

New occurrences of Chonetoidea (Brachiopoda) in the Devonian of Bolivia, Peru and Antarctica

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Abstract

Chonetoidea corresponds to one of the most abundant superfamilies throughout the Malvinokaffric Realm (Argentina, Uruguay, Bolivia, Paraguay, Antarctica, Peru and South-Central Brazil). In this paper we provided a better understanding of the diversity of this superfamily during the Devonian in southern Gondwana. For Bolivian specimens, we corroborate both the occurrence of *Pleurochonetes anteloi* in the Huamampampa Formation, that is, this species may have occurred at least in the Givetian, and the occurrence of *Australostrophia mesembria* in the Pragian-Emsian of Bolivia. We further identify both *Aseptonetes isaacsoni* in the Icla/Gamoneda Formation, which represents the oldest occurrence of this species, and *Chonostrophia truyolsae* in the Belén Formation/Bolivian Altiplano, thereby expanding its geographical distribution. We also provide the first description and illustration of a specimen of Chonetoidea from Antarctica and record the first occurrence of *Australostrophia mesembria*, Devonochonetinae indet. and *Eodevonaria* sp. in the Cabanillas Formation of Peru. Because *A. mesembria* is a typical Malvinokaffric species, this corroborates the extension of this realm into southern Peru.

KEYWORDS: chonetoids; Malvinokaffric realm; Gondwana; systematic paleontology.

INTRODUCTION

The Chonetoidea specimens represents a very characteristic superfamily of brachiopods due to their spines along the hinge of the ventral valve and a pair of antheridia inside the dorsal valve. This superfamily had a global distribution and was very common in the regions covered by the Malvinokaffric Realm (Brazil, Bolivia, Peru, Argentina, Malvinas Islands, Uruguay, Paraguay, Antarctica and South Africa), which was a paleobiogeographic realm characterized by a fauna adapted to shallow cold seas of the Early and Middle Devonian (Clarke 1913, Ritcher 1941, Bosetti *et al.* 2012).

The first studies on the Chonetoidea fauna of Bolivia date back to the end of the 19th century (Ulrich 1893), but the research only intensified in the middle of the 20th century. Currently the Chonetoidea of the Devonian of Bolivia are relatively well known with more than 17 known species (Branisa 1965, Isaacson 1977, Racheboeuf and Branisa 1985, Racheboeuf 1992, Racheboeuf and Isaacson 1993, Racheboeuf *et al.* 2012).

On the other hand, the Chonetoidea of the Devonian of Antarctica and Peru are still poorly known. In Antarctica there are only two papers that comment on the Devonian Chonetoidea and they mention the occurrence of a possible

specimen of *Notiochonetes* in the Mount Wyatt Earp Formation (Lower Devonian), Ellsworth Mountains (Boucot *et al.* 1967, Bradshaw and Webers 1988). In Peru, there is a description and illustration of only a single species of Chonetoidea (*Eodevonaria inca* Isaacson 1977) in the Taya Taya region (Isaacson 1977), while Laubacher (1978) cited the occurrence of *Anoplia?* sp., *Notiochonetes* sp. and *Chonetes arcei* Ulrich, 1893 in the Cabanillas region.

The current paper aimed to contribute to better knowledge on the Chonetoidea fauna in the locations mentioned above. We present new descriptions of this superfamily in the Devonian of Bolivia, Peru and Antarctica.

GEOLOGICAL SETTING

Bolivia

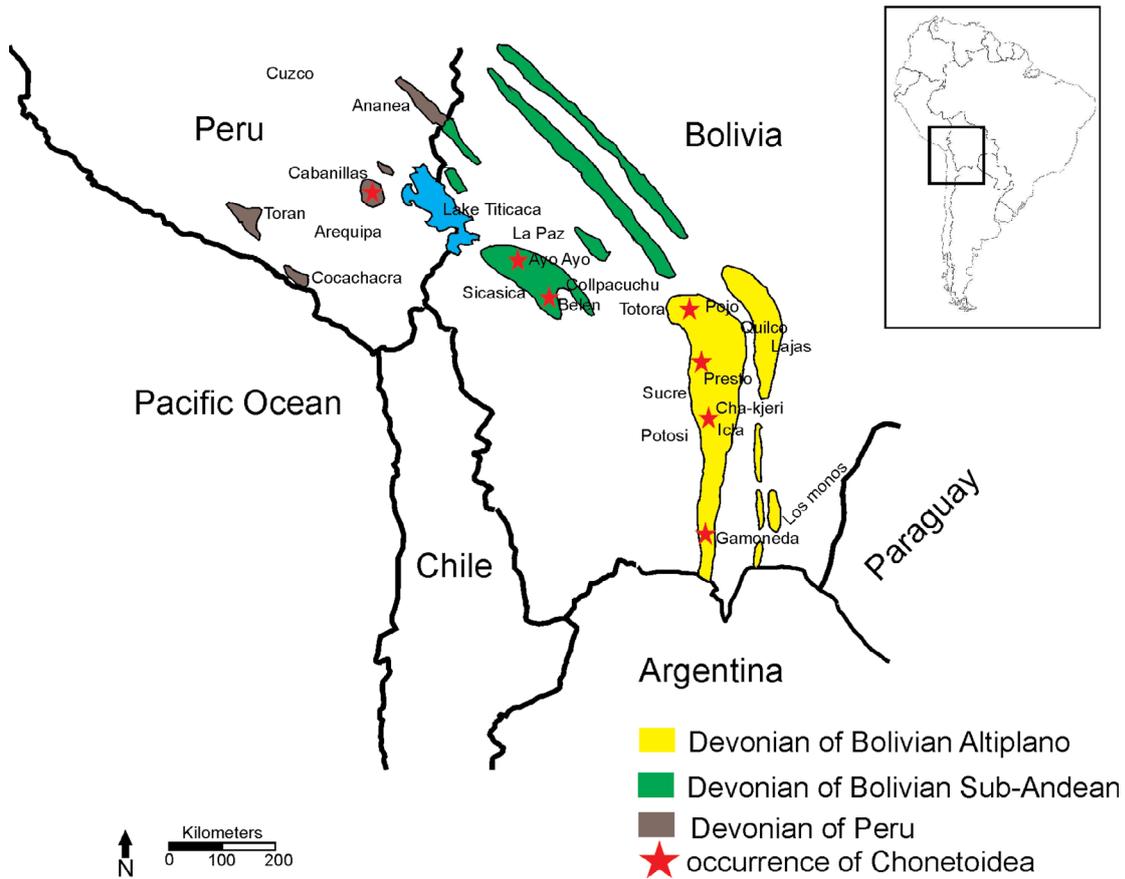
The Bolivian Devonian ranges from Pragian to Frasnian and is known for the good preservation of its fossils (Isaacson and Sablock 1988, Racheboeuf 1992). The Devonian rocks of Bolivia emerge in the west of the country in the Sub-Andean regions (region of Icla, Tarabuco, Pojo, Presto and Tarija) and Altiplano (region of La Paz, Chiarumani, Ayo Ayo and Belén) (Racheboeuf 1992; Figs. 1, 2, 3).

