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ARTICLES

FIRST MIDDLE DEVONIAN BIVALVES FROM ARGENTINA, NEW RECORDS FROM THE PUNTA NEGRA FORMATION AND INSIGHTS ON MIDDLE PALEOZOIC FAUNAS FROM THE PRECORDILLERA BASIN

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Abstract. Middle Devonian bivalves from Argentina are reported for the first time, based on records of the Precordilleran Punta Negra Formation (Emsian–Frasnian?), San Juan Province. This finding is the youngest Devonian record of bivalves from southernmost South America. The impoverished bivalve association in the Punta Negra Formation includes five shallow infaunal deposit feeders, *i.e. Nuculites argentinum* Sánchez, *Anthracoleda (Pseudoleda) minuta* Sánchez, *Praenucula* sp., *Deceptrix* sp. and *Praectenodonta* sp. The distribution of the Silurian–Devonian bivalves from Precordillera shows a decreasing diversity trend during this interval, due to potential biases in sampling and paleoecology and thus suggesting that this trend might be apparent. Early and Middle Devonian bivalves from Precordillera show a strong cosmopolitan paleobiogeographic signature, in contrast with other geographically related basins showing endemic (Malvinokaffric Realm) signals during the Devonian. Contrarily, an endemic composition is recorded in the Precordillera Basin when based on coeval Malvinokaffric groups such as ostracods and trilobites. Although more information is needed, the cosmopolitan character of Devonian bivalve assemblages from the Argentine Precordillera Basin might be interpreted under the light of a unique history driving biogeographic processes affecting different taxonomic groups in different ways.

Key words. Bivalvia. Middle Devonian. Punta Negra Formation. Argentine Precordillera.

Resumen. PRIMEROS BIVALVOS DEL DEVÓNICO MEDIO DE ARGENTINA, NUEVOS REGISTROS DE LA FORMACIÓN PUNTA NEGRA Y APRECIACIONES SOBRE LAS FAUNAS DEL PALEOZOICO MEDIO DE LA CUENCA DE PRECORDILLERA. Se dan a conocer los primeros registros de bivalvos del Devónico Medio (Emsiano–Frasniano?) de Argentina en la Formación Punta Negra, Precordillera de San Juan. Se identificó una asociación empobrecida integrada por cinco bivalvos infaunales detritívoros: *Nuculites argentinum* Sánchez, *Anthracoleda (Pseudoleda) minuta* Sánchez, *Praenucula* sp., *Deceptrix* sp. y *Praectenodonta* sp. La distribución de los géneros de bivalvos en el Silúrico-Devónico de la Precordillera, muestra una diversidad decreciente en este intervalo de tiempo. Sin embargo, esta tendencia podría ser aparente debido a posibles sesgos paleoecológicos o derivados del muestreo en las asociaciones. Los bivalvos del Devónico Temprano y Medio de la cuenca de Precordillera son fuertemente cosmopolitas, en contraposición con los registros de endemismos (malvinocáfricos) de cuencas coetáneas geográficamente relacionadas. Además, es reconocible una signatura paleobiogeográfica endémica en otros grupos de esta cuenca como ostrácodos y trilobites. Si bien se necesita más información, es posible interpretar que el carácter cosmopolita de los bivalvos de la Precordillera Argentina respondería a una historia única de procesos biogeográficos que afectan de manera diferente a cada grupo taxonómico.

Palabras clave. Bivalvos. Devónico Medio. Formación Punta Negra. Precordillera Argentina.

MIDDLE DEVONIAN faunas are poorly known in the Argentine basins. A number of contributions came from the Chigua Formation in the eastern Precordillera (Baldis, 1967; Baldis and Longobucco, 1977; Leanza, 1968), but more recent ones derive from the Central Precordillera region (Herrera and Bustos, 2001; Rustán, 2011; Salas *et al.*, 2013). The Middle Devonian is represented in this area by the Punta Negra Formation (Bracaccini, 1950), known by its scarce paleontological content. Previously identified records include palynomophs (Rubinstein, 2000), plant debris (Frenguelli, 1951, 1952; Menéndez, 1967; Baldis, 1973, 1975; Poiré and Morel, 1996; Edwards *et al.*, 2009), invertebrates and ichnofossils (Baldis, 1967, 1973; Padula *et al.*, 1967; Peralta *et al.*, 1995; Herrera and Bustos, 2001). Only Herrera and Bustos (2001) described a brachiopod assemblage recorded approximately in the middle part of the unit, while other

authors only mentioned the presence of isolated remains.

In this context, the discovery of new fossiliferous beds in the Punta Negra Formation (Rustán and Vaccari, 2010; Rustán, 2011; Salas *et al.*, 2013) including bivalves, ostracods, trilobites, brachiopods, gastropods, hyolithids, cephalopods, crinoids, bryozoans and corals is highly interesting as it contributes to the knowledge on the Middle Devonian fauna from Argentina. Numerous contributions were published by Sánchez (1985, 1989, 1991, 2003, 2005) who over the last decades studied the Early and Middle Paleozoic mollusks from western Argentina. However, only one of her contributions reported a Devonian bivalve fauna in the Precordillera Basin, and this one limited to the Early Devonian Talacasto Formation (Lochkovian–Emsian) in San Juan Province (Sánchez *et al.*, 1995).

In this paper we report palaeotaxodontid bivalves from two classical localities where the Punta Negra Formation is exposed; they are the youngest record of this group in the Devonian of Precordillera. The significance of the diversity and paleobiogeographical insights revealed by this new information are briefly commented in the context of bivalve data from coeval related basins and also other faunas from Precordillera.

GEOLOGICAL SETTING AND PROVENANCE OF THE MATERIAL

The studied Devonian sedimentary rocks are widespread and very well exposed in the Central Precordillera of San Juan Province (central-western Argentina), between the Jáchal River to the north and the San Juan River to the south (Fig. 1). This succession is integrated by the siliciclastic rocks of the Talacasto (early Lochkovian–late Emsian) and Punta Negra (latest? Pragian–early Frasnian?) formations, which together constitute the Gualilán Group (Baldis, 1975).

The Punta Negra Formation unconformably (paraconcordance) overlies the marine succession of mudstones with intercalated sandstone beds of the Talacasto Formation. A guide horizon originally recognized by Keidel (1921) allows a new correlation scheme for the different stratigraphic sections, evidencing the diachronism between these units (Rustán and Vaccari, 2010; Salas *et al.*, 2013).The boundary has been discussed in the literature and it is interpreted as being progressively younger northwards. Hence, the oldest ages of the Punta Negra Formation are latest? Pragian–early Emsian in the south of the basin, whereas they are Emsian–early Frasnian in the north, according the paleontological data summarized by Herrera and Bustos (2001) and Salas *et al.* (2013).

