



New crustacean microcoprolites from the Lower Cretaceous (middle Berriasian–lower Valanginian) of the Neuquén Basin, Southern Mendoza, Argentina

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ABSTRACT

Three new ichnotaxa of crustacean microcoprolites from the Neuquén Basin, Argentina, are described in this paper: *Palaxius rahuensis* Kietzmann n. isp. (early Valanginian), *Palaxius mendozaensis* Kietzmann n. isp. and *Palaxius malarguensis* Kietzmann n. isp. (middle to late Berriasian). In addition, a *Favreina* ichnospecies from the late Berriasian – early Valanginian is reported for the first time for the Neuquén Basin. Controls on the microcoprolite distribution could be related to their biostratigraphic position, sedimentary processes, facies distribution, and diagenesis. Changes in microcoprolite diversity may reflect a shallowing facies trend.

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1. Introduction

Mass accumulations of crustacean faecal pellets are very common in Jurassic and Cretaceous carbonate platforms and ramps settings (Scoffin, 1987; Flügel, 2004). Faecal pellets are mostly produced by gastropods, worms and shrimps (Scoffin, 1987). However, crustacean microcoprolites differ from gastropods and worms pellets because they are internally structured due to the presence of pyloric fingerlets inside the crustacean's gut (Powell, 1974). These structures consist of longitudinal canals that, in cross section, show particular characteristics which allow the discrimination of different taxa (Brönnimann, 1972). Features used for their taxonomic subdivision are the number, shape and arrangement of the internal canals (e.g. Schweigert et al., 1997).

The presence of these particles in the marine successions of the Neuquén Basin can be of enormous interest because it has proved to be useful in paleobiogeographical studies (e.g. Blau et al., 1993; Senowbari-Daryan and Kuss, 1992) and biostratigraphic studies (e.g. Molinari Paganelli et al., 1980, 1986; Senowbari-Daryan and Stanley, 1986; Senowbari-Daryan and Kuss, 1992).

The aims of this paper are to present new ichnospecies of crustacean microcoprolites for the Berriasian and Valanginian of the Neuquén Basin, as well as to discuss their possible biostratigraphic

usefulness in the Jurassic–Cretaceous transition of the basin, based on new material described here and previous studies (Kietzmann and Palma, 2010; Kietzmann et al., 2010). Results could be used for comparison with other localities worldwide so as to provide biostratigraphic implications to the Jurassic–Cretaceous transition of other sedimentary basins of South America, and can contribute to establishing the distribution patterns of crustacean in the Pacific margin of the continent.

2. Geological setting

The Neuquén Basin (Fig. 1) is a retro-arc basin developed in Mesozoic times in the Pacific margin of South America (Legarreta and Uliana, 1991). Their development was controlled by different tectonic regimes (Mpodozis and Ramos, 1990; Legarreta and Uliana, 1991; Ramos and Folguera, 2005), which exerted a first-order control on the sedimentary evolution. During the Late Jurassic and Early Cretaceous a series of marine sequences were developed throughout the basin, grouped under the Mendoza Group (Stipanovic, 1969) or Lower Mendoza Mesosequence (Legarreta and Gulisano, 1989). In the southern Mendoza area the Mendoza Group includes the early Tithonian–early Valanginian Vaca Muerta Formation (Weaver, 1931 *enmend.* Leanza, 1973), the early Valanginian Chachao Formation (Momburú et al., 1978), and the early Valanginian–early Barremian Agrio Formation (Weaver, 1931) (Fig. 2).

This study analyses the deposits of the Vaca Muerta Formation in the southern Mendoza region of the Neuquén Basin. The Vaca

