relatively common in heterorthids. The above mentioned characters separating *Orthis berthois* var. *erratica* from *Drabovinella drabovens* are regarded here as being of generic rather than specific significance, and justify the erection of the new genus *Tunaria* to include the European species *Drabovinella erratica* and the new Bolivian species *Tunaria coxsi* described herein, formerly attributed to *Drabovinella cf. erratica*.

A second conclusion is that the overall features of *Tunaria* gen. nov. are distinctive of heterorthids rather than of draboviids. The heterorthid filiation of *Orthis berthois*? (Roualt) var. *erratica* Davidson was correctly recognized by Cocks (1978), who initially referred the English specimens to the genus *Svobodaina* (albeit with a question mark), but later reassigned the type material to the plectorthoidean *Corineorthis* Cocks and Lockley (1981). Bassett (1981, p. 652), however, in his revision of the Ordovician brachiopods of the Gorran Quartzite of Cornwall, stated that "*Orthis berthois*? var. *erratica* is not an orthacean and that "...the convexity, short hinge and ventral musculature are typical of the Rhipidomellidae and related dalmanellacean brachiopods...". Villas (1995) noted that the arrangement of the ribs intersecting the hinge line in the Iberian specimens of *D. erratica* is a distinctive feature of heterorthids, though it may be incipiently developed in other species of *Drabovinella* such as *D. satrapa* Havlíček, 1977. Well-developed cardinal canals along the posterior margins of ventral valve are present in some heterorthids (e.g., *Tissintia* Havlíček, 1971, *Svobodaina*, Havlíček, 1951, *Tarfaya*, Havlíček, 1971, and in the platyorthid *Crozonorthis* Mélou, 1976, but never have been reported in enteletoids. Another key heterorthid fea-

**Figure 2.** 1–25, *Tunaria coxsi* gen. nov. sp. nov.; 1–2, ventral external mould and latex cast, CEGH-UNC 24847; 3, ventral valve latex cast, CEGH-UNC 24824b; 4, dorsal external mould showing endopunctae, CEGH-UNC 24841; 5–6, dorsal valve latex cast, dorsal and posterodorsal views, CEGH-UNC 24858; 7, dorsal valve latex cast, CEGH-UNC 24825; 8, dorsal valve latex cast, CEGH-UNC 24851a; 9, internal mould of juvenile ventral valve, EGH-UNC 24849b; 10–12, ventral internal mould, latex cast, and detail of apicalium in oblique posteroventral view, CEGH-UNC 24828; 13, internal mould of ventral valve, CEGH-UNC 24827a; 14, internal mould of ventral valve, CEGH-UNC 24827b; 15, internal mould of ventral valve, CEGH-UNC 24840; 16–17, internal mould of ventral valve and detail of cardinal canals, CEGH-UNC 24824a; 18–19, internal mould of dorsal valve and latex cast showing cardinalia, CEGH-UNC 24838; 20, internal mould of dorsal valve, CEGH-UNC 24836; 21, latex cast showing cardinalia, posterior view, CEGH-





UNC 24848e; **22–23**, dorsal internal mould and latex cast showing detail of cardinalia, holotype CEGH-UNC 24835a; **24–25**, dorsal internal mould and detail of cardinalia, CEGH-UNC 24842. Scale bar= 1 cm, except for 4, 12,17, 19, 21, and 23 in which scale bar= 5 mm.



ture is the large semiflabellate ventral muscle field, which in draboviids tends to be oval or subtriangular and confined to the delthyrial cavity. In some Armorican specimens of *Tunaria erratica* the strongly bilobed diductors are reminiscent of those of the heterorthids *Tafilaltia destombesi* Havlíček and *Svobodaina inchyta* (Barrande, 1879), but are also comparable to those of the platyorthid *Crozonorthis muscolosa* Mélou, 1976. The new Bolivian species *Tunaria cocksi* sp. nov. displays a large but less clearly bilobed ventral muscle field, like that of *Arenorthis* but with scalloped margins. The presence of variably developed fulcral plates is another distinctive feature that distinguishes draboviids (and most entelotoideans) from heterorthids. Its absence in *Tunaria* also supports its classification among the heterorthids.

Stubblefield (1939) assigned *Orthis berthoisii* (Roualt) var. *cornubiensis* Davidson, 1881, from the Gorran Quartzite of Cornwall (England), to the plectorthoid *Corineorthis*. Bassett (1981) reviewed this genus and gave a detailed description of the type material of *C. cornubiensis*. Although *Corineorthis* and *Tunaria* are externally rather similar, the former differs internally by its smaller ventral muscle field, its apparently non lobate bulbous myophore, its shorter, non-parallel and strongly converging brachiophore supporting plates, and by the presence of fulcral plates. In addition, endopunctae have not been mentioned in this species. Overall, these features clearly separate *C. cornubiensis* from both *T. erratica* and *T. cocksi* and confirm its placement among the plectorthoids (Williams and Harper, 2000).