The Vila Vila (late Lochkovian), Belén (Pragian-Eifelian), Sicasica (early Givetian-Frasnian) and Collpacuchu (Frasnian) (Isaacson and Sablock 1988, Blicek *et al.* 1996) formations outcrop in the Altiplano zone, while in the Sub-Andean zone outcrop the Tarabuco (early Pridoli-early Lochkovian), Santa Rosa (late Lochkovian-early Pragian), Icla (early Pragian-Eifelian), Huamampampa (early Eifelian-Givetian), Los Monos (Givetian-Frasnian) and Iquiri (Givetian-Frasnian) formations

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Source: adapted from Isaacson and Sablock (1988).

Figure 1. Devonian outcrops in Bolivia and Peru.

Age	Bolivian Altiplano	Bolivian Sub-Andean
Frasnian	Iquiri Fm.	Collpacuchu Fm.
Givetian	Los Monos Fm.	Sicasica Fm.
		Santari Sandstone
		middle Mb.
	Huamampampa Fm.	Cruz Loma Sandstone
Eifelian		Belen Fm.
	Upper Icla Fm.	
Emsian		Condoriquiña Quartzite
Pragian	Lower Icla Fm.	Lower Belen Mb.
Lochkovian	Santa Rosa Fm.	Vila Vila Fm.
	Tarabuco Fm.	Catavi Fm.

Source: adapted from Isaacson and Sablock (1988) and Blicek *et al.* (1996).

Figure 2. Silurian-Devonian stratigraphic units of Bolivia.

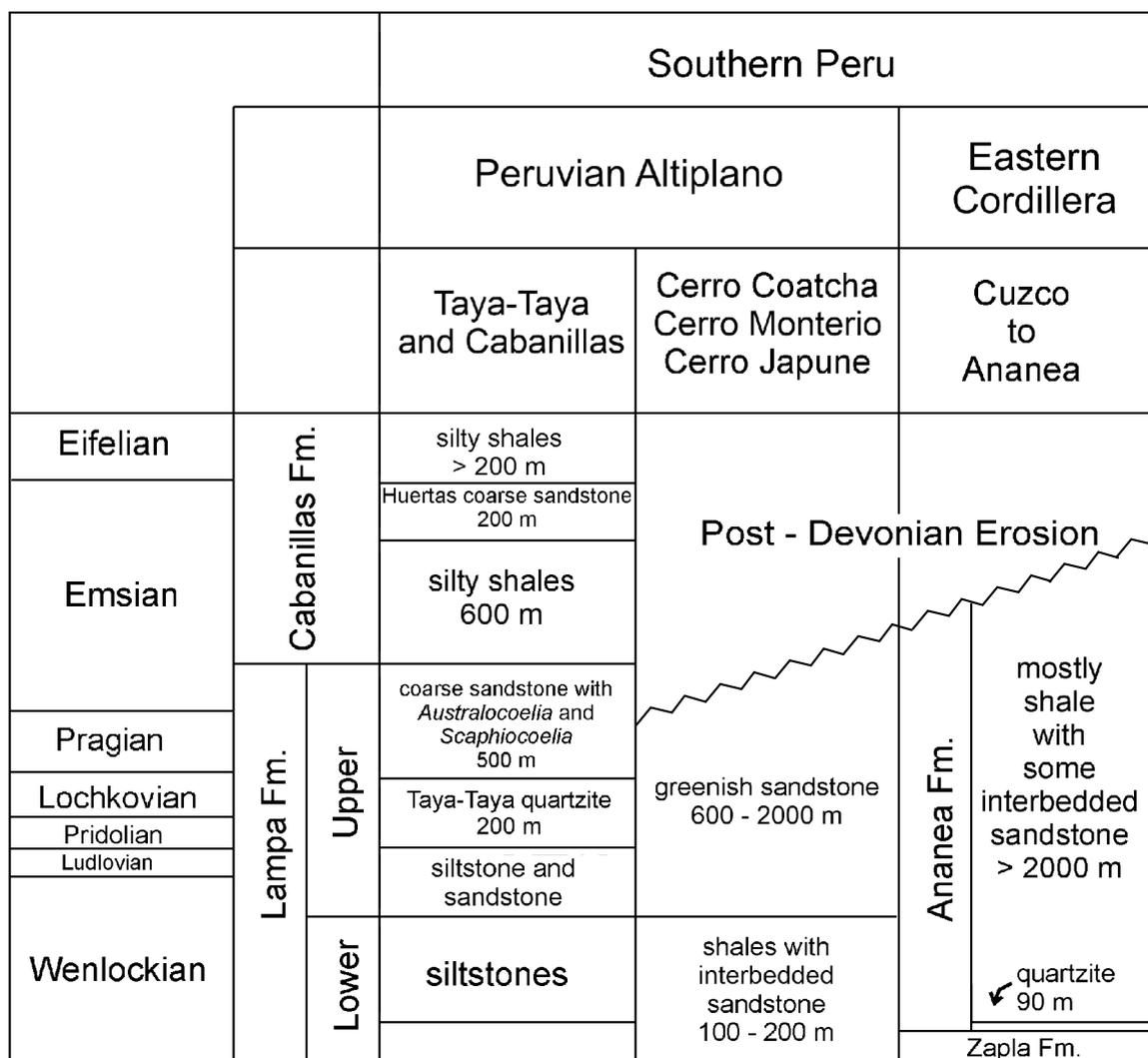
(Grahn 2002). Out of these stratigraphic units the Chonetoidea are found in the Belén, Icla, Huamampampa, Santa Rosa and Sicasica formations (Racheboeuf 1992).