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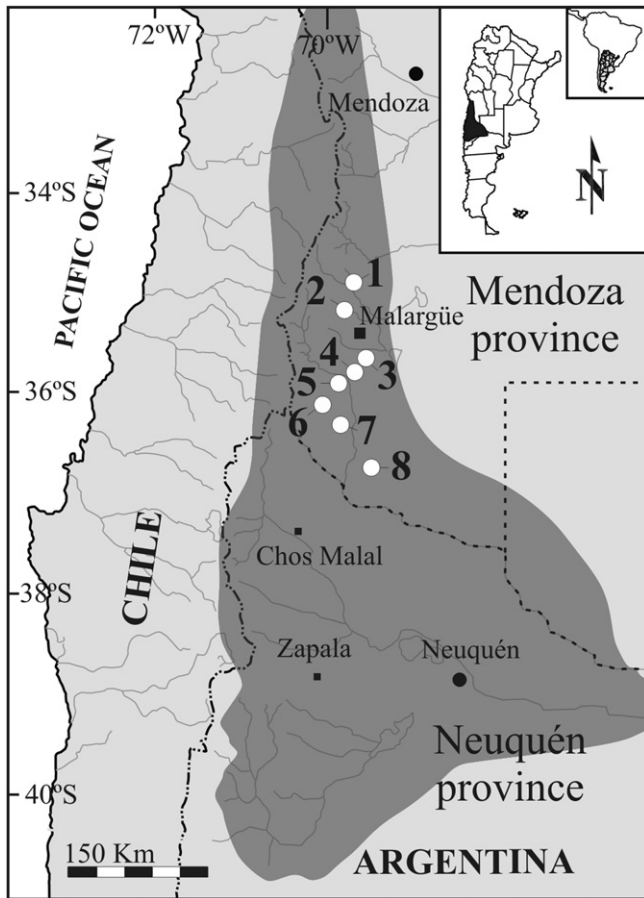


Fig. 1. Location map of the Neuquén Basin showing the studied localities. 1: Tres Esquinas, 2: Salado River, 3: Loncoche creek, 4–5: Bardas Blancas, 6–7: Sierra Azul range (Rahue creek, Yeso creek), 8: Cara Cura range. Modified after Palma et al. (2008).

Muerta Formation is characterized by rhythmic alternation of marls and shales with bioclastic mudstones, wackestones, packstones and floatstones (Kietzmann et al., 2008). These deposits constitute a homoclinal ramp system dominated by basin and outer ramp

Age	Stratigraphy Mendoza area		Sedimentary environment	
Barremian	Mendoza Mesosequence	Upper Mendoza Gr.	outer to inner mixed-carbonate ramp	
Hauterivian				Agrio Fm.
Valanginian				
Berriasian		Lower Mendoza Gr.	basin, outer and middle carbonate ramp	
Tithonian				Vaca Muerta Fm.
Kimmeridgian			fluvial, eolian lacustrine	
		Tordillo Fm.		

Fig. 2. Stratigraphic chart of the Mendoza Group in the Mendoza province.

facies, although they also reach the middle ramp position (Kietzmann et al., 2008; Kietzmann and Palma, 2009a).

3. Studied samples

This study is based on more than 200 thin sections perpendicular to the stratification plane from different locations of the southern Mendoza province (Fig. 1). Systematic determinations were made with a Leica LMP petrographic microscope. The results of this study are part of the microfacies analysis carried out at the outcrops of the Vaca Muerta Formation in the Mendoza province, which were supported on centimetre-scale stratigraphic columns. Facies were defined according to lithologic characteristics, texture, sedimentary structures, geometry, contacts, fossil content, and taphonomic features (e.g. Kietzmann et al., 2008; Kietzmann and Palma, 2009a,b).

Microcoprolites from the Vaca Muerta Formation are found in laminated packstones and wackestones, rich in ammonites, bivalves and radiolarians. These facies are associated with black shales, radiolarian and bioclastic mudstones/wackestones, and storm induced calcareous turbidites (Kietzmann et al., 2008). Microcoprolite preservation is generally poor and the best specimens are found associated with low availability of mud, where the canals can not be filled with micrite. For this reason, it was revised the filling of the ammonite chambers, where the preservation is better (Kietzmann et al., 2010) and stratigraphic position can be established by ammonite zonation, using the schemes of Riccardi et al. (2000) and Riccardi (2008). Selected specimens are housed in the Collection of Palaeontology of the University of Buenos Aires, under the registration numbers CPBA-20675 to 20699.

4. Systematic palaeontology

(by D.A. Kietzmann)

Ichnofamily FAVREINIDAE Vialov, 1978

Ichnogenus FAVREINA Brönnimann, 1955

Type ichnospecies: *Favreina salevensis* (Parejas, 1948)

Remarks: The ichnogenus *Favreina* is characterized by the presence of rounded shaped canals, with a symmetry plane in cross section. It contains 25 known ichnospecies from Triassic to Miocene, but most of the known ichnospecies of *Favreina* are from Jurassic and Cretaceous (Senowbari-Daryan and Kube, 2003; Senowbari-Daryan and Bernecker, 2005; Senowbari-Daryan et al., 2007).

Favreina cf. salevensis (Parejas, 1948)

Fig. 3a

Material: About 30 specimens in thin sections CPBA-N° 20693 and CPBA-N° 20694, Salado River Section, Mendoza province, Argentina (Fig. 1).