*Arenorthis* Havlíček, 1971, is comparable to the new genus *Tunaria* in the large flabellate ventral muscle field, tripartite posterior face of myophore, and broad dorsal median ridge, but clearly differs by its ventribiconvex shell profile, shorter and strongly converging brachiophore bases, and thickened bulbous myophore (see also Benedetto *et al.*, 2013). Another heterorthid resembling *Tunaria* is *Tissintia* Havlíček, 1970, which differs by the ventribiconvex shell profile, bilobed diductor scars almost enclosing suboval adductor scars, and shorter brachiophore plates.

### ***Tunaria cocksi* sp. nov.**

Figures 2.1–25; 3.1

1996. *Drabovinella* cf. *erratica* (Davidson, 1869), Suárez Soruco and Benedetto, p. 214–215, pl. 1, figs. 1–3, 6–10.

non 1996. *Drabovinella* cf. *D. erratica* (Davidson, 1869), Suárez Soruco and Benedetto, pl. 1, figs. 4–5.

**Etymology.** In honor of Professor L.R.M. Cocks.

**Type material.** Holotype: An internal mould of dorsal valve CEGH-UNC 24835a. Paratypes: Three external moulds

and eight internal moulds of ventral valves, CEGH-UNC 24824a-b, 24827, 24828, 24838, 24839, 24840, 24841, 24843, 24847, 24849c-d; two external moulds and nine internal moulds of dorsal valves, CEGH-UNC 24824c-d, 24826, 24835b, 24836, 24837, 24842, 24848e, 24849a-b, 24850, 24851.

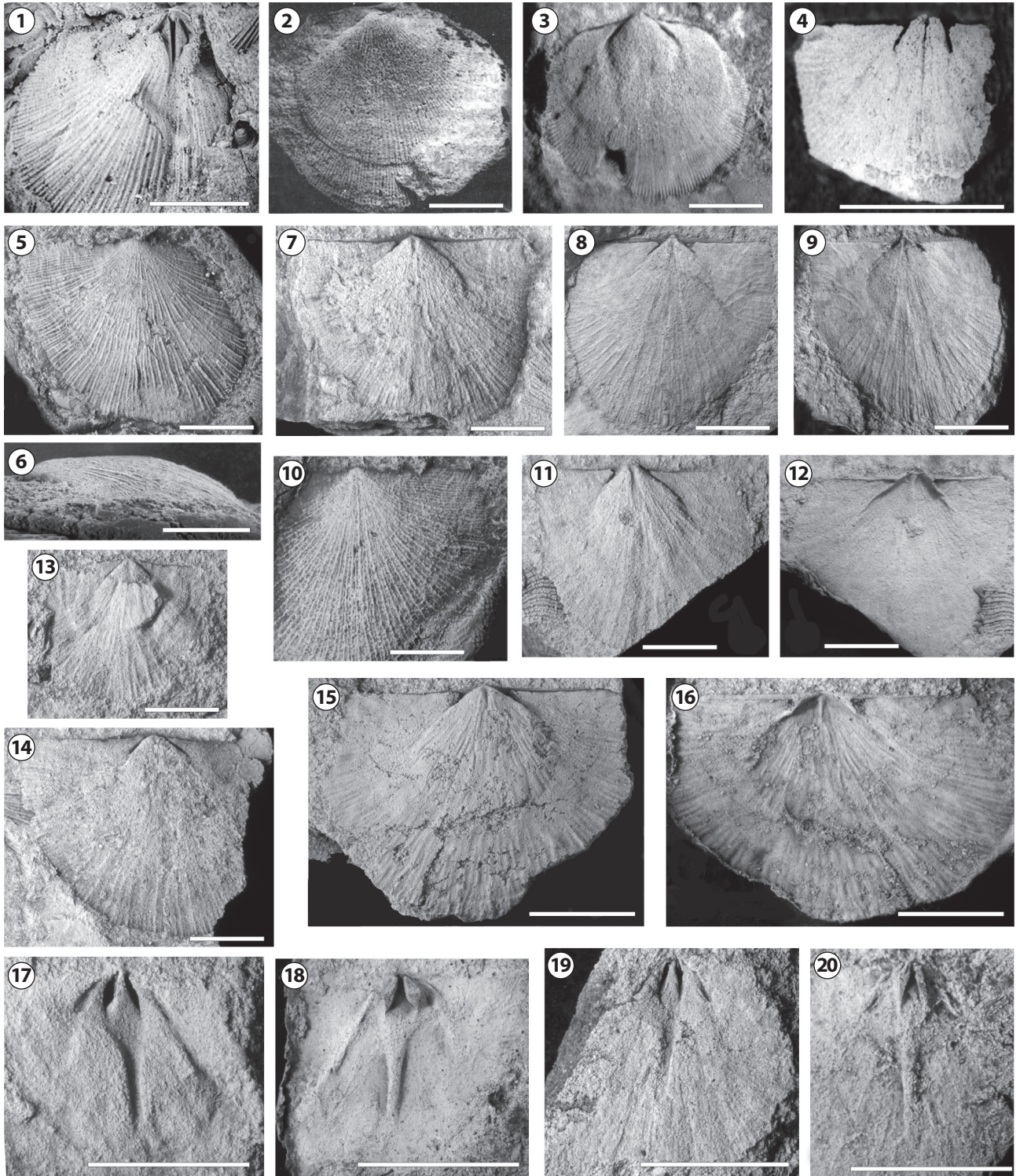
**Additional material.** Twelve variably preserved internal and external moulds of both valves, 24825, 24829–24834, 23844–46, 24858–24859.