The Punta Negra Formation includes a thickening- and coarsening-upward succession of green to blackish green sandstones interbedded with mudstones, reaching up to 1000 meters along the basin (Bustos, 1996). The beds are mainly tabular, 0.2–1.5 m thick, and display a conspicuous rhythmicity and graded sedimentation. However, significant lateral facial changes have been observed toward the northeast and west by Baldis (1973), changing to more greenish colors and a less obvious rhythmical arrangement. The sandy-mudstone succession of Punta Negra Formation is unconformably covered by the glacial diamicritic Upper Carboniferous deposits of the basal Guandacol Formation (Cuerda, 1965).

The depositional environment of this unit was initially deemed to be a submarine fan (González Bonorino, 1975; González Bonorino and Middleton, 1976; Peralta and Ruzycki, 1990; Peralta, 2005; among others), or a delta system (Astini, 1990; Bustos, 1996; Poiré and Morel, 1996; Bustos and Astini, 1997). More recently, however, it has been interpreted as a shallow marine inner shelf to locally continental environment by Edwards *et al.* (2009), as suggested by the taphonomy of plant remains.

The paleontological content of the unit is poor and has received little attention (see a review by Herrera and Bustos, 2001). Specific contributions include palynomorphs (Rubinstein, 2000), plants (Edwards *et al.*, 2009 and references therein), brachiopods (Herrera and Bustos, 2001), trilobites (Rustán and Vaccari, 2010; 2012) and ostracods (Salas *et al.*, 2013).

The studied bivalve fauna comes from two different localities of the Punta Negra Formation, *i.e.*, Las Casitas River and Loma de Los Piojos sections (Fig. 1).

Las Casitas River section

The section runs in an E-W trend approximately 20 km to the southwest of Niquivil locality, San Juan Province (30°31'12" S; 68°48'30" W). In this section, the Punta Negra Formation reaches approximately 190 m thick, unconformably overlies the Talacasto Formation, and underlies the Guandacol Formation by means of an erosive

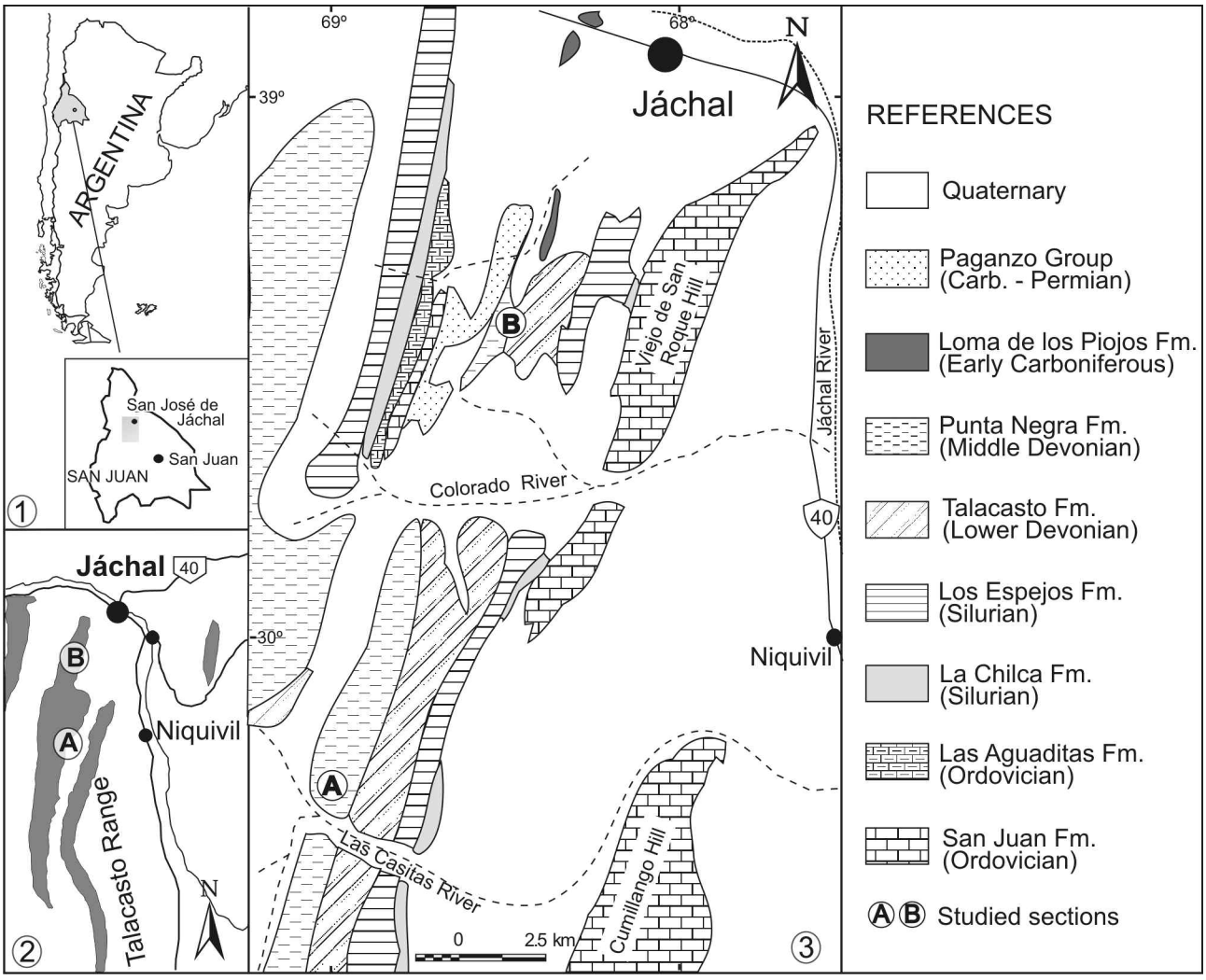

Figure 1. 1-2, Geographic location of the fossiliferous localities. 3, Geologic map showing the studied area: **A**, Las Casitas River; **B**, Loma de los Piojos.

discordance. The succession starts with a thick green pelitic interval, while a sandy coarsening- and thickening-upward interval completes the upper part of the formation. The bivalves were collected from two levels. The lower fossil-bearing bed is characterized by fossil nests dispersed within the pelitic matrix, nearly 45 m above the base. The upper bivalve bearing-level is a thin (10–20 cm) light brownish tabular layer of coarse micaceous sandstone lying 171.5 m from the base (Fig. 2). The associated fauna includes brachiopods, ostracods (Salas *et al.* 2013), crinoids, gastropods, corals and hyolithids, preserved as oxidized molds in the sedimentary plane.

According to Salas *et al.* (2013) this productive level is interpreted as stratigraphically equivalent to the one bearing brachiopods reported by Herrera and Bustos (2001) from the Las Chacritas River section, a few kilometers to the west.