Description: In cross section the rod-like microcoprolite has a circular to triangular outline of about 500 µm in diameter. Internally, the coprolite is penetrated by about 26 or 28 canals that show a circular to oval outline in cross section. These are arranged bilaterally to the symmetry plane in two groups; each consisting of 1 folded row of 11 canals, straight close to the symmetry plane and curved toward the periphery. A second row of 3 canals apparently develops in the “central” zone of each group.

Comparison: *Favreina cf. salevensis* is comparable with *F. salevensis* (Parejas, 1948) because of the number of canals and the similar internal arrangement (Fig. 3b–c). According to Parejas

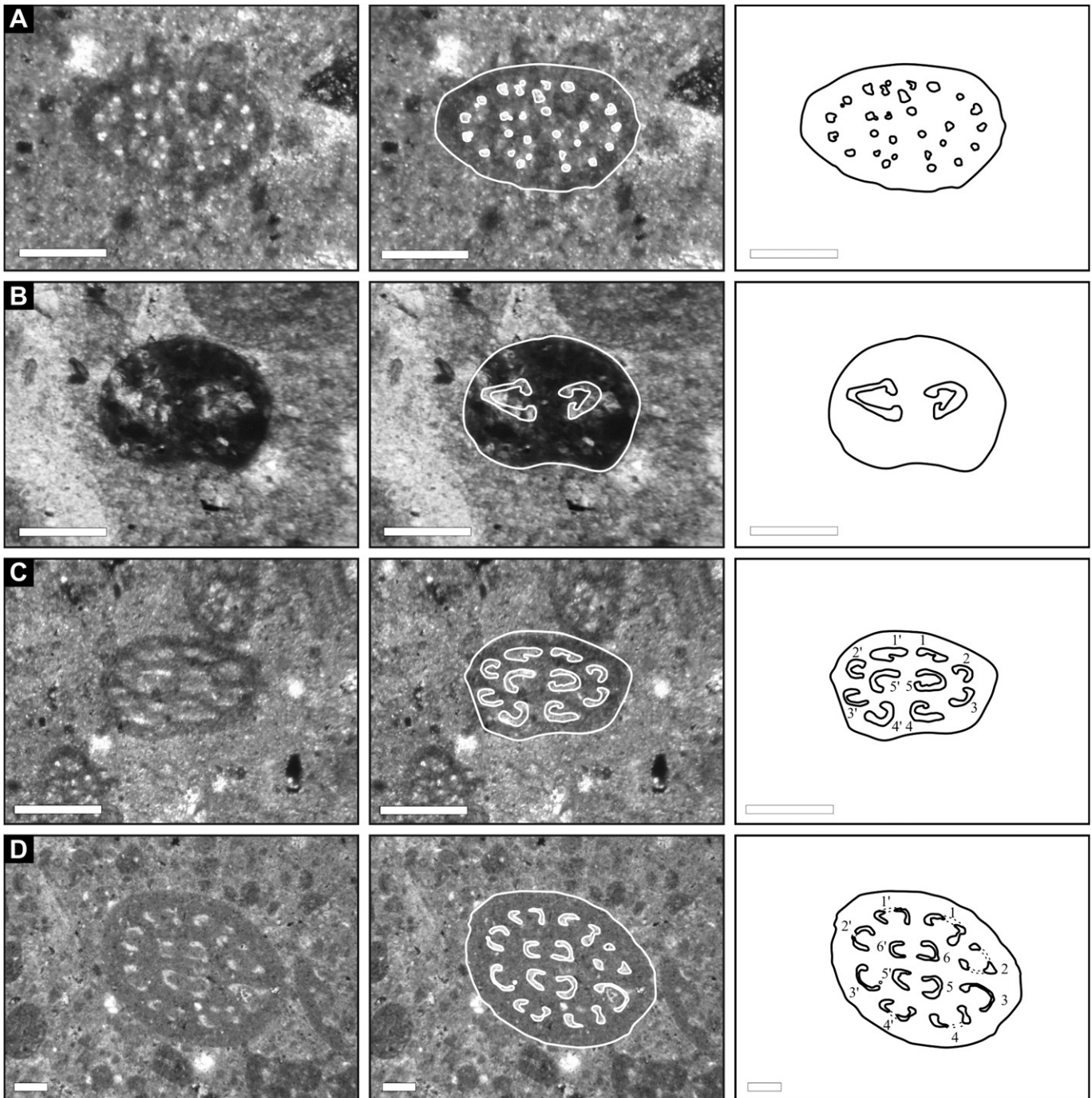


Fig. 3. New crustacean microcoprolites from the Vaca Muerta Formation. (a) *Favreina* cf. *salevensis* (Parejas, 1948), CPBA-20696 (*Spiticeras damesi* Ammonite Zone, upper Berriasian); (b) *Palaxius rahuensis* n. isp., CPBA-20675 (*Lissonia riveroi* Ammonite Zone, lower Valanginian); (c) *P. malarguensis* n. isp., CPBA-20696 (*S. damesi* Ammonite Zone, upper Berriasian); (d) *P. mendozaensis* n. isp., CPBA-20699 (*Argentiniceras noduliferum* Ammonite Zone, middle Berriasian). Scale bar: 200 μ m.

(1948) some extra canals can appear outside the arrangement. However, the preservation state of the studied material does not allow a better classification.

Age and stratigraphic distribution: *Favreina* cf. *salevensis* was recognized at different levels corresponding to the *Spiticeras damesi* Zone (upper Berriasian) and the *Neocomites wichmani* Zone (lower Valanginian) in the Salado River and Tres Esquinas sections of the Vaca Muerta Formation (Fig. 1). *F. salevensis* was originally reported by Parejas (1948) from the Portlandian and Berriasian deposits of

Turkey, but it is known from numerous localities (Molinari Paganelli et al., 1980)

Ichnotaxonomy: Ichnotaxonomy Brönnimann and Norton, 1960

Type Ichnospecies: *Palaxius habanensis* Brönnimann and Norton, 1960

Remarks: The ichnotaxonomy *Palaxius* is characterized by the presence of crescent or hook-shaped longitudinal canals, with a symmetry

plane in cross section (Brönnimann and Norton, 1960; Brönnimann, 1972). It contains 27 known ichnospecies from Late Carboniferous to Miocene, besides the 3 new species described in this paper (see Kietzmann et al., 2010).

Palaxius rahuensis Kietzmann n. isp.