The Santa Rosa formation consists of micaceous sandstones with layers of silty argillites. It was dated, based on assemblages of chitinozoa, as late Lochkovian to early Pragian (Grahn 2002).

The Icla Formation is divided into an upper and a lower portion (Racheboeuf *et al.* 1993, Grahn 2002) and consists of silty argillites rocks interspersed with sandstones (Grahn 2002). Based on chitinozoa assemblages, Grahn (2002) stated that the lower portion of the Icla Formation is Pragian in age, while the upper portion of the Icla Formation is aged between the late Emsian and the early Eifelian. Isaacson (1977) described the Gamoneda Formation, in the homonym region, however the difference between this formation and the type-section of the Icla Formation lies only in the thickness and better development of the sandy levels. With this in mind, Suárez-Soruco and Martínez (1996) and Racheboeuf *et al.* (1998) considered that the “Gamoneda Formation” is only a lateral variation of the Icla Formation, which is followed in this contribution.

The Huamampampa Formation consists of sandstones interspersed with silty argillites. It was dated, through chitinozoan assemblages, as late Eifelian to early Givetian (Grahn 2002).

The Belén Formation is divided into the lower Belén, Quartzite Condoriquina and upper Belén members (Isaacson 1977, Isaacson and Sablock 1988). The lithology is composed of argillites, siltstones and fine to coarse sandstones. The Belén Formation is related to the Icla Formation and has been dated, through



Source: adapted from Laubacher *et al.* (1982).

Figure 3. Stratigraphic units from the Ordovician-Devonian of Peru.

macrofossiliferous content, as Pragian to Eifelian (Isaacson and Sablock 1988, Blicek *et al.* 1996, Holloway and Carvalho 2009).

Finally, the Sicasica Formation is divided into the Cruz Loma Sandstone, Middle Member and Santari Sandstone members (Isaacson 1977, Isaacson and Sablock 1988). The Cruz Loma Sandstone is composed of micaceous and occasionally well cemented fine to medium sandstone; the Middle Member is mainly constituted by micaceous siltstone without the presence of fossils and the Santari Sandstone is constituted by medium-grained and micaceous sandstones. Through the macrofossiliferous content it was possible to date this formation as Givetian to Frasnian (Isaacson and Sablock 1988, Blicek *et al.* 1996, Holloway and Carvalho 2009).

Peru

The Devonian in Peru (Figs. 1 and 3) was initially studied by Douglas (1920) and Newell (1949). It outcrops throughout the entire country and can be divided into three main geographic regions: north and central, south (Altiplano) and southwest (coastal). Despite its great geographical extension, the Devonian of Peru is still poorly understood.

In the Altiplano region (close to Lake Titicaca), the Cabanillas Formation outcrops. Newell (1949) recognized

that the lithology of the Cabanillas Formation and the Icla and Sicasica series are very similar, but he preferred to name the Peruvian sequence with a different name, due to the type-section present in the Icla series and the very remote location of the Sicasica series. The Cabanillas Formation is composed of an intercalation of sandstones, argillites, shales and siltstones (Isaacson and Sablock 1988). Based on the macrofossil content, this stratigraphic unit is considered to have an age between the Emsian and the Eifelian (Laubacher *et al.* 1982).

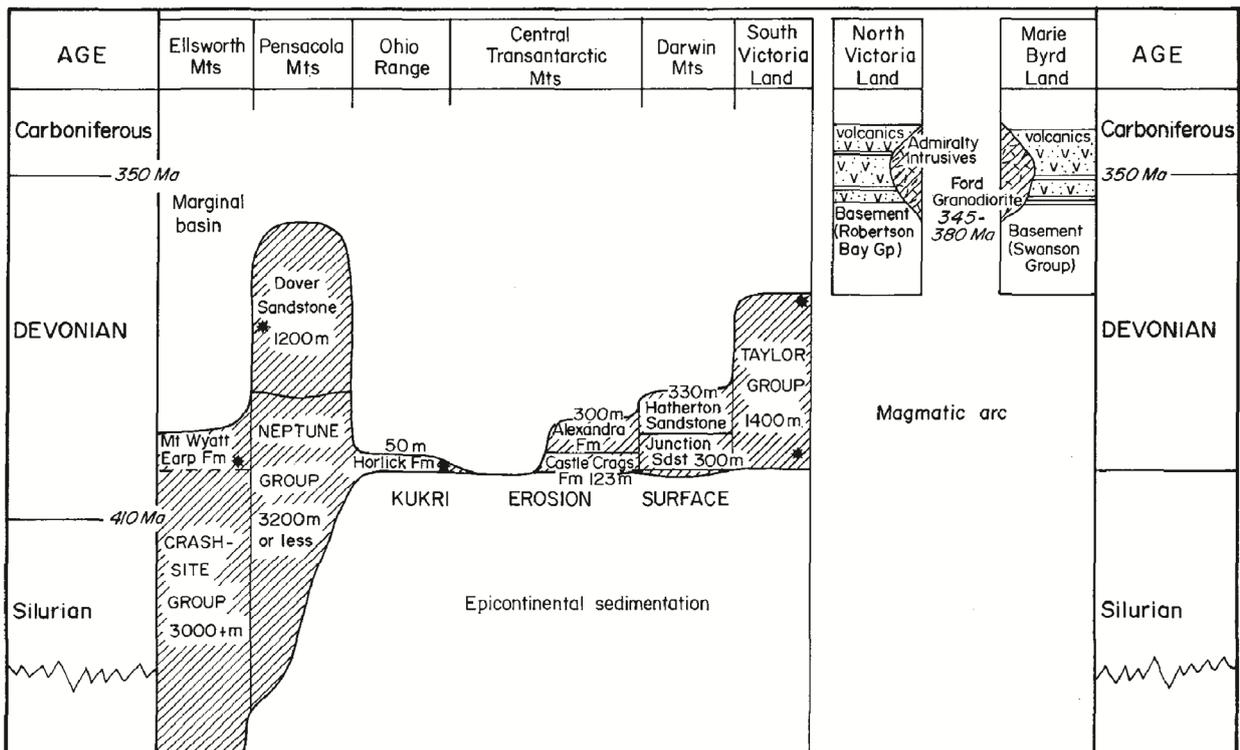
The Peruvian fossils analyzed in this article come from the Cabanillas region and the presence of Chonetidae and Eodevonariidae ensures a Devonian age for the deposits where they were collected. This, coupled with siltite lithology, allowed us to position them safely in the Cabanillas Formation, differentiating it from the Silurian-Early Devonian Lampa Formation, which also appears in the region and in its Devonian portion is characterized by coarse grained sandstones and quartzites (Laubacher *et al.* 1982).