Loma de Los Piojos section

This section is located *ca.* 8 km southwest from the city of Jáchal (30° 18.504' S; 68° 47.399' W). The section of the Punta Negra Formation reaches here a thickness of approximately 310 m, being very similar to that of the Las Casitas River section. Bivalves were recorded 245 m above the base of the formation in a 50 cm-thick bed of greenish dark-grey and slightly micaceous massive mudstones, with frequent 1-3 mm diameter quartz pebbles and oblate nodules. This bed is included in an interval of intercalated greenish-gray sandstones and shales (Fig. 2). This horizon

(fossil locality LP 2) contains an abundant and diverse marine fauna, including trilobites (Rustán and Vaccari, 2010), ostracods (Salas *et al.*, 2013), brachiopods, gastropods, hyolithids, nautiloids, tentaculitids, crinoids, bryozoans and corals, accompanied by plant remains, and trace fossils. In spite of some fragmentation, preservation in this level is usually very good, and fossils are loosely dispersed into the sedimentary matrix and show different orientations.

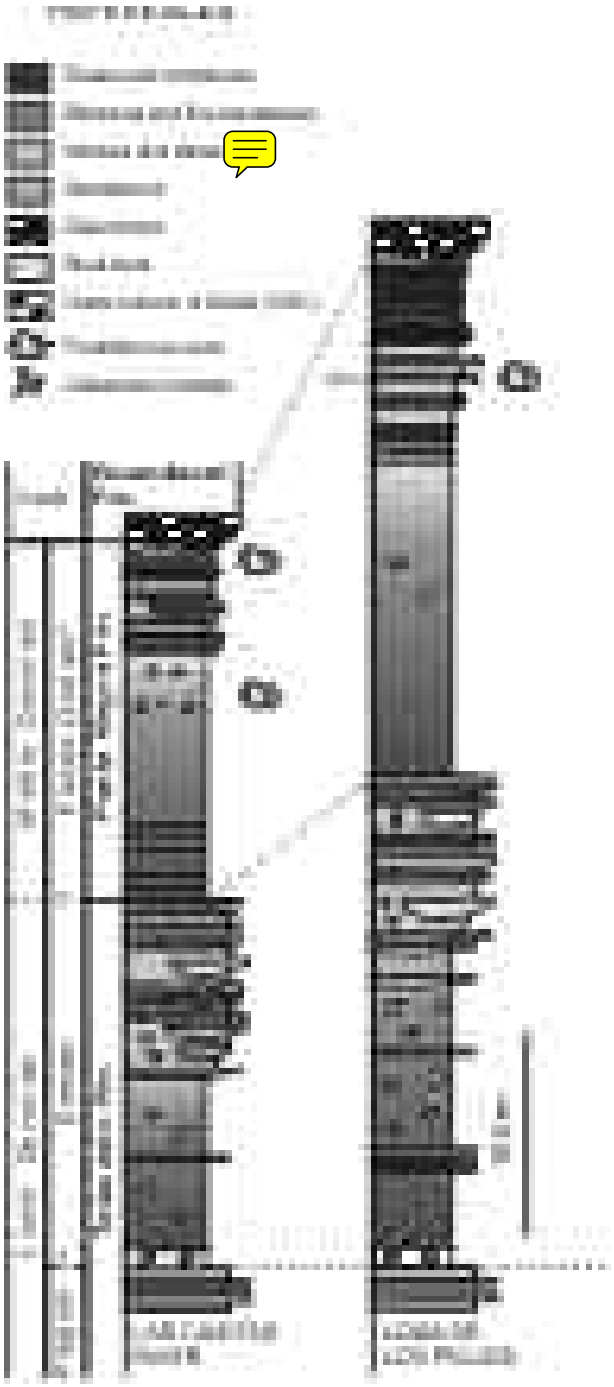

Figure 2. Stratigraphical columns of the Punta Negra Formation in the Las Casitas River and Loma de los Piojos sections.

Salas *et al.* (2013) interpreted this productive level as stratigraphically equivalent to that one in the Las Chacritas River section reported by Herrera and Bustos (2001) and the upper level of the Las Casitas River section (Fig. 1). Salas *et al.* (2013) interpreted a Middle Devonian age for all these levels. This age was based on the trilobite *Acanthopyge* (*Lobopyge*) *balliviani* (Kozłowski, 1923), from productive level LP2 at the Loma de los Piojos section (Rustán and Vaccari, 2010).

MATERIAL AND METHODS

Field-collecting was undertaken checking bed by bed. Specimens are mainly represented by internal and external molds, with only a few retaining the original shell. Fossils were prepared mechanically, using pneumatic vibrators and thin needles. In the case of external casts, latex molds were obtained using black colored latex.

Specimens were coated with ammonium chloride for photography and illuminated with flash light. Images were captured using a Canon Power Shot S50 digital camera mounted on a Leica MZ75 binocular magnifier. The new classification proposed by Carter *et al.* (2011) is adopted here.

Institutional abbreviation. The material is housed in the paleontological collection of the Centro de Investigaciones Paleobiológicas (**CIPAL**) at the Universidad Nacional de Córdoba, Córdoba, Argentina (**CEGH-UNC**).

SYSTEMATIC PALEONTOLOGY

Superorder Nuculiformii Dall, 1889

Order Nuculida Dall, 1889

Superfamily Nuculoidea Gray, 1824

Family Praenuculidae McAlester, 1969

Subfamily Praenuculinae McAlester, 1969

Genus ***Praenucula*** Pfab, 1934

Type species. *Praenucula dispar expansa* Pfab, 1934. Middle Ordovician, Czech Republic.

Praenucula sp.

Figures 3.2–4, 7

Material. Three left valves and three right valves preserved as internal or composite molds. Figured specimens are three: CEGH-UNC 25691, 25692, 25693. Additional non figured specimens are CEGH-UNC 25964a, 25964b and 25695.

Geographic and stratigraphic occurrence. Upper part of the Punta Negra Formation, (level LP2), in the Loma de los Piojos section (Fig. 2), Argentine Precordillera.

Description. Shell small, outline subtriangular or subovate. Subtriangular specimens with anterior and posterior margins sharply rounded and short cardinal margin. Subovate specimens with marked anterior elongation. Inflation moderate to strong, with a maximum near the umbo. Umbo narrow, prominent and opisthogyrous, incurved above dorsal margin and placed one-third of the shell length from the posterior margin. Umbonal slopes pronounced and rounded. Resilifer absent. Continuous teeth below the umbo. Anterior and posterior teeth row similar in length and in teeth-size. External teeth convex and internal teeth straight, in both series. Hinge fully preserved only in three specimens: CEGH-UNC 25961 with eight teeth in the anterior row and seven in the posterior one, CEGH-UNC 25962 with seven teeth in the anterior row and six in the posterior, and CEGH-UNC 25963 exhibiting four teeth in each row. Muscle scars unknown. Shell sculpture not preserved. See dimensions in Table 1.