Fig. 3b

Etymology: Named after its occurrence in the Rahue creek section.

Holotype: The specimen shown in Fig. 3b, thin section CPBA-N° 20675.

Type level: At approximately 340 m from the base of the Vaca Muerta Formation, *Olcostephanus* (*Olcostephanus*) *atherstoni* Zone (lower Valanginian).

Locality: Rahue creek, Sierra Azul range, Mendoza province, Argentina (Fig. 1).

Material: Five specimens in thin sections CPBA-N° 20675 and CPBA-N° 20695.

Diagnosis: Species of the ichnogenus *Palaxius* with 2 internal canals clustered around a symmetry plane. The canals exhibit a sharp crescent morphology (hook-shaped) and are oriented with their concave side facing the symmetry plane (Fig. 3).

Description: In cross section the rod-like microcoprolite has a circular outline with ventral groove. Internally, the coprolite is penetrated by 2 longitudinal canals that show a hook-shaped outline in cross section. These are arranged bilaterally to the symmetry plane (1:1) and their concave sides point towards the centre of the coprolite. The internal arrangement is reconstructed in Fig. 3.

Comparison: *P. rahuensis* Kietzmann n. isp. differs from comparable ichnospecies (*Palaxius darjaensis* Silantiev in Senowbari-Daryan and Silantiev, 1991, *Palaxius groesseri* Blau et al., 1993, *Palaxius monteranoensis* Blau and Grün, 1989, and *Palaxius rhomboideus* Brönnimann et al., 1972) in the hook-shaped morphology of the canals, which are oriented with their concave side facing the symmetry plane. Canals in *P. groesseri* and *P. rhomboideus* are oriented with the concave side facing the symmetry plane, while in *P. darjaensis* and *P. monteranoensis* the morphology of the canals are crescent (Fig. 4). Its morphology is comparable with that of *Fundalutum sendjiensis* Masse, 1979 (4 canals), but it is probably that *F. sendjiensis* should also be included as a *Palaxius* species.

Age and stratigraphic distribution: The new species was recognized in levels corresponding to the *Lissonia riveroi* Zone (lowermost lower Valanginian) and *Olcostephanus* (*Olcostephanus*) *atherstoni* Zone (uppermost lower Valanginian) in the Rahue creek section of the Vaca Muerta Formation (Fig. 1).

Palaxius malarguensis Kietzmann n. isp.

Fig. 3c

Etymology: Named after its occurrence in the Malargüe area, Mendoza province.

Holotype: The specimen presented in Fig. 3c, thin section CPBA-N° 20696.