**Horizon and locality.** Upper part of the San Benito Formation, Cordillera del Tunari, Titiri syncline, Cochabamba Department, Bolivia.

**Diagnosis.** Convexiplane, subcircular shells with ramicostellate or fascicostellate ornament of 5–6 costae per 5 mm at anterior margin. Ventral muscle field large, suboval, extending for about 42% of valve length. Cardinal process expanded into a prominent, often trilobate myophore occupying the whole notothyrial platform. Thick brachiophores supported by proportionally short bases converging medially towards floor of valve.

**Description.** Shells convexiplane, up to 26 mm wide, most specimens ranging in width from 18 to 22 mm; outline transversely elliptical, length/width ratio 0.70–0.83 (average 0.74). Cardinal extremities rounded, maximum width commonly at valve midlength. Hinge line about 65% of maximum shell width. Ventral valve gently convex around the umbo becoming subplanar both anteriorly and laterally, with a median carina defined by a thickened costa, which reaches the anterior margin. Ventral interarea moderately high, approximately 30% of valve length, slightly concave, strongly apsacline to catacline, with open subtriangular delthyrium. Dorsal valve increasingly convex with age; largest specimens up to 3.2 mm thick (average thickness/width ratio = 0.22), with maximum thickness at about one third of length. Relatively deep median sulcus originating at umbo, becoming shallow on the anterior third of the valve in most specimens. Dorsal interarea low, anacline. Radial ornament ramicostellate to slightly fascicostellate, with rounded costellae of subequal size and equally spaced, numbering 11–13 per 5 mm along the anterior margin of mature specimens. Costellae increasing in number mainly by bifurcation, but intercalations are also present on both valves. Costellae strongly incurved posterolaterally to intersect hinge line at high angle. Ventral valve with 4–7 cardinal canals indenting the internal surface of the hinge line. Densely packed and randomly distributed endopunctae on the entire surface of internal moulds.





**Figure 3.** 1, *Tunaria cocksi* gen. nov. sp. nov. 1, dorsal internal mould, MHNC-8129d; 2–4, *Hirnantia* cf. *H. transgrediens* (Havlíček, 1950); 2–3, ventral valve, latex cast of exterior and internal mould, MHNC-8125a; 4, internal mould of dorsal valve, MNHC-8125c. 5–20, *Rafinesquina pseudo-loricata* (Barrande, 1848); 5–7, latex cast of exterior of a ventral valve, lateral view, and internal mould, CEGH-UNC 24851b; 8–9, internal mould of ventral valve and latex cast, CEGH-UNC 24848b; 10, latex cast of ventral valve exterior, CEGH-UNC 24854; 11–12, internal mould of ventral valve and latex cast, CEGH-UNC 24853; 13, internal mould of ventral valve of juvenile specimen, CEGH-UNC 24850; 14, internal mould of ventral valve, CEGH-UNC 24852; 15–16, internal mould of ventral valve and latex cast, CEGH-UNC 24855; 17–18, internal mould of dorsal valve and latex cast, CEGH-UNC 24848c; 19–20, internal mould of dorsal valve and latex cast, CEGH-UNC 24857. Scale bar= 1 cm).



Ventral interior with well-developed pedicle callist forming a short platform in the apical region of delthyrial chamber. Teeth subtriangular in lateral profile, with shallow crural fossettes, supported by short dental plates that continue anteriorly into widely divergent ridges posterolaterally bounding the muscle field. Ventral muscle field large, extending slightly beyond the valve midlength in medium sized specimens but reaching up to the two thirds of valve length in largest valves. Diductor scars large, flabellate, with scalloped margins; adductor scars undifferentiated or poorly impressed, not enclosed by diductors.