Discussion. Several discussions were performed about *Praenucula* and its similarity with *Praeleda* Pfab, 1934, and *Deceptrix* Fuchs, 1919 (Bradshaw, 1970; Pojeta, 1978; Tunnicliff, 1982; Babin and Gutiérrez-Marco, 1991; Cope 1997, 1999; Kříž and Steinová, 2009). McAlester (1968, 1969) proposed *Deceptrix* as senior synonym of *Praeleda* and agreed on the differentiation of the genera *Praenucula* and *Deceptrix* based on the characters of the teeth row. In *Praenucula* the anterior and posterior teeth are similar in size and number, while in *Deceptrix* the posterior teeth are smaller and more numerous than the anterior. Moreover, according to Tunnicliff (1982) the umbo in *Praenucula* is placed in the posterior half, while in *Deceptrix* it usually lies in the anterior half. Babin and Gutiérrez-Marco (1991) were of the same opinion.

Different is the classification of Cope (1997), who in several occasions discussed some Ordovician palaeotaxodonts. In this sense, Cope (1997) proposed the generic name *Homilodonta* Cope, 1997 for some of the gradidentate praenuculid palaeotaxodonts which had been figured under the name *Deceptrix* by other authors. In this paper we adopt the conservative criterion of McAlester.

In Punta Negra Formation it was possible to recognize both genera, *Praenucula* and *Deceptrix*, based on the umbo and the teeth row. However, a third difference based on the position of the adductor muscle scars was not observed in our material. In spite of the lack of the latter character, our material is assigned to *Praenucula* based on the general shape of the valves and dentition features. The genus *Praenucula* is widely distributed in the Ordovician of Laurentia (Tunnicliff, 1982) and Gondwana, although in basins from South America it has previously been recorded only in the

TABLE 1. Measurements (in mm) of **Praenucula** *sp.*

Specimen		*L*	*H*	*H/L*	*Cx*	*da*	*dp*
CEGH-UNC 25961	*LV*	*3.5*	*3*	*0.85*	*1*	*8*	*8*
CEGH-UNC 25962	*RV*	*9.5*	*6.5*	*0.68*	*2*	*8*	*6*
CEGH-UNC 25963	*LV*	*4.5*	*3.5*	*0.77*	*1.5*	*4*	*4*
CEGH-UNC 25965	*LV*	*4.5*	*3.5*	*0.77*			
CEGH-UNC 25964a	*RV*	*4*	*3.5*	*0.,87*	*1*		
CEGH-UNC 25964b	*RV*	*9*	*7*	*0.,77*	*1.5*		

Abbreviations: ***LV,*** *left valve;* ***RV****, right valve;* ***L,*** *maximum length;* ***H,*** *maximum height;* ***Cx,*** *convexity (one valve);* ***da,*** *anterior teeth;* ***dp,*** *posterior teeth.*

Lipeón Formation (Silurian) by Sánchez (1989). The recognition of *Praenucula* in the Middle Devonian of the Punta Negra Formation represents the youngest record of the genus.

Our *Praenucula* specimens are very similar in shell-outline and dentition to *Praenucula plicata* Sánchez, 1989, from the Lower Silurian in northwestern Argentina (Sánchez, 1989); yet, the lack of preserved muscle scars and ornamentation does not allow a more precise comparison.

Three species from the Silurian of Bolivia were identified by Dalenz-Farjat (2005). *Praenucula quichua* Dalenz-Farjat, 2005, and *Praenucula* sp. 1 (Ludlow–Přídolí) differ from our specimens in shell- outline, number of teeth and major convexity of the shell. Most similar is *Praenucula*? sp. 2 but it can be distinguished from our material by its narrower and more prominent umbo.

The type species *Praenucula dispar* Barrande in Polechová, 2013, from the Middle Ordovician of the Prague