Type level: At approximately 280 m from the base of the Vaca Muerta Formation, *S. damesi* Zone (upper Berriasian).

Locality: Salado River Section, Mendoza province, Argentina.

Diagnosis: Ichnospecies of the ichnogenus *Palaxius* with 10 internal canals clustered around a symmetry plane (2–3:3–2). The “central” canals are oriented with the concave side to the symmetry plane.

Material: Five specimens in thin sections CPBA-N° 20696 and CPBA-N° 20697.

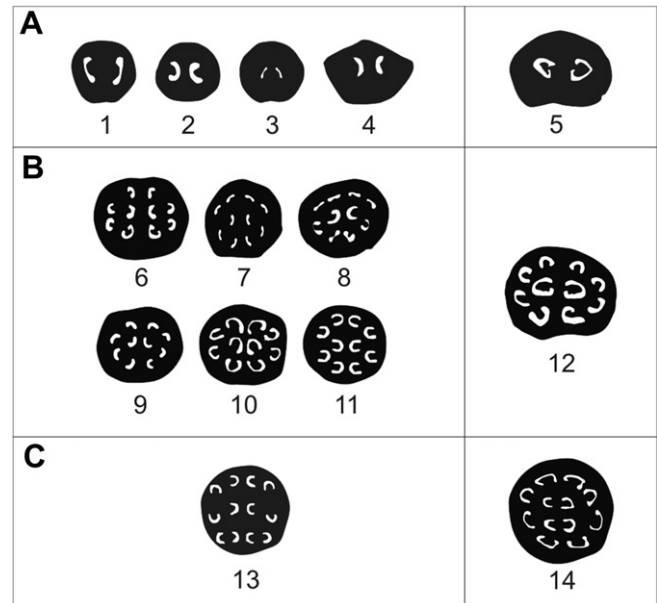


Fig. 4. Schematic diagrams of the different ichnospecies of *Palaxius* compared in this work (not to scale). A) *Palaxius* ichnospecies with two canals: 1, *P. monteranoensis* Blau and Grün, 1989; 2, *P. groesseri* Blau et al., 1993; 3, *P. darjaensis* Silantiev in Senowbari-Daryan and Silantiev (1991); 4, *P. rhomboideus* Brönnimann et al., 1972; 5, *P. rahuensis* n. isp. (this work). B) *Palaxius* ichnospecies with ten canals: 6, *P. colombiensis* Blau et al., 1993; 7, *P. decaochetarius* Palik, 1965; 8, *P. caracuraensis* Kietzmann in Kietzmann et al. (2010); 9, *P. habanensis* Brönnimann and Norton, 1960; 10, *P. decemlunulatus* (Parejas, 1948); 11, *P. decemporatus* Senowbari-Daryan, 1979; 12, *P. malarguensis* n. isp. (this work). C) *Palaxius* ichnospecies with twelve canals: 13, *P. veliensis* Senowbari-Daryan and Vartis-Matarangas, 1989; 14, *P. mendozaensis* n. isp. (this work).

Description: In cross section the rod-like microcoprolite has a circular outline without ventral groove. The holotype has a diameter of 500 μm in cross section. Internally, the coprolite is penetrated by 10 longitudinal canals that show a hook-shaped outline with rounded protuberant extremities in cross section. These are arranged bilaterally to the symmetry plane (2–3:3–2). Canals 1/1' to 3/3' and canal 5/5' are oriented with their concave sides facing the symmetry plane. Canal 4/4' is oriented at 45° respect to the symmetry plane.

Comparison: *P. malarguensis* Kietzmann n. isp. is the only *Palaxius* form with 10 canals with canal 5/5' oriented with their concave sides facing the symmetry plane. It differs also from *Palaxius decaochetarius* Palik, 1965, *P. habanensis* Brönnimann and Norton, 1960 and *Palaxius caracuraensis* Kietzmann (in Kietzmann et al., 2010) in the hook shaped morphology of the canals. In *Palaxius decemporatus* (Senowbari-Daryan, 1979) all canals are oriented with their convex sides facing the symmetry plane; *Palaxius decemlunulatus* (Parejas, 1948) differs in the orientation of canal 4/4', which is oriented 30° respect to the symmetry plane, and canal 5/5', which is oriented with their convex sides facing the symmetry plane at 160°. Finally, *Palaxius colombiensis* Blau et al., 1993 differs in the orientation of canals 1/1' and 5/5', which face with their convex sides the symmetry plane (Fig. 4).