Antarctica

The Devonian in Antarctica is obscure, but it is known that it outcrops across the continent (both in the eastern and western portion) (Boucot *et al.* 1967, Bradshaw and Webers 1988) (Figs. 4 and 5). Four main regions present Devonian rocks in



Source: adapted from Bradshaw and Webers (1988).
Figure 4. Devonian outcrops in Antarctica.



Source: adapted from Bradshaw and Webers (1988).
Figure 5. Silurian-Carboniferous stratigraphic units of Antarctica.

Antarctica: Transantarctic Mountains, Ellsworth Mountains, Northern Victoria Land and Marie Byrd Land. However, across the continent, only one specimen of the Devonian Chonetoidea (Ellsworth Mountains) is recorded.

The Ellsworth Mountains are located in West Antarctica and its Devonian rocks form the upper part of the strongly folded and very thick (at least 13 km) conformable sequence of predominantly shallow marine or alluvial sediments that were deposited in a basin steadily subsiding since the Middle Cambrian (Bradshaw and Webers 1988). The only specimen of Chonetoidea comes from the Mount Wyatt Earp Formation, which consists of gray, red or brown quartz sandstones/quartzites, with poorly selected grains, argillites, conglomerates and fragments of volcanic rocks in some places (Bradshaw and Webers 1988, Spörl 1992, Webers *et al.* 1992). Based on its fossiliferous content, which features elements of the typical Malvinokaffric fauna, this stratigraphic unit was dated as Lower Devonian, most likely early Emsian (Boucot *et al.* 1967, Bradshaw and Webers 1988).

MATERIALS AND METHODS

The specimens analyzed are preserved at the Department of Paleobiology in the National Museum of Natural History/Smithsonian Institution (USNM). For taxonomic identification, we consulted the Treatise on Invertebrate Paleontology (Racheboeuf 2000) and other papers that address the Chonetoidea from the Malvinokaffric and Eastern Americas realms, in addition to the Brazilian basins of Amazonas and Parnaíba (Tab. 1). The standards proposed by Racheboeuf (2000), and Fonseca (2001) were used to assess the size and transversal elongation of the Chonetoidea shells.

SYSTEMATIC PALEONTOLOGY

Phylum Brachiopoda Duméril, 1806

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer and Popov, 1996

Class Strophomenata Williams, Carlson, Brunton, Holmer and Popov, 1996

Order Productida Sarytcheva and Sokolskaya, 1959

Suborder Chonetidina Muir-Wood, 1962

Superfamily Chonetoidea Bronn, 1862

Family Strophochonetidae Muir-Wood, 1962

Subfamily Strophochonetinae Muir-Wood, 1962

Genus *Australostrophia* Caster, 1939

Type-species: *Leptostrophia? mesembria* Clarke, 1913

***Australostrophia mesembria* (Clarke, 1913)** (Figs. 6B, 6C and 6I)

1913 *Leptostrophia? mesembria* Clarke; Clarke, p. 286, pl. 22, fig. 33-41.

1975 *Australostrophia mesembria* (Clarke); Boucot, pl. 1, figs. 1-12.

1977 *Australostrophia mesembria* (Clarke); Isaacson, p. 165-167, pl. 3, fig. 13-20, pl. 4, fig. 1-8.

Material: USNM 209050, USNM 209051, USNM 209052, USNM 209053, USNM 209054, USNM 209055, USNM 209056, USNM 305212 and USNM PAL 771570.

Provenance: Bolivia, Gamoneda, "Gamoneda Formation" (Pragian - Emsian), Pojo and Totorá, lower Icla Formation (Pragian); and Peru, Cabanillas region (Emsian-Eifelian).

Description: medium to very large shell, with length ranging from 11.2 to 33 mm, and width ranging from 14 to 40 mm, distinctly transverse to slightly transverse (C/L between 0.61 and 0.82); shell presenting several concentric growth lines (*fila*), not very prominent umbo and specimens with spines were not found. Ornamentation was constituted, on average, by 16/5 mm close to the anterior commissure, sparse pseudopunctuation. **Ventral interior:** large flabelled muscular field, diverging at most 90° and occupying up to 67% of the valve (USNM 17976), long myofragm, large, triangular and previously rounded diductor scars, narrow and sub elliptical adductor scars. **Dorsal interior:** pair of slightly divergent anteridia, little thick and long median dorsal septum, absence of accessory septa.