Dorsal interior with slender brachiophores supported by long subparallel plates strongly converging onto, and fused with, a slightly elevated concave notothyrial platform prolonged into a broad median ridge extending up to about one third of valve length, often continuous with elevation corresponding to external median sulcus. Cardinal process slender, ridge-like in small shells, differentiated into a thick long shaft (as long as the brachiophore plates), and a bulbous, posteriorly trilobed myophore that in mature specimens entirely fills the notothyrial cavity. Dental sockets subtriangular, excavated directly in the valve floor without evidence of fulcral plates. Dorsal muscle field and vascular system not impressed.

**Discussion.** *T. cocksi* is close to the European species *Tunaria erratica* from which it can be distinguished externally by showing a coarser radial ornament, an enlarged median costa on the ventral valve, and a deeper dorsal sulcus. Internally, the Bolivian new species differs by having a subtriangular, widely splayed ventral muscle field with flabellate diductor scars whereas in *T. erratica* it tends to be elongately bilobed with subparallel or slightly divergent lateral margins.

Superfamily ENTELETOIDEA Waagen, 1884

Family DRABOVIIDAE Havlíček, 1950

Subfamily DRABOVIINAE Havlíček, 1950

Genus *Hirnantia* Lamont, 1935

**Type species.** *Orthis saggitifera* M'Coy 1851. Upper Ordovician (Sandbian)–Lower Silurian.

*Hirnantia* cf. *H. transgrediens* (Havlíček, 1950)

Figures 3.2–4

1996. *Hirnantia?* sp., Suárez Soruco and Benedetto, p. 216, pl. 1, fig. 11.

1996. *Drabovinella* cf. *D. erratica* (Davidson 1869), Suárez Soruco and Benedetto, pl. 1, figs. 4–5.

**Material.** A ventral valve, both the external and internal moulds MHNC 8125a, and a single internal mould of dorsal valve, MHNC 8125c.

**Horizon and locality.** Upper part of the San Benito Formation, Cordillera del Tunari, Titiri syncline, Cochabamba Department, Bolivia.

**Description.** Shell dorsibiconvex, up to 28 mm wide. Ventral valve subcircular in outline, slightly convex, maximum width at valve midlength. Hinge line width about 60% of maximum valve width. Dorsal valve semielliptical, evenly and moderately convex. Ornament finely and uniformly multicostellate, with 15–16 costellae per 5 mm measured on the anterior third of the valve.

Ventral interior with conspicuous subtriangular pedicle callist. Teeth small, trigonal, supported by high and strongly divergent dental plates continuous with arched ridges posterolaterally bounding the muscle field. Ventral muscle field bilobed, approximately as wide as long, extending forward for about 30% of valve length. Adductor scars narrower and shorter than diductors, limited anteriorly by a thickening of valve floor.

Dorsal interior with cardinal process formed by a slightly enlarged myophore and a short shaft continuing anteriorly with a thin median ridge, which extends forward to about one-third of valve length. Brachiophore bases subvertical, diverging anteriorly at about 45°. Fulcral plates short, bordering narrow dental sockets. Dorsal muscle field not discernible.

**Discussion.** The two available specimens from the San Benito Formation can be attributed confidently to *Hirnantia* on the basis of the bilobate subtriangular ventral muscle field bounded posterolaterally by prolongations of dental plates, blade-like cardinal process, high diverging brachiophore plates, and presence of fulcral plates, together with the multicostellate radial ornament and the dorsibiconvex shell. Among the described pre-Hirnantian species, most of which come from the Berounian and Kralodvorian of the Czech Republic (Havlíček, 1977), our material is close to *H. transgrediens* (Havlíček, 1950), a characteristic species from the Zahořany Formation of Bohemia (late Sandbian–lower Katian), from which it differs by its finer ornament, and slightly wider adductor scars. The Bolivian material, however, is too scarce for a reliable specific identification.

Order STROPHOMENIDA Öpik, 1934

Superfamily STROPHOMENOIDEA King, 1846

Family RAFINESQUINIDAE Schuchert, 1893

Subfamily RAFINESQUININAE Schuchert, 1893

Genus *Rafinesquina* Hall and Clarke, 1892

**Type species.** *Leptaena alternata* Conrad, 1838. Upper Ordovician–Lower Silurian.



***Rafinesquina pseudoloricata* (Barrande, 1848)**

Figures 3.5–20

**Material.** Three external moulds and seven internal moulds of ventral valves, and two internal moulds of dorsal valves, CEGH- UNC 24848a-b-c, 24849-24857.

**Horizon and locality.** Upper part of the San Benito Formation, Cordillera del Tunari, Titiri syncline, Cochabamba Department, Bolivia.