Age and stratigraphic distribution: The new ichnospecies was recognized in levels corresponding to the *S. damesi* Zone (upper Berriasian) in the Salado River and Yeso creek sections of the Vaca Muerta Formation (Fig. 1).

Palaxius mendozaensis Kietzmann n. isp.

Fig. 3d

Etymology: Named after its occurrence in the Mendoza province of Argentina.

Holotype: The specimen presented in Fig. 3d, thin section CPBA-N° 20698.

Type level: At approximately 230 m from the base of the Vaca Muerta Formation, *Argentincerases noduliferum* Zone (middle Berriasian).

Locality: La Tosca creek, Cara Cura Range, Mendoza province, Argentina (Fig. 1).

Diagnosis: Species of the ichnogenus *Palaxius* with 12 internal canals clustered around a symmetry plane (2–4:4–2), with the concave side of the “central” canals facing the symmetry plane (Figs. 3 and 4).

Material: Four specimens in thin sections CPBA-N° 20698 and CPBA-N° 20699.

Description: Cylindrical coprolite with circular outline in cross section and without ventral groove. The holotype has a diameter of 1500 µm in cross section. Internally, the coprolite is penetrated by 12 longitudinal hook-shaped canals arranged bilaterally to the symmetry plane (2–4:4–2). Each group of canals consists of two “external” canals (canals 2/2’ to 3/3’) and four “central” canals (1/1’, 4/4’, 5/5’ and 6/6’). The canals are strong crescent shaped with their concave sides facing the symmetry plane, and show rounded protuberances in their extremities. Canals 1/1’ to 4/4’ are oriented at 45° respect to the symmetry plane. Canals 5/5’ and 6/6’ are oriented at 90° respect to the symmetry plane.

Comparisons: *P. mendozaensis* Kietzmann n. isp. differs from *Palaxius veliensis* Senowbari-Daryan and Vartis-Martarangas (with 12 canals) in the internal arrangement (3–3:3–3) and in the orientation of all canals respect to the symmetry plane (Fig. 4).

Age and stratigraphic distribution: The new ichnospecies was recognized in levels corresponding to the *A. noduliferum* Zone (middle Berriasian), in La Tosca creek section (Cara Cura Range) and

Tres Esquinas section (Atuel depocentre) of the Vaca Muerta Formation (Fig. 1).

5. Discussion

In the Tithonian–Valanginian interval of the Neuquén Basin Kietzmann et al. (2010) observed two informal assemblages of crustacean microcoprolites (MA-1 and MA-3, Fig. 5): one from the middle Tithonian–lower Berriasian, with *P. caracuraensis* Kietzmann, *P. decaochetarius* Palik and *Palaxius* isp. B, and the other from the lower Valanginian, with *Palaxius* isp. A and B, *Palaxius azulensis* Kietzmann, *Helicerina* isp. B and *Helicerina?* isp. A aff. *Helicerina siciliana* Senowbari-Daryan, Schäfer and Catalano. The new material described in this paper allows the characterization of the middle and upper Berriasian interval (*A. noduliferum* and *S. damesi* ammonite zones), which comprise *P. mendozaensis* Kietzmann n. isp., *P. malarguensis* Kietzmann n. isp., *Favreina* cf. *salevensis* (Parejas), and *Helicerina?* isp. A aff. *H. siciliana* Senowbari-Daryan, Schäfer, and Catalano (MA-2, Fig. 5).

Crustacean microcoprolites described in this paper are new ichnotaxa, and therefore their comparison with other records worldwide has not been possible. *Helicerina* ichnospecies were unknown in Upper Jurassic and Lower Cretaceous, while only three *Palaxius* ichnospecies are known from Tithonian–Valanginian in other regions: *Palaxius biserialis* (Kristan-Tollmann), *P. decaochetarius* Palik, and *Palaxius tetraochetarius* Palik. Nevertheless, five *Favreina* ichnospecies have been described for this interval: *F. salevensis* (Parejas), *Favreina guinchoensis* Brönnimann, *Favreina murciensis* Cuvillier, Bassoulet and Fourcade, *Favreina prusensis* (Parejas), and *Favreina tabasensis* Brönnimann (see Molinari Paganelli et al., 1980; Senowbari-Daryan and Kuss, 1992).