Remarks: externally, *A. mesembria* (Clarke, 1913) differs from *A. senegalensis* Racheboeuf and Villeneuve, 1989 in its larger size, as it presents thinner ribs and a dorsal median septum (Racheboeuf and Villeneuve 1989). *A. mesembria* differs from *A. clarkei* Racheboeuf and Herrera, 1994, externally in the more transverse contour, thicker ribs (at most

Table 1. Origin of the analyzed samples.

Locality	Outcrop	Material
Bolivia	Pojo	USNM 209050, USNM 209051, USNM 209052, USNM 209053, USNM 209054, USNM 209055 and USNM 209056.
	Totorá	USNM 305212
	Gamoneda	USNM 209059, USNM 209060, USNM 209061, USNM 209062 and USNM PAL 771566
	Junacas	USNM 209063
	<i>Metacryphaeus</i> zone	USNM PAL 771562 and USNM PAL 771563
	<i>Asteropyge</i> zone	USNM PAL 771564
	Unknown	USNM PAL 771561
Peru	Cabanillas region	USNM PAL 771567, USNM PAL 771568, USNM PAL 771569, USNM PAL 771570 and USNM PAL 771571
Antarctica	Heritage Range, Ellsworth Mountains	USNM PAL 771565

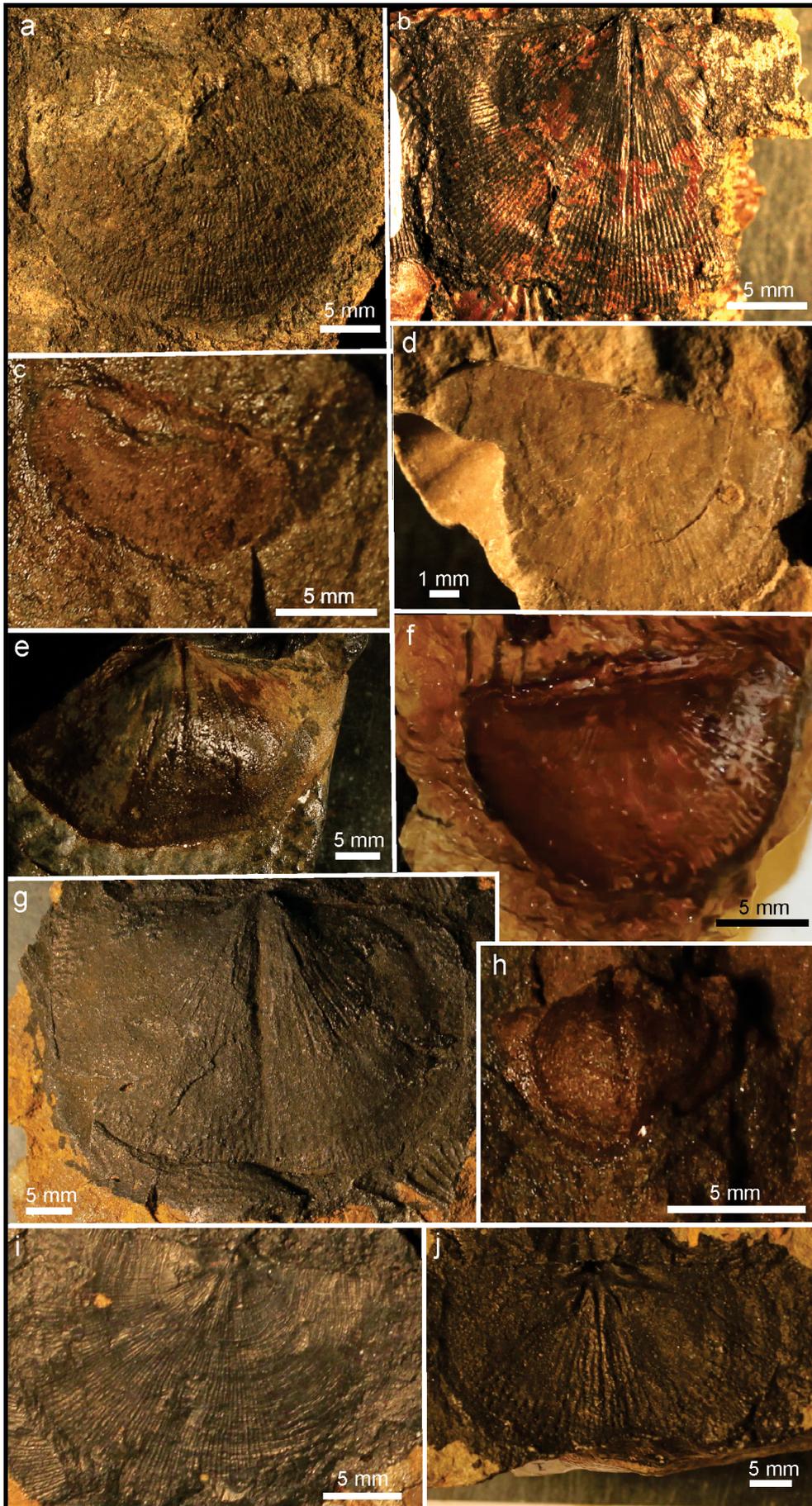


Figure 6. Chonetoidea from the Devonian of Bolivia, Peru and Antarctica: (A) *Australostrophia?* sp. (USNM PAL 771563), Antarctica, ventral valve?; (B) *Australostrophia mesembria* (USNM 209050), Bolivia, ventral valve; (C) *Australostrophia mesembria* (USNM PAL 771570), Peru, ventral valve; (D) *Chonostrophia truyolsae* (USNM PAL 771564), Bolivia, dorsal valve; (E) *Eodevonaria* sp. (USNM PAL 771571), Peru, ventral valve; (F) *Aseptonetes isaacsoni* (USNM PAL 771566), Bolivia, articulated valves; (G) *Pleurochonetes anteloi* (USNM 209063), Bolivia, ventral valve; (H) Devonochonetinae indet. (USNM PAL 771567), Peru, ventral valve; (I) *Australostrophia mesembria* (USNM 209055), Bolivia, dorsal valve; (J) *Pleurochonetes anteloi* (USNM 209059), Bolivia, dorsal valve.