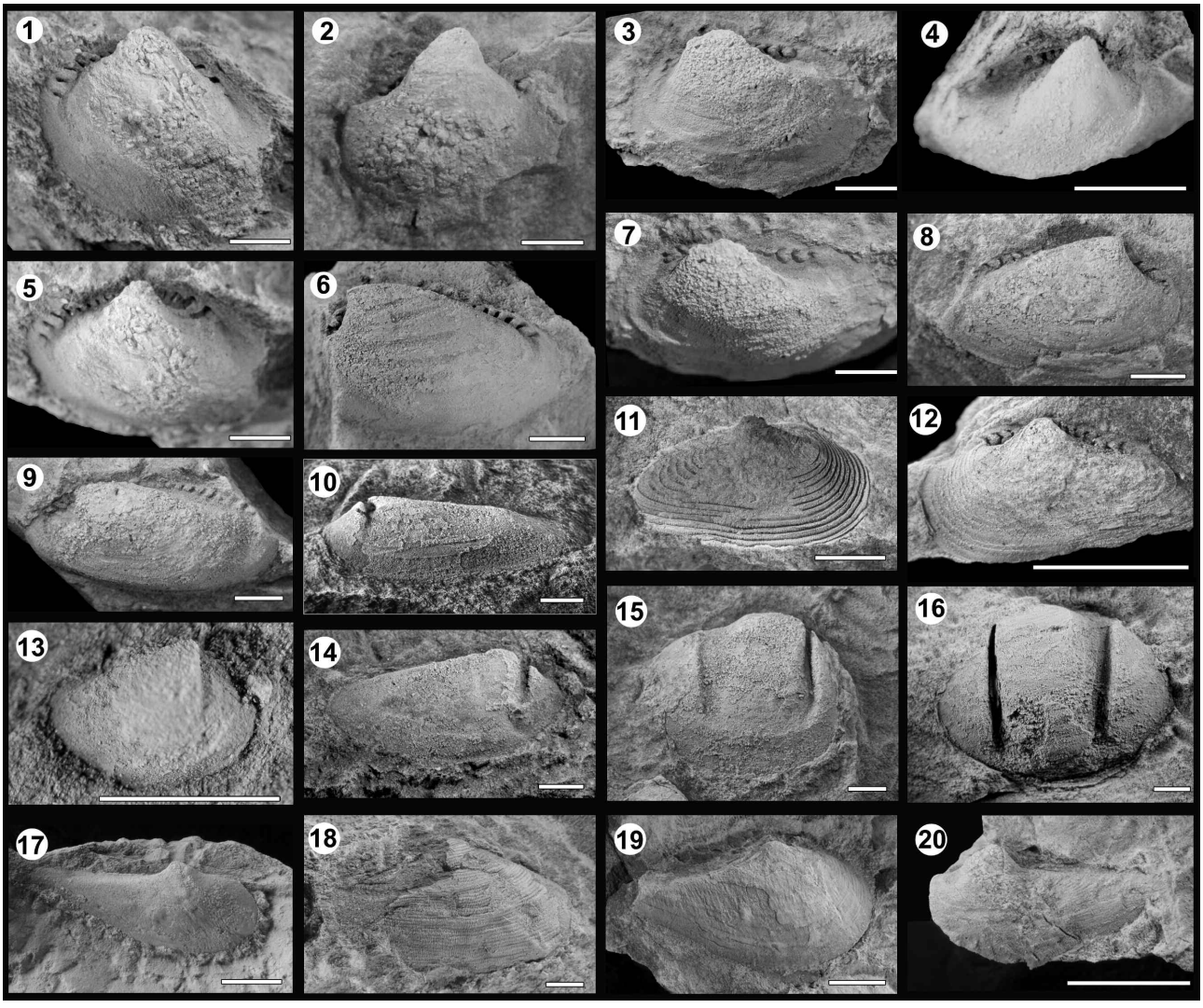

Figure 3. **1, 5–6, 8–9,** ***Deceptrix*** sp., **1,5,** CEGH-UNC 25966, lateral view and dorso-lateral view of internal mold of right valve; **6,** CEGH-UNC 25968, composite internal mould of left valve; **8,** CEGH-UNC 25969, internal mould of right valve; **9,** CEGH-UNC 25967, internal mould of left valve; **2–4, 7** ***Praenucula*** sp., **2,** CEGH-UNC 25961, internal mould of left valve; **3,7,** CEGH-UNC 25962, lateral view and dorso-lateral view of right valve; **4,** CEGH-UNC 25963, internal mould of right valve; **11–12,** ***Praectenodonta*** sp., CEGH-UNC 25973, external and internal mould of left valve; **10, 13–16,** ***Nuculites argentinum*** Sánchez; **10**, CEGH-UNC 25975, composite internal mould of left valve; **13**, CEGH-UNC 25976, internal mould of right valve; **14**, CEGH-UNC 25977, internal mould of right valve; **15**, CEGH-UNC 25978, internal mould of right valve; **16**, CEGH-UNC 25979, internal mould of left valve; **17–20**, ***Anthracoleda (Pseudoleda) minuta*** Sánchez; **17**, CEGH-UNC 25982, internal mould of right valve; **18**, CEGH-UNC 25983, external mould of right valve; **19**, CEGH-UNC 25984, composite internal mould of right valve; **20**, CEGH-UNC 25985, internal mould of left valve. Scale bar= 1 mm (Figures 1-8). Scale bar= 2 mm (Figures 9-20).

Basin, shows a similar shape and dentition, but the muscle scars were not comparable.

Praenucula dispersa Tunnicliff*, P. praetermissa* Tunnicliff and *P. infirma* Tunnicliff, described by Tunnicliff (1982) for the Ordovician of Ireland, differ from the studied material by their smaller size, less elongated shell, more prominent umbo and lower number of teeth.

All in all, until better material is available, we report the species in open nomenclature.

Genus ***Deceptrix*** Fuchs, 1919

Type species. *Deceptrix carinata* Fuchs, 1919, Lower Devonian, Germany.

Deceptrix sp.

Figures 3.1, 5–6, 8–9

Material. Four left valves and four right valves preserved as internal or composite molds, CEGH-UNC. Figured specimens are CEGH-UNC 25966, 25967, 25968, 25969. Additional specimens not figured are CEGH-UNC 25970, 25971, 25972.

Geographic and stratigraphic occurrence. Upper part of the Punta Negra Formation (level LP2), in the Loma de los Piojos section (Fig. 2), Argentine Precordillera.

Description. Shell small, regularly inflated and subovate in outline. Dorsal and ventral margins slightly convex, anterior and posterior margins broadly rounded. Umbo moderately prominent, prosogyrate and situated in the forward quarter of the valve. Anterior hinge plate short and broad with 4–5 large teeth. Posterior hinge plate long with about 17 teeth. Teeth of the anterior set scarcely bigger than those of posterior set. In both series, teeth become smaller near the umbo. Dentition unknown below the umbo. Some specimens preserved part of the shell showing fine and regular commarginal ridges. Other characters unknown due to poor preservation. See dimensions in Table 2.

Discussion. The studied material is assigned to *Deceptrix* Fuchs, 1919, mainly because of the subovate outline of the shell and features of the plate hinge: dentition continuous below the umbo, with few and large anterior teeth and numerous and small posterior ones (McAlester, 1969). The genus *Deceptrix* is typically Devonian, although its record reaches back to the Middle Ordovician. In South America *Deceptrix* is found in Silurian levels of Bolivia (Pojeta *et al.*, 1976), Venezuela (Arnold and Smith, 1964; Sánchez, 1985), northwestern Argentina (Sánchez, 1989, 1991); and in the Lower Devonian of the Talacasto Formation in the Argentine Precordillera.

Sánchez *et al.* (1995) defined the Subgenus *Devonodeceptrix* Sánchez based on the zigzag pattern of shell ornamentation, and placed those species exhibiting a regular commarginal ridge sculpture in the Subgenus *Deceptrix* Fuchs. The particular zigzag sculptural pattern is clearly observable in specimens that retain recrystallized parts of the shell, such as those from the Talacasto Formation at Loma de Los Piojos (see fig. 3.2 in Sánchez *et al.*, 1995). The material recorded in the Punta Negra Formation is similar to *Deceptrix (Devonodeceptrix) jachalensis* Sánchez, 1995, in general outline and dentition, but the new specimens show a smaller size and the ornamentation is virtually unknown

TABLE 2. Measurements (in mm) of* Deceptrix *sp.

Specimen		*L*	*H*	*H/L*	*Cx*	*da*	*dp*
CEGH-UNC 25966	*RV*	*8,5*	*6,5*	*0.76*	*2,5*	*5*	*10*
CEGH-UNC 25967	*LV*	*8*	*5*	*0.62*	*2*	*5*	*17*
CEGH-UNC 25968	*RV*	*12*	*8*	*0.66*	*2*		*17*
CEGH-UNC 25969	*RV*	*10*	*6,5*	*0.65*	*1,5*	*3*	*9*
CEGH-UNC 25970	*LV*	*9,5*	*7*	*0.73*	*2*		

Abbreviations: ***LV,*** *left valve;* ***RV,*** *right valve;* ***L,*** *maximum length;* ***H,*** *maximum height;* ***Cx,*** *convexity (one valve);* ***da,*** *anterior teeth;* ***dp,*** *posterior teeth.*

because the external surface of the shell is preserved (poorly) in only a couple of specimens.

The material described is substantially different from *Deceptrix elongata* Sánchez, 1989, and *D. subtrigonalis* Sánchez, 1989, from the Lipeón Formation (Lower Silurian) of the Sierra de Zapla, northwestern Argentina (Sánchez, 1989), by its small size, greater elongation and uniformly ovate shape.

Tunnicliff (1982) recognized four *Deceptrix* species in the Lower Ordovician of Ireland, based mainly on internal molds. Among these, *D. regularis* Portlock, 1843, and *D. subtruncata* Portlock, 1843, show a greater similarity of their shell outline with the material studied herein. However, since the muscle scars are unknown, a more accurate comparison was impossible.