**Description.** Shell moderately concavoconvex, transversely semielliptical, largest specimens up to 31 mm wide; length averaging 82% of width; maximum width at hinge line. Cardinal angles normally orthogonal, slightly auriculate in some specimens. Ventral valve moderately convex with maximum thickness in the posterior third, depth about 10% of length. Ventral interarea planar, anacline, height approximately 6% of valve length in largest specimens. Delthyrium partially closed by a small pseudodeltidium bearing an apical foramen. Dorsal valve gently concave with very narrow, anacline interarea covered apically by a small chilidium. Radial ornament subequally parvicostellate, with 15–16 costellae per 5 mm measured on the anterior third of the ventral valve; a slightly enlarged median costa confined to the posterior third of the ventral valve, undifferentiated anteriorly. Radial ornament crossed by closely spaced fila and sporadic growth lines that coincide with undulations or minor changes in the growth direction of costellae.

Ventral interior with small, transversely elongated teeth supported by strong, moderately long dental plates diverging at an angle of 90°–100°, extending anteriorly into gently curved muscle bounding ridges. Muscle field large, subtriangular, deeply impressed posteriorly becoming progressively shallow and ill-defined anteriorly, extending forward to about the valve midlength. A short rounded ridge bisect the posterior part of muscle field fading anteriorly. Diductor scars large, flabellate, radially striated, enclosing a small, elongate oval adductor field.

Dorsal interior with slender and elongate cardinal process lobes projecting ventrally and resting nearly perpendicular to valve floor, diverging forward at about 35°; in the largest specimen, cardinal process lobes robust and thickened anteriorly, their bases bounding laterally a well-defined elongated notothyrial platform which continues into a broad median ridge. Socket ridges strong, slightly curved and thickened distally, diverging at 80°–90°, extended forward slightly beyond the anterior ends of cardinal process lobes. Shallow subtriangular sockets open anterolaterally. Dorsal muscle field faintly impressed, bisected by the median ridge and

bounded posterolaterally by rounded low ridges originated at the end of socket ridges, with suboval anterior adductor scars and smaller, roundly subtriangular posterior adductor scars.

**Discussion.** The Bolivian specimens display most of the diagnostic features of *Rafinesquina pseudoloricata* (Barrande, 1848), the type material of which comes from the Zahořany Formation at Lodnice, Prague Basin. This species is present in almost all localities where this formation is exposed, and was also recorded in the overlying Bohdalec Formation. The few differences that can be observed in our material, such as the larger ventral muscle field, and the inferred longer dorsal median ridge (no complete valves are available) fall within the morphological variability of the Bohemian material (Havlíček, 1977, pl. 10, figs. 7–14). *R. pseudoloricata* has also been recorded in the late Sandbian Fombuena Formation of the Iberian Chains (Villas, 1985). The Spanish material is very similar to that from the San Benito Formation, but differs slightly by its somewhat finer ornamentation. The material from the Central Iberian zone of Spain referred to as *R. cf. pseudoloricata* by Villas (1995) is also closely comparable to our specimens. The material recovered from the Lower Ktraoua Formation of Morocco attributed to this species by Havlíček (1971) is too scarce for a detailed comparison.

**ACKNOWLEDGEMENTS**

I am especially indebted to my colleague R. Suárez Soruco for showing me the fossil localities, collecting the first specimens, and making them available for this study. I thank L. Popov and the anonymous reviewer for their valuable contributions leading to the improvement of this paper. This research has been supported by grants PICT 2004-21857 from FONCYT (Agencia Nacional de Promoción Científica y Tecnológica) and PIP 5599 from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

**REFERENCES**

- Ahlfeld, F. and Branisa, L. 1960. *Geología de Bolivia*. Ed. Don Bosco, La Paz, 215 p.
- Albanesi, G.L. and Astini, R.A. 2002. Faunas de conodontes y *Sacabambaspis janvieri* (Vertebrata) en el Ordovícico medio de la Cordillera Oriental Argentina: implicancias estratigráficas y paleobiogeográficas. 8° Congreso Argentino de Paleontología y Bioestratigrafía (Corrientes), *Resúmenes*, p. 17.
- Albanesi, G.L., Benedetto, J.L. and Gagnier, P.G. 1995. *Sacabambaspis janvieri* (Vertebrata) y conodontes del Llandeiliano temprano en la Formación La Cantera, Precordillera de San Juan, Argentina. *Boletín de la Academia Nacional de Ciencias* 60: 519–544.
- Álvarez, J.J., Vennin, E., Villas, E., Destombes, J. and Vizcaíno, D. 2007. Pre-Hirnantian (latest Ordovician) benthic community assemblages: Controls and replacements in a siliciclastic-dominated platform of the eastern Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245: 20–36.
- Barrande, J. 1848. Ueber die Brachiopoden der silurischen Schichten von Böhmen. II. *Naturwissenschaftliche Abhandlungen* 2: 155–256.