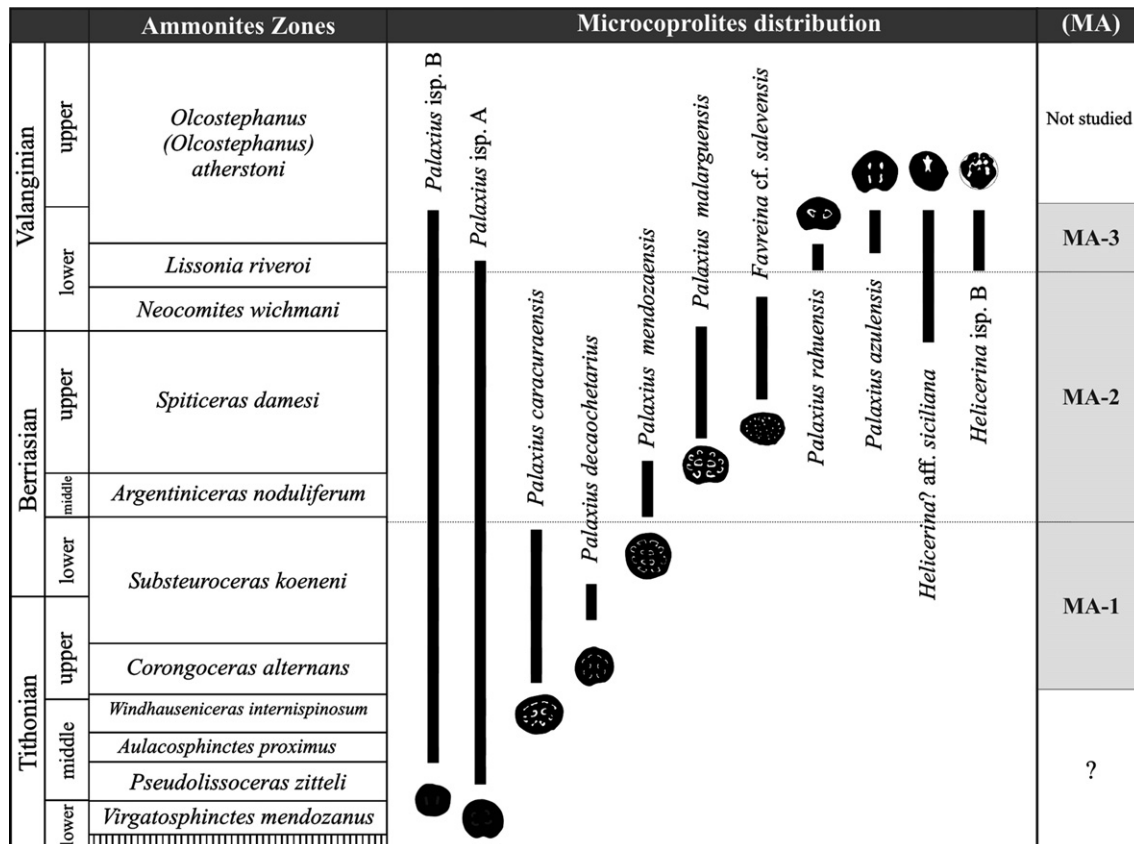


Fig. 5. Microcoprolites distribution in the Tithonian–Valanginian interval of the Neuquén Basin. Ammonite Zones according to Riccardi et al. (2000) and Riccardi (2008), modified after Kietzmann et al. (2010).

Among the crustacean microcoprolites described in South America are those from the Upper Triassic of Peru, including *Palaxius salataensis* Brönnimann, Caron and Zaninetti, *Parafavreina thoronetensis* Brönnimann, Caron and Zaninetti, and *Parafavreina huaricolcanensis* Senowbari-Daryan and Stanley (Senowbari-Daryan and Stanley, 1986), from the Lower Jurassic of Peru, with *P. thoronetensis* and *Favreina peruviansis* Blau, Rosas and Senff (Blau et al., 1994), from the Upper Triassic of Colombia, including *P. grosseri* Blau, Grün and Senff, *P. colombiensis* Blau, Grün and Senff, *P. salataensis* Brönnimann, Caron and Zaninetti, *Payandea shastaensis* (Kristan-Tollmann), *P. thoronetensis*, *Thoronetia quinaria* Brönnimann, Caron and Zaninetti, *Favreina martellensis* Brönnimann and Zaninetti, from the Upper Cretaceous of Colombia, containing *Palaxius caucaensis* Blau, Moreno and Senff (Blau et al., 1995), from the Upper Cretaceous of Venezuela, with *Favreina* isp. (De Romero and Galea-Alvarez, 1995), and from the Upper Jurassic of Chile that contain *Favreina multicanalis* Förster and Hillebrandt (Förster and Hillebrandt, 1984).