According to the internal and external features discussed by Sánchez *et al.* (1995), the material from the Punta Negra Formation is assigned to the genus *Deceptrix.* However, the absence of well-preserved shell does not allow a subgeneric assignment.

Order Solemyida Dall, 1889
Superfamily Solemyoidea Gray, 1840
Family Ctenodontidae Wöhrmann, 1893

Genus ***Praectenodonta*** Philip, 1962

Type species. *Palaeoneilo raricostae* Chapman, 1908; Silurian, Australia.

Praectenodonta sp.
Figures 3.11–12

Material. Internal and external mold of a left valve CEGH-UNC 25973, fragmentary left valve CEGH-UNC 25974.

Geographic and stratigraphic occurrence. Upper part of the Punta Negra Formation (level LP2), in the Loma de los Piojos section (Fig. 2), Argentine Precordillera.

Description. Subovate shell outline, posteriorly elongated and moderately convex. Anterior margin broadly rounded. Ventral margin gently curved, and sharp posterior extremity. Cardinal margin straight to moderately convex. Umbo acute, not prominent, orthogyrous and situated in the anterior half of shell. Continuous taxodont dentition below the umbo. Anterior row shorter than the posterior, including 6 and 9 teeth, respectively. Teeth small and straight near the umbo and large and convex in the external part. External ornamentation of sharp and homogeneous commarginal ridges and very fine radial ribs between ridges. Muscle scars are not preserved.

Dimensions. Length 7,5 mm; height 4 mm; anterior length 3 mm (specimen CEGH-UNC 25973).

Discussion. Based on Babin (1966) and McAlester (1968), our specimens clearly belong to *Praectenodonta* Philip due to the subequilateral outline of the shell, the dentition, and the concentric ornamentation. *Praectenodonta* is a cosmopolitan genus and its record reached the Early Devonian (McAlester, 1969). In the Malvinokaffric Realm the genus is known from the Silurian (Ludlow) of the Precordillera Basin and northwestern Argentina (Sánchez, 1989; Sánchez *et al.*, 1995), and Bolivia (Dalenz-Farjat, 2005). The finding of *Praectenodonta* in the Punta Negra Formation extends the temporal record of the genus up to the Middle Devonian.

The species geographically closest to our material is *Praectenodonta alternata* Sánchez, 1989, from the Lower Silurian of Precordillera and northwestern Argentina (Sánchez, 1989; Sánchez *et al.*, 1995). However, our specimens are distinguished from these by their small size and rows of teeth of different length. In addition, the studied material lacks the typical alternating coarse and fine commarginal ridges, having instead a regular arrangement of fine ridges.

Two species recorded by Dalenz-Farjat (2005) in the Late Silurian (Ludlow) of Bolivia resemble our specimens. The argentinian material is closely related to *Praectenodonta* sp. A from the Catavi Formation, but it differs from the latter by its higher posterior margin and irregular commarginal ridges. Regarding *P. boliviensis* Dalenz-Farjat, 2005, from the Tarabuco Formation, the differences are mainly in the size, general outline of the shell, subcentral umbo and concave-convex shape of the teeth of the bolivian species.

P. attenuata Babin, 1966, from the Middle Devonian of the Armorican Massif differs from our specimen by its subcentral umbo, its rows of teeth of similar length and the alternated commarginal ridges. *P. elegans* (Khalfin, 1948) from the Late Silurian–Devonian in Russia (Krasilova, 1963) and the Devonian in Turkey (Babin, 1973) is different from the studied material because it has a more widely rounded anterior margin and the posterior one lower.

The scarcity and fragmentary preservation of this material only allow a generic assignment.

Superorder NUCULANIFORMII Carter *et al.*, 2011
Order NUCULANIDA Carter *et al.*, 2011
Superfamily MALLETIOIDEA Adams and Adams, 1858
Family MALLETIIDAE Adams and Adams, 1858

Genus ***Nuculites*** Conrad, 1841

Type species. *Nuculites oblongatus* Conrad, 1841; Middle Devonian, United States.

Nuculites argentinum Sánchez in Sánchez *et al.*, 1995
Figures 3.10, 13–16

Material. Several specimens preserved as internal or composite molds of left valves and right valves. Figured specimens are CEGH-UNC 25975, 25976, 25977, 25978, 25979. Additional specimens not figured are CEGH-UNC 25980, 25981.

Geographic and stratigraphic occurrence. Upper levels of the Punta Negra Formation, in the Las Casitas River section, 45m and 171.5 m from the base, and in the Loma de los Piojos section (LP2) (Fig. 2), Argentine Precordillera.

Remarks. Based on the variable shape of the shell and the presence of a myophoric septum, this material was assigned to *Nuculites argentinum*, originally defined by Sánchez in Sánchez *et al.* (1995) from the Los Espejos and Talacasto formations (Ludlow–Emsian). This species is characterized by its outline, which varies from subtriangular to elliptical; by the deep, narrow and strongly marked, variably long anterior septum that extends ventrally from the dorsal margin; and by the posterior septum, only present in some specimens, which is wider and shallower than the anterior one. However, the wide range of variability in the shape of the shelves and presence-absence of posterior septum, are very common features in several species of *Nuculites* (Costa-Machado, 1999 and references cited therein).

The genus *Nuculites* is cosmopolitan and several species have been recorded in all the Gondwanan basins. This report includes the youngest record of *Nuculites* in the Precordillera Basin, reaching the Eifelian–Givetian? in the Punta Negra Formation.

Superfamily NUCULANOIDEA Adams and Adams, 1858
Family NUCULANIDAE Adams and Adams, 1858

Genus ***Anthracoleda*** Benedetto, 1980
Subgenus *Anthracoleda (Pseudoleda)* Sánchez in Sánchez *et al.*, 1995

Type species. *Anthracoleda radiata* Benedetto, 1980, Carboniferous, Venezuela.

Anthracoleda (Pseudoleda) minuta Sánchez in Sánchez *et al.*, 1995
Figures 3.17–20

Material. Two left valves and three right valves preserved as internal and composite moulds and one external mold. Figured specimens are CEGH-UNC 25982, 25983, 25984, 25985. Additional specimens not figured are CEGH-UNC 25986, 25987.

Geographic and stratigraphic occurrence. Upper part of the Punta Negra Formation (level LP2), in the Loma de los Piojos section (Fig. 2), Argentine Precordillera.

Remarks. Features such as the elongate outline and the posteriorly expanded shell, the relatively small size and the ornamentation patterns allow to assign the studied material to *Anthracoleda (Pseudoleda) minuta* defined by Sánchez in Sánchez *et al.* (1995) for the Silurian and Lower Devonian of Los Espejos and Talacasto formations, respectively. The genus *Anthracoleda* was originally defined by Benedetto (1980) for nuculanid species with radial ornamentation from the Carboniferous of Venezuela, although the differences with the genus *Phestia* Chernyshev, 1951 are not clear. Ever since, *Anthracoleda* was only recorded in the Argentine Precordillera by Sánchez *et al.* (1995), who defined the subgenus *Pseudoleda* based on its general shape. The genus *Anthracoleda* needs to be revised, because the differences with the genus *Phestia* are not clear (as previously remarked by Dalenz-Farjat, 2000). The poorly preserved material does not allow a more precise analysis.