20 ribs, instead of 21 to 24 along the anterior commissure) and by the longer spines erect (about 50° instead of between 25 and 30°); the ventral interior has posterior ridges limiting the muscular field; less divergent (70° to 90° instead of 90° to 112°). Presence of low median septum and a less divergent anderidia pair (about 30° instead of between 32° and 40°) (Racheboeuf and Isaacson 1993). However, regarding the difference between *A. mesembria* and *A. clarkei*, it is necessary to make some considerations:

- Herrera (1995) stated that in *A. clarkei* the septum median does not exceed the length of the anderidia pair, however dorsal valve specimens from the *A. mesembria* type-series (Clarke 1913) also share this characteristic (Boucot 1975);
- the question of *A. clarkei* being less transversal than *A. mesembria* is relative, since samples from the *A. clarkei* type-series are more transversal than the lectotype by *A. mesembria* (DGM 241-I), C/L ratio = 0.63 in the first and 0.70 in the second species (Clarke 1913, Racheboeuf and Herrera 1994).

Finally, *A. mesembria* differs from *A. penoensis* Herrera, 1995, from the Argentinian Pragian (Talacasto Formation) (Herrera 1995), outwardly in less dense ornamentation and more erect spines. In the dorsal interior, the two species mainly differ in the presence of accessory septa in *A. penoensis* (absent in *A. mesembria*), and in the shape and length of the median septum, which is low, wide and short in *A. mesembria*, not reaching half of the valve, whereas in *A. penoensis*, it reaches 50% to 60% of the length of the valve (Herrera 1995). The specimens USNM 209050, USNM 209051, USNM 209052, USNM 209053, USNM 209055, USNM 209056 and USNM 305212 were described and classified by Isaacson (1977) as *A. mesembria*, but when Racheboeuf and Herrera (1994) created the *A. clarkei* species, they considered that all specimens identified as *A. mesembria* by Isaacson (1977) would be synonymous with *A. clarkei*. The analysis of these specimens showed that the specimens of Isaacson (1977) have several ribs/5 mm and divergences in the muscular field and the pair of anderidia is very similar to *A. mesembria*. Bearing this in mind and comparing it with the specimens of the type-series of *Australostrophia mesembria* preserved in the collection found in the Rio de Janeiro office (Geological Survey of Brazil (CPRM/RJ)), we consider the validity of identification as *Australostrophia mesembria* of Isaacson's (1977) specimens. Later Boucot *et al.* (2001) did not describe the Isaacson (1977) specimens as a synonym of *A. clarkei*, but did not explain the reasons. The USNM 20056 specimen represents the first occurrence of *A. mesembria* in the Devonian of Peru.

Occurrence of the species *Australostrophia mesembria*: late Lochkovian-late Emsian, Brazil (*e.g.* Clarke 1913, Petri 1948, Lange 1954, Lange and Petri 1967, Melo 1985, Quadros 1987, Boucot *et al.* 2001, Souza 2007, Cerri 2013); Pragian-Emsian, Bolivia (Isaacson 1977, Racheboeuf *et al.* 1998); Pragian-Emsian, Malvinas Islands (Clarke 1913); ?Lochkovian-late Pragian, Argentina (Castellaro 1966; for

age see García-Muro *et al.* 2018); ?Lower Devonian, Paraguay (Harrington 1950 *apud* Proyecto PAR 83/005 1986) and late Pragian-early Emsian, Uruguay (Mendez-Alzola 1938; for age see Daners *et al.* 2017).

***Australostrophia?* sp. (Fig. 6A)**

Material: USNM PAL 771565.

Provenance: Antarctica, Heritage Range, Ellsworth Mountains, Mt. Wyatt Earp Formation (early Emsian?).

Description: large shell, about 23 mm long and 31 mm wide, with maximum extension in the middle of the valve; presence of *fila* and about 15 ribs/5 mm. **Ventral interior:** not found in the analyzed material. **Dorsal interior:** not found in the analyzed material.

Remarks: this specimen is classified as a likely *Australostrophia* due to its size, shape of the valve and the presence of a *fila*, however the absence of further details prevents a classification with closed nomenclature. Specimens of Chonetoidea from the Devonian of Antarctica have never been described or figured formally; however, we believe that the same specimen described has been cited in previous papers (*e.g.* Boucot *et al.* 1967, Bradshaw and Webers 1988) as a possible *Notiochonetes* due to its large size. We believe that, since the only paper citing Chonetoidea from the Antarctic Devonian is Boucot *et al.* (1967), Bradshaw and Webers (1988) cite the material of this paper. The description by Boucot *et al.* (1967) matches that of the analyzed specimens: “a single incomplete specimen of large articulate brachiopods, possibly referable as *Chonetes*”. In addition, the specimen was collected in 1965 by Gerald Frank Webers, one of the co-authors in the Boucot *et al.* (1967) paper. The specimen here studied was part of the so-called Boucot Collection, a collection that belonged to paleontologist Arthur James Boucot and was later donated to NMNH/SI. In any case, we do not agree that the specimen is a *Notiochonetes*, as it has a *fila* which is uncommon in this genus, but is widely found in *Australostrophia*.

Occurrence of the *Australostrophia* genus: Lochkovian-Emsian of Brazil, Argentina, Bolivia and Guinea (Racheboeuf 2000).

Family Chonostrophiiidae Muir-Wood, 1962

Genus *Chonostrophia* Hall and Clarke, 1892

Type-species: *Chonetes reversa* Whitfield, 1882

***Chonostrophia truyolsae* (Racheboeuf 1992) (Fig. 6D)**

1992 *Chonostrophia truyolsae* Racheboeuf; Racheboeuf, p. 50, pl. 1.16-24.

1993 *Chonostrophia truyolsae* Racheboeuf; Racheboeuf and Isaacson, p. 106-107, Fig. 6G and 6H.

