REVISTA DE LA
ASOCIACIÓN GEOLÓGICA
ARGENTINA
www.geologica.org.ar

Volumen 77 (3):
DESARROLLOS RECIENTES EN
ICNOLOGÍA ARGENTINA

Septiembre 2020

Palaxius chosmalalensis n. isp., a new crustacean microcoprolite from the Lower Cretaceous of Argentina and new criteria for the classification of ichnospecies of *Palaxius*

Diego A. KIETZMANN[1,2] and Mariana S. OLIVO[1,2]

[1]Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Geológicas, Ciudad Autónoma de Buenos Aires.

[2]CONICET-Universidad de Buenos Aires, Instituto de Geociencias Básicas, Ambientales y Aplicadas de Buenos Aires (IGeBA).

Email: diegokietzmann@gl.fcen.uba.ar

Editor: Graciela S. Bressan y Diana E. Fernández

Recibido: 12 de mayo de 2019
Aceptado: 2 de agosto de 2019

ABSTRACT

Crustacean microcoprolites are abundant constituents in the Upper Jurassic–Lower Cretaceous of the Neuquén Basin (Argentina). A new record of these particles is described from the lowermost *Olcostephanus* (*O.*) *atherstoni* ammonite Zone (lower Valanginian) in the Mulichinco Formation at Puerta Curacó section, north of the Neuquén province. Coprolites come from shallow-water oyster-dominated biostromes and belong to a new ichnospecies, *Palaxius chosmalalensis* n. isp., which was previously described as *P. decemlunulatus* (Paréjas) from the Upper Cretaceous of Egypt. As a consequence of the description of the new ichnospecies, we propose to incorporate quantitative criteria regarding the angle with which the canals are oriented, as well as its position with respect to the center of symmetry of the coprolite.

Keywords: pellets, Callianassidae, ichnology, Cretaceous.

RESUMEN

Palaxius chosmalalensis *n. isp., un nuevo microcoprolito de crustáceos del Cretácico Inferior de la Cuenca Neuquina, Argentina.*
Los microcoprolitos de crustáceos son constituyentes abundantes en el Jurásico Superior - Cretácico Inferior de la Cuenca Neuquina. Se describe un nuevo registro de estas partículas proveniente de la parte inferior de la Zona de amonites de *Olcostephanus* (*O.*) *atherstoni* (Valanginiano inferior) en la Formación Mulichinco, sección Puerta Curacó, norte de Neuquén. Los coprolitos provienen de biostromas de aguas someras dominados por ostras y pertenecen a una nueva icnoespecie, *Palaxius chosmalalensis* n. isp., que fue previamente descripta como *P. decemlunulatus* (Paréjas) para el Cretácico Superior de Egipto. Como consecuencia de la descripción de la nueva icnoespecie, se propone incorporar criterios cuantitativos con respecto al ángulo con el que se orientan los canales, así como su posición con respecto al centro de simetría del coprolito.

Palabras clave: pellets, Callianassidae, icnología, Cretácico.

INTRODUCTION

Crustacean microcoprolites are common particles in carbonate platforms. Although carbonate marine pellets can also be produced by mollusks or annelids, those produced by crustaceans differ from other fecal pellets by a characteristic internal structuring. They are rod-shaped cylindrical particles traversed internally by longitudinal canals caused by folds of the inner layer of crustacean's intestine (Powell 1974). In cross section, the arrangement, number, and shape of the canals allow their ichnotaxonomic subdivision. Ichnotaxonomy of crustacean microcoprolites was established by Brönimann (1955, 1972) and improved in recent decades, allowing the definition of 12 ichnogenera and more than 80 ichnospecies.

Molinari Paganelli et al. (1980, 1986) showed that this kind of microcoprolites can be used for biostratigraphical purposes. In fact, Blau et al. (1993) obtained good correlations between the Late Triassic of the Tethyan realm and western Gondwana, and Senowbari-Daryan and Kuss (1992) proposed a correlation for the Late Cretaceous of Egypt. More recently, Bujtor (2012) and Jáger et al. (2012) reported some concordance in the temporal distribution of Valanginian species of *Favreina* Brönnimann.

The stratigraphic record of crustacean microcoprolites in South America is fragmentary and restricted to Mesozoic times. They have been reported from the Norian Chambara Formation in central Perú (Senowbari-Daryan and Stanley 1986), the Norian Payandé Formation of Colombia (Blau et al. 1993), the Pliesbachian–Toarcian Condorsinga Formation of Perú (Blau et al. 1994), the Kimmeridgian of Chile (Förster and Hillebrandt 1984), the Tithonian–Valanginian Lower Mendoza Subgroup of Argentina (Kietzmann and Palma 2010a,b, 2014, Kietzmann et al. 2010), the Campanian La Luna Formation of Venezuela (De Romero and Galea-Alvarez 1995), and the Campanian-Maastrichtian Nogales Formation of Colombia (Blau et al. 1995).