- Barrande, J. 1879- Système Silurien du centre de la Bohême. Première Partie. Recherches paléontologiques, vol. 5, Classe des Mollusques, Ordre des Brachiopodes. Prague and Paris, 226 p.
- Bassett, M.G. 1981. The Ordovician brachiopods of Cornwall. *Geological Magazine* 118: 647–664.
- Benedetto, J.L. 1998. Early Palaeozoic brachiopods and associated shelly faunas from western Gondwana: its bearing on the geodynamic history of the pre-Andean margin. In: R.J. Pankhurst and C.W. Rapela (Eds.), *The proto-Andean margin of Gondwana. The Geological Society, London, Special Publications* 142: 57–83.
- Benedetto, J.L. 1999. El género *Drabovinella* (Brachiopoda) en el Caradociano de la Sierra de Mojotoro, Provincia de Salta, Argentina. *Ameghiniana* 36: 235–238.
- Benedetto, J.L. 2004. The allochthony of the Precordillera ten years later (1993-2003): A new paleobiogeographic test of the microcontinental model. *Gondwana Research* 7: 1027–1039.
- Benedetto, J.L. and Sánchez, T.M. 1996. Paleobiogeography of brachiopod and molluscan faunas along the South American margin during the Ordovician. In: B.A. Baldis and F.G. Aceñolaza (Eds.), *El Paleozoico inferior del Noroeste de Gondwana. Serie Correlación Geológica (INSU-GEO)* 12: 23–38.
- Benedetto, J.L. and Suárez Soruco, R. 1998. Los braquiópodos del Silúrico de la Cordillera del Tunari (Cochabamba, Bolivia) y su correlación con otras sucesiones sedimentarias gondwánicas. *13º Congreso Geológico Boliviano* (Potosí), *Memorias* 1: 153–159.
- Benedetto, J.L., Vaccari, N.E., Waisfeld, B.G., Sánchez, T.M. and Foglia, R.D. 2009. Cambrian and Ordovician paleobiogeography of Andean margin of Gondwana and accreted terranes. In: M.G. Bassett (Ed.), *Early Palaeozoic Peri-Gondwanan Terranes: New Insights from Tectonics and Biogeography. The Geological Society, London, Special Publications* 325: 199–230.
- Benedetto, J.L., Halpern, K. and Galeano-Inchausti, J.C. 2013. Higher-latitude Hirnantian (latest Ordovician) brachiopods from the Eusebio Ayala Formation of Paraguay, Paraná Basin. *Palaentology* 56: 61–78.
- Cocks, L.R.M. 1978. A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's Monograph. *Monograph of the Palaeontological Society* 131: 1–256.
- Cocks, L.R.M. and Lockley, M.G. 1981. A reassessment of of the Ordovician brachiopods from the Budleigh Salterton Pebble Bed, Devon. *Bulletin of the British Museum Natural History (Geology)* 35: 11–124.
- Conrad, T.A. 1838. Report on the palaeontological department of the survey. *New York State Geological Survey, Annual Report* 3: 57–66.
- Davidson, T. 1869. British Silurian Brachiopods.. *Palaeontographical Society Monographs* 3, Part 7 (3): 169–248.
- Davidson, T. 1881. A monograph of the British fossil Brachiopoda. On the Devonian and Silurian Brachiopoda that occur in the Triassic Pebble-Bed of Budleigh-Salterton near Exmouth, in Devonshire. *Palaeontographical Society Monographs* 4, Part 4: 317–368.
- Davies, N.S., Sansom, I.J., Albanesi, G.L. and Céspedes, R. 2007. Ichnology, palaeoecology and taphonomy of a Gondwanan early vertebrate habitat: Insights from the Ordovician Anzaldo Formation, Bolivia. *Palaeoecology, Palaeoclimatology, Palaeoecology* 249: 18–35.
- Díaz-Martínez, E. and Grahn, Y. 2007. Early Silurian glaciation along the western margin of Gondwana (Peru, Bolivia and northern Argentina): Palaeogeographic and geodynamic setting. *Palaeoecology, Palaeoclimatology, Palaeoecology* 245: 62–81.
- Fatka, O. and Mergl, M. 2009. The 'microcontinen' Perunica: status and story 15 years after conception. In: M.G. Bassett (Ed.), *Early Palaeozoic Peri-Gondwanan Terranes: New Insights from Tectonics and Biogeography. The Geological Society, London, Special Publications* 325: 65–101.
- Gagnier, P.Y., Blicek, A. and Rodrigo, G. 1986. First Ordovician vetebrate from South America. *Geobios* 19: 629–634.
- Gagnier, P.Y., Blicek, A., Emig, C.C., Sempere, T., Vachard, D. and Van-guestaine, M. 1996. New paleontological and geological data on the Ordovician and Silurian of Bolivia. *Journal of South American Earth Sciences* 9: 329–347.