Material: USNM PAL 771561, USNM PAL 771562 and USNM PAL 771564.

Provenance: Bolivia, Belén Sequence (Belén Formation), *Asteropyge* zone (Eifelian, see Lieberman and Kloc 1997) and *Metacryphaeus* zone (Emsian-Eifelian, see Carbonaro *et al.* 2018).

Description: small, lightly resupinate shells, between 8 and 10 mm long and between 10 and 14.5 mm wide (USNM PAL 771561 and USNM PAL 771564 respectively); sub elliptical contour, transverse (C/L between 0.68 and 0.80), small umbo,

maximum width before hinge line. About 3 ribs/mm close to the anterior commissure, multiplying mainly by intercalation, presence of at least three oblique orthomorph spines on each side of the umbo. **Ventral interior:** small, triangular muscle field, medium-sized myofragm. **Dorsal interior:** absence of dorsal median septum.

Remarks: ornamentation with very sparse ribs, straight dental pits and small *Chonostrophia truyolsae* Racheboeuf, 1992 that can be differentiated from the other species of *Chonostrophia*: *C. dawsoni* (Billings, 1874), *C. cartieri* Racheboeuf and Lespérance, 1995, *C. montrealensis* Schuchert, 1901 and *C. elenae* Herrera, 1995. The USNM PAL 771562 and USNM PAL 771564 specimens represent the first occurrence of *C. truyolsae* in the Belén Formation and consequently the first occurrence in the Bolivian Altiplano.

Occurrence of the *Chonostrophia truyolsae* species: late Eifelian, Bolivia (Racheboeuf 1992).

Family Eodevonariidae Sokolskaja, 1960

Genus *Eodevonaria* Breger, 1906

Type-species: *Chonetes arcuatus* Hall, 1857

***Eodevonaria* sp.** (Fig. 6E)

Material: USNM PAL 771571.

Provenance: Cabanillas region, Peru (Emsian-Eifelian).

Description: medium shell 23 mm long and 40 mm (?) wide, transverse (C/L - 0.58), heavily concave-convex valve, poorly preserved but apparently thin ribs, presence of pseudopunctuations, denticular hinge with 12 poorly preserved teeth in 5 mm. **Ventral interior:** thin myofragm, reaching approximately half the length of the valve, striated muscle field, large and poorly defined. **Dorsal interior:** not found in the studied material.

Remarks: the specimen presents the typical characteristics of *Eodevonaria*, however the absence of the dorsal valve prevents classification at a specific level with certainty (see Boucot and Harper 1968). The specimen differs from *Eodevonaria imperialis* Caster, 1939 from the Devonian of Colombia and Venezuela (Caster 1939, Benedetto 1984) due to its smaller umbo, the muscle field has a different morphology and is less inflated. *Eodevonaria* sp. differs from *Eodevonaria inca* (Isaacson 1977) of the Devonian of Peru (Isaacson 1977) in that it is apparently more inflated and has a larger muscular field.

Occurrence of *Eodevonaria* genus: Pragian-Emsian, Appalachian Mountains (North America) (Racheboeuf 2000); Emsian, Canada (Racheboeuf and Lespérance 1995); Devonian, Colombia (Caster 1939); Devonian, Venezuela (Benedetto 1984); Devonian, Peru (Isaacson 1977).

Family Chonetidae Bronn, 1862

Subfamily Devonochonetinae Muir-Wood, 1962

Genus *Aseptonetes* Isaacson, 1977

Type-species: *Aseptonetes boucoti* Isaacson, 1977

***Aseptonetes isaacsoni* Racheboeuf and Branisa, 1985** (Fig. 6F)

1985 *Aseptonetes? isaacsoni* Racheboeuf and Branisa; Racheboeuf and Branisa, p. 1441, fig. 5. 10-21.

1992 *Aseptonetes isaacsoni* Racheboeuf and Branisa; Racheboeuf, p.37.

1993 *Aseptonetes isaacsoni* Racheboeuf and Branisa; Racheboeuf and Isaacson, p. 110, fig. 8N-R.

Material: USNM PAL 771563 and USNM PAL 771566.

Provenance: Bolivia, Belén Formation (Eifelian), *Metacryphaeus* zone (Emsian-Eifelian, see Blicek *et al.* 1996) and Gamonedá, “Gamonedá Formation” (Pragian-Emsian).

Description: small to medium inflated shells, between 7 and 8 mm in length; width between 5,5 and 7,5 mm; sub elliptical contour, slightly transverse (C/L ratio between 0.75 and 0.85), maximum width at the hinge line, between 9 and 12 ribs/5mm, with V-shaped interspaces; presence of at least 3 oblique orthomorph spines on each side of the umbo, forming an angle greater than 90° in relation to the hinge. **Ventral interior:** large, triangular muscular field; thin and long myofragm. **Dorsal interior:** pair of well developed anderia, median septum relatively long and thin.

Remarks: the high-angle orthomorph spines and the V-spaces make the specimens described to be of the genus *Aseptonetes*. *A. isaacsoni* (Racheboeuf and Branisa, 1985) differing from *A. boucoti* Isaacson, 1977 in that it is less transversal, more inflated and has spines making a greater angle with the hinge. The presence of *A. isaacsoni* in the “Gamonedá Formation” (USNM PAL 771566), from Pragian to Emsian age (Isaacson 1977, Racheboeuf *et al.* 1998), represents the oldest occurrence of this species. Until then, it was believed that it was restricted to the Eifelian (Racheboeuf 1992).

Occurrence of the *Aseptonetes isaacsoni* species: Eifelian, Bolivia (Racheboeuf 1992).

Subfamily Devonochonetinae Muir-Wood, 1962

Devonochonetinae indet. (Fig. 6H)

Material: USNM PAL 771567, USNM PAL 771568 and USNM PAL 771569.

Provenance: Cabanillas region, Peru.