In the Neuquén Basin only eleven ichnospecies of microcoprolites were described from early Tithonian-early Valanginian carbonate ramp deposits (Vaca Muerta and Chachao Formations), showing a distinctive stratigraphic distribution (Kietzmann and Palma 2010b, 2014, Kietzmann et al. 2010). A new record of crustacean microcoprolites is described from the lowermost *Olcostephanus* (*O.*) *atherstoni* ammonite Zone (lower Valanginian) in the Mulichinco Formation at Puerta Curacó section, north of the Neuquén province. Coprolites come from shallow-water oyster-dominated biostromes located in the middle member of this unit, and belong to a new species, which was previously reported from the Upper Cretaceous of Egypt as *P. decemlunulatus* (Paréjas) (Senowbari-Daryan and Kuss 1992), and the Middle Jurassic of the Iranian Zagros Zone as *Palaxius* isp. (Motaharian et al. 2014).The increase in the number of ichnospecies in recent years, as well as the comparison between remarkably similar ichnospecies give us the opportunity to review and discuss some of the criteria established for the classification of crustacean microcoprolites.

GEOLOGICAL SETTING AND STUDIED SECTION

The Neuquén Basin was a retro-arc basin developed in Mesozoic times along the Pacific margin of South America (Fig. 1). Its stratigraphy was defined by Groeber (1946, 1953) and Stipanicic (1969), who recognized three sedimentary cycles, i.e. *Jurásico, Ándico* and *Riograndico*. Legarreta and Gulisano (1989) updated this framework and emphasized the importance of eustatic changes in the development of depositional sequences.

Different tectonic regimes exerted a first-order control in basin development and sedimentary evolution (Legarreta and Uliana 1991, 1996). An extensional regime was established during the Late Triassic–Early Jurassic. It was characterized by a series of narrow, isolated depocenters controlled by large transcurrent fault systems filled mainly with continental deposits of the Precuyo cycle (Gulisano 1981, Vergani et al. 1995, D'Elia et al. 2012, 2015, Buchanan et al. 2017).

The Early Jurassic–Late Cretaceous was characterized by a thermal subsidence regime with localized tectonic events. Depocenters were filled by continental and marine siliciclastic, carbonate and evaporite successions (Cuyo, Lotena, and Mendoza Groups; Gulisano et al. 1984, Legarreta and Gulisano 1989, Legarreta and Uliana 1991, 1996, Arregui et al. 2011, Kietzmann et al. 2014, 2016a, b). Under these tectonic conditions, a series of marine sequences were developed throughout the basin during the Late Jurassic–Early Cretaceous. These are included in the Mendoza Group (Stipanicic 1969, Leanza 2009) (Fig. 2). Finally, a compressive deformation regime was established during the Late Cretaceous and lasting throughout the Cenozoic alternating with extensional events (Ramos and Folguera 2005, Ramos 2010).

The Mendoza Group was divided by Legarreta and Gulisano (1989) in three mesosequences (Lower Mendoza, Middle Mendoza, and Upper Mendoza Mesosequences), that should be treated as subgroups according to Leanza (2009) (Fig. 2). The Mulichinco Formation is part of the Middle Mendoza Subgroup, which extends from the Intra-Valanginian unconformity