The stratigraphic distribution of the different crustacean microcoprolites ichnospecies in the studied interval of the Neuquén Basin suggests some biostratigraphic implications (Fig. 5). Nonetheless, we must take into account the fact that different factors may have influenced the content of the microcoprolite assemblages, such as diagenesis and facial restriction of the producer species.

As proposed by Blau et al. (1993), crustacean microcoprolites could be considered as stratigraphic correlation fossils, since the larvae of the crustaceans can easily migrate through the oceans. The occurrence of morphologically similar microcoprolite taxa in the Late Triassic of Europe, Asia, North America and South America demonstrates an exceptional worldwide biogeographic distribution of decapod crustaceans over the Tethyan and Panthalassan Oceans (Blau et al., 1993; Senowbari-Daryan et al., 2010).

It is also important to point out that crustacean microcoprolites could be useful in local and regional studies (Senowbari-Daryan and Kuss, 1992; Blau et al., 1993; Schweigert et al., 1997). In fact, studies conducted by Senowbari-Daryan (1979) and Senowbari-Daryan and Stanley (1986) have also demonstrated the value of crustacean microcoprolites for the stratigraphic subdivision of Triassic limestones-dominated shelves of Austria and Peru. Similar results were obtained by Senowbari-Daryan and Kuss (1992) for Albian and Turonian limestones of Egypt and Jordan, using different ichnospecies of the genera *Palaxius* and *Favreina*.

An interesting difference that allows to distinguish the assemblage MA-1 from the assemblage MA-2 is the change in the internal pattern of the *Palaxius* ichnospecies. In the “Tithonian” MA-1 the concave sides of the central canals are pointing outwards of the coprolite, while in the “Berriasian” MA-2 they are pointing inside the coprolite. Almost certainly, this difference is due to the presence of different crustacean species for each time interval. Nonetheless, the different ichnospecies of each assemblage could represent different ontogenetic stages of the same crustacean species (see Schweigert et al., 1997). Although this feature should be tested, it could be a good indicator of the Tithonian–Berriasian transition.

The control of the diagenetic processes on the microcoprolites preservation is easily observable (Kietzmann and Palma, 2010), but it is extremely difficult to determine if diagenesis affect the specific content of the assemblages. Neomorphism is an early diagenetic process which implies the loss of the internal structure of microcoprolites. However, this process usually affects the entire muddy deposit so it cannot be considered a determining factor controlling the composition of an assemblage. The only possibility in which neomorphism might influence the composition of the microcoprolite assemblage would be if diverse species were composed of different carbonate mud mineralogy (calcite or aragonite).

Microcoprolites are found in thin sections of laminated and HCS-packstones and wackestones, mostly transported during storms (Kietzmann and Palma, 2010). Transport could have affected the associations by grain size selection due to differential hydraulic behaviour of the different ichnospecies (Pryor, 1975). An additional problem is the mud filling of the internal canals, which could affect more frequently those specimens with larger canals or those where the capillary pressure is higher.

The effect of facial control on MA can be recognized in microcoprolites distribution illustrated in Fig. 5, where a correlation between the shallowing trend and the increasing diversity of crustacean microcoprolites is clearly evident. *Palaxius* ichnospecies seem to dominate the deeper facies, while *Favreina* and *Helicerina* ichnospecies seem to dominate the shallower facies of the carbonate ramp. This problem could be tested in other South American marine basins with more significant facial variations, which is not the case of the Late Jurassic–Early Cretaceous carbonate ramp deposits of the Neuquén Basin.

In summary, the biostratigraphic usefulness of microcoprolite assemblages should be carefully considered, since diagenesis, sedimentary process and facial changes may control the assemblage content. Consequently, its real biostratigraphic value could be only demonstrated by analyzing different sedimentary successions of South America.

6. Conclusions

In this paper three new ichnotaxa of crustacean microcoprolites from the Neuquén Basin are described: *P. rahuensis* Kietzmann n. isp., *P. mendozaensis* Kietzmann n. isp. and *P. malarguensis* Kietzmann n. isp. It is also described for the first time a *Favreina* ichnospecies classified as *Favreina* cf. *salevensis* (Parejas). Excluding the Valanginian ichnospecies (*P. rahuensis* Kietzmann n. isp.), the Berriasian interval of the Vaca Muerta Formation is characterized by the described crustacean microcoprolites.

The Jurassic–Cretaceous transition in the Vaca Muerta Formation could be characterized by a change in the internal pattern of the *Palaxius* ichnospecies. However, the biostratigraphic utility of microcoprolite should be carefully considered, because associations may be controlled by diagenesis, sedimentary process and facial changes.

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