COMMENTS ON BIVALVE FAUNAS

Devonian bivalves in South American basins

This new finding in the Punta Negra Formation is the first Middle Devonian (Eifelian–Givetian?) bivalve record from Argentina and the youngest Devonian record from southernmost South America.

The bivalves identified define a scarce and poorly diversified taxodontid assemblage integrated by *Nuculites ar-*

gentinum, *Anthracoleda (Pseudoleda) minuta*, *Praenucula* sp., *Deceptrix* sp. and *Praectenodonta* sp. These five genera have been documented in the Precordillera Basin since the Silurian as typical elements of more diversified associations, according to data from the Silurian Los Espejos Formation and the Early Devonian Talacasto Formation (Sánchez *et al.*, 1995).

Considering that Sánchez and collaborators reported as many as 12 genera from the Silurian–Lower Devonian of the Argentine Precordillera, a preliminary analysis of integrated taxonomic and stratigraphic information suggests a decreasing trend in bivalve diversity in the Precordillera Basin during the Middle Paleozoic. In fact, and despite a strong disparity of available data sources (*i.e.* highly sampled basins such as the Bolivian ones *vs.* other virtually unknown ones such as Malvinas), coeval bivalve associations from other closely related basins seem to exhibit a comparatively higher abundance and diversity. Thus, the most important record of Devonian bivalves in Gondwana comes from Bolivian basins (in the Andean region) with as many as 22 genera, of which nine correspond only to the Lower Devonian and three are only recorded in the Middle–Upper Devonian (Suarez-Riglós and Dalenz-Farjat, 1991; Babin and Dalenz-Farjat, 1993; Dalenz-Farjat, 2000) (Table 3). The Brazilian basins (which include the best intracratonic records), are mainly represented by the Early Devonian Ponta Grossa Formation in the Paraná Basin, from which Clarke (1899), Morsh (1983, 1984, 1986) and Kotzian (2003) reported a total of 20 genera. The Middle–Upper? Devonian bivalve records from Brazil come from the Amazonas Basin (Pará) and Tujano-Jatobá Basin (NE Brazil), characterized by seven genera, following Clarke (1912) and Costa Machado (1999). In this context, the southernmost extent of the Brazilian Paraná Basin is represented by the poorly known Early Devonian bivalve faunas from Uruguay where seven genera were recorded in the El Durazno Group (Méndez-Alzola, 1938; Sprechmann *et al.*, 1993). With regards to the Antarctic bivalves 12 Early Devonian genera were described from the Horlick Formation (McAlester, 1965; Bradshaw and McCartan, 1991). There are also seven bivalves identified in Early to Middle Devonian sediments of the Fox Bay Formation in the Islas Malvinas by Clarke (1913), Baker (1924) and Cocks *et al.* (1998, in Aldiss and Edwards, 1999). With respect to South Africa, 16 genera were recorded in the Bokkeveld Group (Emsian–lower Givetian), only five reach the Upper Devonian (Witteberg Group, upper Givetian–Famennian) (Reed, 1925; Hiller, 1990). In Venezuela, the Devonian Cachiri Group includes 17 genera (Sánchez *et al.*, 1995 and references therein), with five and six genera in the Middle and Upper Devonian, respectively (Benedetto, 1979; Sánchez and Benedetto, 1983) (Table 3).

As mentioned earlier, although our information seems to suggest a pattern of decreasing bivalve diversity throughout the Middle Paleozoic in the Precordillera Basin, in our opinion this could be apparent. The Middle Devonian bivalve assemblage reported herein is exclusively composed by shallow infaunal deposit-feeders with no participation of deep infaunal nor byssate epifaunal taxa typical of the Lower Devonian of Precordillera (e.g. *Actinopteria* Hall, 1884) which indicates an important ecological bias. In addition, it must be noticed that except for a couple of specimens coming from the Las Casitas River section, virtually all the material reported in this contribution has been collected in only one section, Loma de Los Piojos (LP2 level) (Fig. 2). According to sedimentological and stratigraphic features (see Geological setting), this section might correspond to turbid waters and muddy bottom conditions, environmentally related to important supplies of organic matter (noticeably plant remains) probably with fluvial (*i.e.* deltaic) influence (Bustos, 1996; Bustos and Astini, 1997; Edwards *et al.*, 2009). Hence, and because knowledge on the entire Devonian bivalve faunas from Argentina is still in a preliminary stage, further conclusions on comparative bivalve diversity among different basins as well as diversity trends, should be interpreted cautiously, based on the data reported herein and those reported by Sánchez *et al.* (1995).

Affinities of the bivalve and associated fauna

Regarding paleobiogeographic implications, the bivalves of the Punta Negra Formation should be interpreted in the context of the Malvinokaffric Realm, a major marine Early–Middle Devonian Southern Circumpolar region (including basins from southern South America, South Africa and Antarctica). This Realm is characterized by a high level of supra-generic endemic taxa and scarcity (or absence) of some typical Paleozoic groups such as stromatoporoids, graptolites and conodonts (Boucot and Racheboeuf, 1993). Following pioneering proposals by Clarke on the "austral"

TABLE 3. Devonian bivalve genera from Antarctica and South America localities. Data from: (1) Sánchez et al. *(1995) and this work; (2) Branisa (1965), Suarez-Riglos and Dalenz-Farjat (1991); Babin and Dalenz-Farjat (1993), Dalenz-Farjat (2000); (3) Clarke (1912, 1990), Morsh (1983, 1984, 1986), Kotzian (2003); (4) Reed (1908, 1925), Hiller (1990); (5) Méndez-Álzola (1938), Sprechmann* et al. *(1993); (6) McAlester (1965), Bradshaw and McCartan (1991); (7) Clarke (1913), Baker (1924), Cocks* et al. *(1998), Aldiss and Edwards(1999); (8) Benedetto (1979), Sánchez and Benedetto (1983).*