- Gutiérrez-Marco, J.C., Goldman, D., Reyes-Abril, J. and Gómez, J. 2011. A preliminary report on some Sandbian (Upper Ordovician) graptolites from Venezuela. In: J.C. Gutiérrez-Marco, I. Rábano and D. García-Bellido, *Ordovician of the World. Instituto Geológico y Minero de España, Cuadernos del Museo Geominero* 14: 199–206.
- Hall, J. and Clarke, J.M. 1892. *An introduction to the study of the genera of Palaeozoic Brachiopoda. Natural History of the New York, Palaeontology, volume 2, part 1.* New York Geological Survey, Albany, 394 p.
- Hamman, W. 1992. The Ordovician trilobites from the Iberian Chains in the province of Aragón, NE-Spain. *Beringeria* 6: 1–144.
- Harper, D.A.T. 2000. Dalmanellidina. In: A. Williams, C. H. C. Brunton, and S. J. Carlson (Eds.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, revised, 3.* The Geological Society of America and The University of Kansas, Boulder, Colorado, p. 782–844.
- Havlíček, V. 1950. The Ordovician Brachiopoda from Bohemia. *Rozprawy Ústředního ústavu Geologického* 13:1–133.
- Havlíček, V. 1970. Heterorhthidae (Brachiopoda) in the Mediterranean Province. *Sborník Geologických Věd, Paleontologie* 12: 7–50.
- Havlíček, V. 1971. Brachiopodes de l'Ordovicien du Maroc. *Notes et Mémoires du Service Géologique du Maroc* 230: 1–135.
- Havlíček, V. 1977. Brachiopods of the Order Orthida in Czechoslovakia. *Rozprawy Ústředního ústavu Geologického* 44: 1–327.
- Havlíček, V. 1990. Mediterranean and Malvinokaffric Provinces: new data on the Upper Ordovician and Lower Silurian brachiopods. *Casopis pro Mineralogii a Geologii* 35: 1–14.
- Havlíček, V. and Branisa, L. 1980. Ordovician brachiopods of Bolivia. *Rozprawy Československé Akademie Věd* 90: 1–54.
- Havlíček, V., Van k, J. and Fatka, O. 1994. Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic associations). *Sborník Geologických Věd, Geologie* 46: 23–56.
- Hints, L. 1971. A new genus of rhipidomellid brachiopods from the middle Ordovician of the Moscovian syncline. *Esti MSV Yeaduste Akademia Toimetised* 22: 248–256 [in Russian].
- Hughes, C.P. 1978. A brief review of the Ordovician faunas of northern South America. *2º Congreso Argentino de Paleontología y Bioestratigrafía* (Buenos Aires), *Actas* 1: 11–22.
- Hughes, C.P., Rickards, R.B. and Williams, A. 1980. The Ordovician fauna from the Contaya Formation of eastern Perú. *Geological Magazine* 117: 1–21.
- King, W. 1846. Remarks on certain genera belonging to the class Pallio-branchiata. *Annals and Magazine of Natural History (series 1)* 18: 26–42.
- Lamont, A. 1935. The Drummuck Group, Girvan: a stratigraphic revision with descriptions of new fossils from the lower part of the group. *Transactions of the Geological Society of Glasgow* 19: 288–334.
- M'Coy, F. 1851. On some new Cambro-Silurian fossils. *Annals and Magazine of Natural History (series 2)* 8: 387–409.
- Mélou, M. 1976. Orthida (Brachiopoda) de la Formation de Postolonnec (Ordovicien) Finistère, France. *Géobios* 9: 693–717.
- Mélou, M. 1985. Revision d' "Orthis" berthoisii Roualt, 1949, Orthida (Brachiopoda) de l'Ordovicien du Massif Armoricain. *Géobios* 18: 595–603.
- Mergl, M. 1983. New brachiopods (Cambrian-Ordovician) from Algeria and Morocco (Mediterranean Province). *Časopis pro Mineralogii a Geologii* 28: 337–352.
- Milani, E.J., Gonçalves de Melo, J.H., De Souza, P., Fernández, L.A. and Barros França, A. 2007. Bacia do Paraná. *Boletim de Gociencias Petrobras* 15: 265–287.
- Moore, R.C. 1952. Brachiopoda. In: R.C. Moore, C.G. Lalicker and A.G. Fisher (Eds.), *Invertebrate Fossils*, McGraw-Hill, New York, 766 p.
- Öpik, A.A. 1934. Über Klitamboniten. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis) series A* 26: 1–239.
- Pérez-Leyton, M.A. 1996. [Informe palinológico de la sección del Titirí-Sikhiri, Cochabamba. Informe Interno Yacimientos Petrolíferos Fiscales Bolivianos (CTP 08-2908), Santa Cruz. Inédito].