Description: small shell at around 5 mm in length and around 7 mm in width, transverse (C/L - 0.71), heavily concave-convex, sub elliptical contour, presence of oblique cyrtomorph spines (?), small umbo, narrow ribs, presence of about 6 ribs in 1 mm. **Ventral interior:** large, poorly defined muscle field, small myofragm. **Dorsal interior:** not found in the studied material.

Remarks: the poor preservation of the specimens prevents a more detailed taxonomic classification, however due to the characteristics described it is possible to classify them as belonging to the Devonochonetinae subfamily. The specimens resemble the genus *Montsenetes* due to their external morphology, which has records in Venezuela, Bolivia and Brazil in South America (Racheboeuf 1992, 2000, Fonseca 2004), however this genus is generally larger, has thicker ribs and a better developed myofragm than that of the analyzed specimens. Therefore, it is necessary to analyze more specimens to corroborate this hypothesis. This is the first record of a Devonochonetinae in the Devonian of Peru.

Occurrence of the Devonochonetinae subfamily: this subfamily occurred between the Emsian and the Frasnian and had a cosmopolitan distribution (Racheboeuf 2000).

Subfamily Notiochonetinae Racheboeuf, 1992

Genus *Pleurochonetes* (Isaacson, 1977)

Type-species: *Chonetes* (*Pleurochonetes*) *lauriata* Isaacson, 1977

***Pleurochonetes anteloi* (Isaacson, 1977)** (Figs. 6G and 6J)

1977 *Gamonetes anteloi* Isaacson; Isaacson, p. 168, pl. 4, figs. 9-21.

1977 *Notiochonetes falklandica* (Morris and Sharpe); Isaacson, pl. 5, figs. 1-11.

1985 *Notiochonetes falklandicus* (Morris and Sharpe); Racheboeuf and Branisa, p. 1446, figs. 9.7-9.14.

1992 *Pleurochonetes anteloi* (Isaacson); Racheboeuf, p. 46, pl. 2, figs. 1-10.

1993 *Pleurochonetes anteloi* (Isaacson); Racheboeuf and Isaacson, p. 112, fig. 11E-K.

Material: USNM 209059, USNM 209060, USNM 209061, USNM 209062 and USNM 209063.

Provenance: Bolivia, Gamoneda and Junacas, Huamampampa Formation (Eifelian-Givetian?).

Description: small to large slightly inflated shell, ranging from 8 to 30 mm in length and 9 to 43 mm in width; sub elliptical contour, slightly to markedly transverse (C/L ratio between 0.52 and 0.80), maximum width at the hinge line; about 9 to 10 ribs/5mm, V-shaped ribs, straight pseudopunctuation aligned to the interspaces, appears to present growth lines. **Ventral interior:** large, wide muscular field, diverging more than 90°, long well developed myofragm. **Dorsal interior:** pair of slightly divergent anderidia, thin and short dorsal median septum, although absent in the youngest specimens; internal ridges of the dental pit curved towards the anterior margin.

Remarks: the classification of the specimens as *Pleurochonetes* occurred due to the pair of anderidia being poorly developed, on account of the large muscular field and morphology of the dental pits. *P. anteloi* (Isaacson, 1977) differs from *P. falklandicus* (Morris and Sharpe, 1846) by its larger size, the different development of certain structures in the dorsal interior: more developed median septum, larger and more developed cardinal process and less developed accessory septa (Racheboeuf 1992, Racheboeuf and Isaacson 1993). *P. anteloi* differs from *P. surucoi* Racheboeuf, 1992 in that the shell is less inflated, the ribs are less widely spaced, the divergence of the pair of anderidia is less predominant, as well as the internal ridges of the pits (Racheboeuf 1992, Racheboeuf and Isaacson 1993). We reinforce the fact that *Pleurochonetes anteloi* occurs in the Huamampampa Formation. We have analyzed the specimens described and illustrated by Isaacson (1977) and agree with Racheboeuf (1992) that the specimens USNM 209060, USNM 209061, USNM 209062 and USNM 209063 classified by Isaacson (1977) as *Gamonetes anteloi* or *Notiochonetes falklandica* are actually *Pleurochonetes anteloi*. However, for unknown reasons Racheboeuf (1992) and Racheboeuf and Isaacson (1993) do not report the occurrence of *P. anteloi* in the Huamampampa Formation.

Occurrence of the *Pleurochonetes anteloi* species:

Emsian-Eifelian, Bolivia (Isaacson 1977, Racheboeuf 1992, Racheboeuf *et al.* 1998).

FINAL CONSIDERATIONS

In this paper we contribute to a better understanding of the diversity of Chonetoidea of the Malvinokaffric Realm. It was possible to realize that even in places where there is already more consolidated knowledge, such as in Bolivia, there is still a need for more taxonomic papers. In regards to Bolivian specimens, we corroborate the occurrence of *Pleurochonetes anteloi* in the Huamampampa Formation, that is, this species may have occurred at least during the Givetian; we corroborate the occurrence of the *Australostrophia mesembria* in the Pragian-Emsian of Bolivia, as this species occurs at this same age in Brazil, the Malvinas Islands, Uruguay and Paraguay and it is impossible to determine where this species arose; we identified the occurrence of the *Aseptonetes isaacsoni* in the Icla/Gamoneda Formation, representing the oldest specimen of this species found to date and we also identified the first occurrence of the *Chonostrophia truyolsae* in the Belén Formation/Bolivian Altiplano, expanding at least its geographical occurrence.

In relation to Antarctica, we provide the first description and illustration of a specimen of Chonetoidea from this continent and, finally, in relation to the Peruvian specimens, we record the first occurrence of the *Australostrophia mesembria*, Devonochonetinae indet. and *Eodevonaria* sp. in the Cabanillas Formation. *A. mesembria* is a typically Malvinokaffric species, thus corroborating, through the Chonetoidea fauna, that this realm extended to the south of Peru.

The taxonomic identifications made in this paper serve as subsidies for a better understanding the paleobiogeography and paleoenvironments in southern Gondwana during the Devonian.

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