Devonian genera in different basins	*Argentine Precordillera (1)*		*Bolivia (2)*		*Brazil (3)*		*South Africa (4)*		*Uruguay (5)*	*Antarctica (6)*	*Malvinas (7)*	*Venezuela (8)*	
	Lower	*Middle*	*Lower*	*Middle*	*Lower*	*Middle*	*Lower*	*Middle*	*Lower*	*Lower*	*Lower-Mid.e*	*Lower*	*Middle*
Allorisma?	x												
Andinomorpha			x										
Anthracoleda	x	x											
Cardiola			x	x			x	x					
Cardiomorpha			x	x	x	x	x	x			x		
Cypricardella						x							x
Cypricardinia												x	
Deceptrix	x	x											
Edmondia					x								
Glossites	x				x		x			x			
Goniophora							x		x			x	x
Grammysia			x		x		x	x		x			
Grammysioidea	x				x								
(L) Leiopteria					x								
(L) Leptodesma			x										
Modiomorpha	x		x	x	x	x	x	x	x	x	x		
Mytilarca										x			
Notonucula				x	x	x				x			
Nuculana/Phestia	x		x	x	x	x	x	x	x				
Nuculites	x	x	x	x	x	x	x	x	x	x	x		
Nuculoidea	x												
Orthonota					x			x		x			
(P) Actinopteria	x		x				x	x		x		x	x
(P) Ptychopteria			x										
Palaeosolen										x			
Paleoneilo	x		x	x	x	x	x	x	x	x	x		
Pholadella	x		x	x	x	x							
Pleurodapis			x	x	x				x				
Praecardium			x				x	x					
Praectenodonta		x	x										
Praenucula		x											
Prothyris/Paraprothyris			x	x	x	x	x	x		x			
Pseudoaviculopecten				x								x	x
Pterinopectinidae												x	
Sanguinolites			x		x	x	x	x					
Solemyacea			x	x	x		x	x	x		x		
Sphenotomorpha			x		x	x	x	x					
Sphenotus							x	x					

signature of its faunas, the Malvinokaffric Realm was formally proposed as a Devonian biogeographic province by Richter and Richter (1942), based on a noticeable endemic distribution of trilobites and later recognized as a Realm considering distribution of other well-known groups such as brachiopods (Boucot, 1975). Ever since, discussions have been focused on the evolutionary and geographical origin of its faunas and proposals of provincial biogeographic divisions.

Preliminary conclusions about the Early Devonian bivalve associations from the Argentine Precordillera reported by Sánchez *et al.* (1995), accounted for a strongly cosmopolitan paleobiogeographic signature. This fact is remarkable since even the most geographically related basins in South America exhibit a pronounced Malvinokaffric endemism in Early Devonian bivalve faunas. For example, endemic or typically Malvinokaffric genera such as *Pleurodapis* Clarke, 1913, from Bolivia, Brazil, Venezuela and Ghana; *Notonucula* Bradshaw, 1991, from Bolivia, Antarctica and New Zealand; and *Andinomorpha* Dalenz-Farjat, 2000, from Bolivia (Saul *et al.*, 1963; Morsch, 1986; Bradshaw and McCartan, 1991; Dalenz-Farjat, 2000), have not been recognized so far in the Precordillera Basin. In the Pragian–Emsian of Bolivia, Dalenz-Farjat (2000) observed the highest endemism in the basin and proposed migratory routes between Bolivia, Brazil, Uruguay, and South Africa. Malvinokaffric affinities are also recognized during the Early Devonian in Antarctica and New Zealand (Bradshaw and McCartan, 1991).

With respect to the bivalve assemblage reported herein, it includes one Gondwanan genus (*Anthracoleda*, known only from Argentina and Venezuela), while the remaining genera exhibit undoubted global distribution. Therefore, a strong cosmopolitan biogeographic signature is also recognizable in bivalves from the Early and Middle Devonian of the Argentine Precordillera.

The biogeographic information coming from the studied area derived from other taxonomic groups besides bivalves offers contrasting insights. For example, the paleobiogeographic pattern of the ostracod fauna shows mixed affinities in the Lower Devonian (equivalent to the levels of Sánchez *et al.*, 1995), while the upper Lower and Middle Devonian exhibit a typical Malvinokaffric association (Salas *et al.*, 2013; Salas, 2014). Data on the distribution of Lower Devonian corals also agree with Malvinokaffric affinities (Carrera *et al.*, 2013). In turn, an external faunal influence, mainly from the eastern American Realm, has supported the proposal of a 'mixed area' in the case of the Lower Devonian brachiopod faunas of the Argentine Precordillera (Herrera and Racheboeuf, 1997; Herrera *et al.*, 1998; Isaacson, 2007). Regarding trilobites, although overall endemic signatures cannot be neglected, recent reports have indicated unexpected extra-Malvinokaffric affinities for some aulacopleurids and dalmanitids (Rustán and Vaccari, 2010, 2012), and a true worldwide distribution in some Lower Devonian phacopids (*i.e. Reedops bronni* Barrande, 1846) recorded in the Precordillera Basin (Holloway and Rustán, 2011).

In contrast to the Early Devonian situation, the cosmopolitan pattern might be interpreted as a fading Malvinokaffric biogeographical signal in taxonomic composition of faunas from these basins during the Middle–Upper Devonian. This phenomenon has been discussed in relation with the time and causes of the disappearance of the Malvinokaffric Realm as a main Devonian paleobiogeographic division. It has been linked to the major mass extinction related to the Frasnian–Famennian boundary (Copper, 1977; Isaacson, 1978). Other arguments frequently cited in favor of the fading of the Malvinokaffric Realm are a tempering of waters linked to climatic amelioration along with rising sea level allowing faunal exchange (Boucot and Theron, 2001; Isaacson, 2007; Pinto Bosetti *et al.*, 2010, 2012). In this regard, for example, a strong extra-Malvinokaffric influence has been noticed in bivalve faunas from Andean South America since the late Emsian to Givetian (Dalenz-Farjat, 2000, p. 337). The study by Costa-Machado (1999) shows a similar trend in *Nuculites* during the Devonian in Brazilian basins.

However, although more information is needed, we hypothesize that the cosmopolitan character of Devonian bivalve assemblages from the Argentine Precordillera can be interpreted in light of a unique history driving biogeographic processes affecting different taxonomic groups in different ways. This argument was already cited for proposing that the term "Malvinokaffric" should be restricted to trilobites, while brachiopods had to be excluded due to their contrasting boreal-linked biogeographic pattern (Baldis, 1979). So, although the causes are not clear, we interpret that this

phenomenon is especially recognizable in bivalves from the Middle Devonian in the Precordillera Basin. In our opinion, their cosmopolitan pattern distribution is not related to a process of "dilution" of a Malvinokaffric faunal composition during the Middle Devonian. Evidences against this alternative explanation include classic and well-known Malvinokaffric Middle Devonian faunal records from upper Icla and Belén formations in Bolivia, Maecurú and Pimenteiras formations in Brazil and Voorstehoek and overlying formations from South Africa. In the particular case of the Argentine Precordillera, an undoubtedly Malvinokaffric affinity is demonstrated during the Middle Devonian by calmoniids trilobites recorded in the Chigua Formation (Baldis, 1967; Baldis and Longobucco, 1977), which from a geochronological point of view is a coeval lateral equivalent of the Punta Negra Formation (Amenábar, 2009). Additionally, as already mentioned, ostracods recorded in the same layers bearing bivalves reported herein suggest a clear Malvinokaffric signature, as was discussed by Salas *et al.* (2013).

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