- Sánchez, T.M. and Astini, R.A. 2011. A new species of the Gondwanan genus *Cardiolaria* Munier-Chalmas in the Sandbian of northwestern Argentina: Paleobiogeographic considerations. *Journal of South American Earth Sciences* 31: 306–311.
- Sánchez, T.M. and Suárez Soruco, R. 1996. Primer registro de lyrodesmátidos (Bivalvia, Heteroconchia) en América del Sur (Formación San Benito, Ordovícico Superior de Bolivia). *12º Congreso Geológico Boliviano*(Tarija), *Actas* 1: 217–219.
- Schönian, F., Egenhoff, S.O., Marcinek, J. and Erdtmann, B.D. 1999. Glaciation at the Ordovician–Silurian boundary in southern Bolivia. *Acta Universitatis Carolinae, Geologica* 43: 175–178.
- Schuchert, C. 1893. Classification of the Brachiopoda. *American Geologist* 11: 141–167.
- Schuchert, C. 1913. *Class Brachiopoda. The Lower Devonian deposits of Maryland*. Maryland Geological Survey, Baltimore, p. 290–449.
- Schuchert, C. and Cooper, G.A. 1932. Brachiopod genera of the suborders Orthoidea and Pentamerioidea. *Memoirs of the Peabody Museum of Natural History* 4: 1–270.
- Servais, T. and Sintubin, M. 2009. Avalonia, Armorica, Perunica: terranes, microcontinents, microplates or palaeogeographic provinces? In: M.G. Bassett (Ed.), *Early Palaeozoic Peri-Gondwanan Terranes: New Insights from Tectonics and Biogeography*. *The Geological Society, London, Special Publications* 325: 103–115.
- Steinmann, G. and Höek, H. 1912. Das Silur und Kambrium des Hochlandes von Bolivien und ihre Fauna. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 34: 176–252.
- Stubblefield, C.J. 1939. Some Devonian and supposed Ordovician fossils from south-west Cornwall. *Bulletin of the Geological Survey of Great Britain* 2: 63–71.
- Suárez Soruco, R. 1976. El Sistema Ordovícico en Bolivia. *Revista Técnica Yacimientos Petrolíferos Fiscales Bolivianos* 5: 11–123.
- Suárez Soruco, R. (Ed.) 2000. Compendio de geología de Bolivia. *Revista Técnica Yacimientos Petrolíferos Fiscales Bolivianos* 18: 1–213.
- Suárez Soruco, R. and Benedetto, J.L. 1996. Primeros datos sobre la fauna de braquiópodos de la Formación San Benito en la Cordillera del Tunari, Cochabamba, Bolivia. *12º Congreso Geológico Boliviano*(Tarija), *Actas* 1: 211–216.
- Villas, E. 1985. Braquiópodos del ordovícico Medio y Superior de las Cadenas Ibéricas Orientales. *Memorias del Museo Paleontológico de la Universidad de Zaragoza* 1: 1–223.
- Villas, E. 1995. Caradoc through early Ashgill brachiopods from the Central-Iberian Zone (Central Spain). *Geobios* 28, 49–84.
- Villas, E., Vizcaíno, D., Álvaro, J.J., Destombes, J. and Vennin, E. 2006. Biostratigraphic control of the latest-Ordovician glaciogenic unconformity in Alnif (Eastern Anti-Atlas, Morocco), based on brachiopods. *Geobios* 39: 727–737.
- Villeneuve, M. 2005. Paleozoic basins in West Africa and the Mauritanide thrust belt. *Journal of African Earth Sciences* 43: 166–195.
- Waagen, W. 1884. Salt Range fossils, volume 1, part 4, *Productus* Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontology Indica*, 13: 729–770.
- Waisfeld, B.G. and Henry, J.L. 2003. *Huemacaspis* (Trilobita, Kerfornellinae) from the Late Ordovician of the Argentine Cordillera Oriental. *Geobios* 36: 491–499.
- Williams, A. 1974. Ordovician Brachiopoda from the Shelve District, Shropshire. *Bulletin of the British Museum (Natural History), Geology, Supplement* 2: 1–163.
- Williams, A. and Harper, D.A.T. 2000. Orthida. In: A. Williams, C.H.C. Brunton, and S.J. Carlson (Eds.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, revised, 3*. The Geological Society of America and The University of Kansas, Boulder, Colorado, p. 714–782.

doi: 10.5710/AMGH.05.03.2013.558

**Recibido:** 29 de noviembre de 2011**Aceptado:** 5 de marzo de 2013