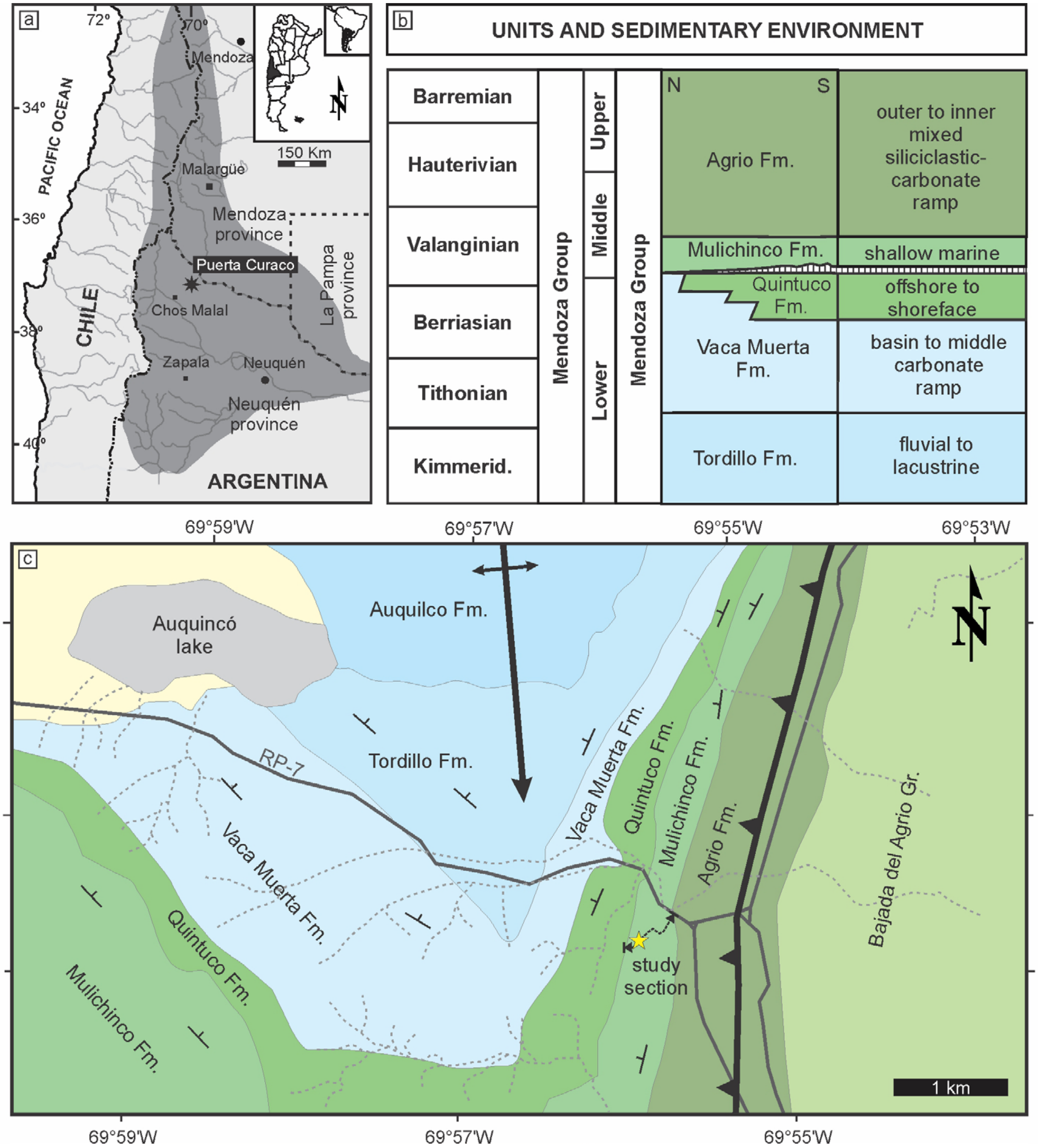


Figure 1. a) Location map of the Neuquén Basin and studied section; b) Stratigraphic chart for the Mendoza Group in northern Neuquén province (modified from Kietzmann et al. 2016b); c) Geologic map of the Puerta Curacó area, showing the trace of the studied section and position of the coprolite-bearing samples (yellow star).

to the Intra-Hauterivian unconformity (Legarreta and Gulisano 1989, Leanza 2009, Schwarz and Howell 2005, Schwarz et al. 2011, 2016). The study area is located in the northern Neuquén province, along the Chos Malal folds and thrust belts, at the classical Puerta Curacó section (Fig. 1), where the Middle Mendoza Subgroup includes mixed siliciclastic-carbonate shallow marine deposits of the Mulichinco Formation, and mixed siliciclastic-carbonate distal marine rhythmic deposits of the Agrio Formation (Fig. 2) (Legarreta and Gulisano 1989, Schwarz et al. 2006, Kietzmann and Paulin 2019).

The Mulichinco Formation in this area was divided into three informal members by Schwarz (1999). The Lower and Upper Members are dominated by siliciclastic sediments, while carbonates are more abundant in the Middle Member. The Lower Member and Upper Members were interpreted by this author as outer shelf to the lower shoreface, whereas the upper member includes upper shoreface facies. The Middle Member is characterized by oyster accumulations interpreted by Schwarz and Howell (2005) as low-energy facies of an epeiric carbonate ramp. The ichnological content of the Mulichinco Formation in the studied area was described by Echevarria et al. (2012) in the Lower Member, who analyzed trace fossils produced by bivalves, and Wesolowski et al. (2017), who examined the ichnology of the Middle and Upper Members with respect to the generation of parasequences.

MATERIAL AND METHODS

The results of this study are part of the microfacies analysis carried out in outcrops of the Mulichinco Formation in the northern Neuquén Province, which are supported on centimeter-scale stratigraphic columns. A detailed sedimentological section of the Mulichinco Formation was measured and described at Puerta Curacó (315 m), in the central Neuquén Basin, along the Chos Malal fold and thrust belt. Facies were defined according to lithologic characteristics, texture, sedimentary structures, geometry, contacts, fossil content, and taphonomic features. Time constraints were based on ammonite biozones published by Schwarz et al. (2011).

More than 40 thin sections were studied following standard microfacial criteria (Flügel 2004) and searched for structured crustacean microcoprolites. In two of these samples, microcoprolites with moderate preservation were found, which allowed their classification. The documented material is housed in the Paleoinvertebrate Collection of the University of Buenos Aires under the collection number CPBA 23720–23721. Specimens were studied using a Leica DM 750 petrographic microscope with attached digital camera. For systematic descriptions, we used the diagnostic features defined by Brönnimann (1955, 1972), which include the number, shape, and arrangement of internal canals, the presence/absence of a ventral cap and size (diameter) of the coprolite. In this work, the orientation angle -measured with respect to the horizontal plane that crosses the centroid- and the position of the canals with respect to the centroid of the coproliteare also included as a criterion for differentiation (see discussion).

SYSTEMATIC ICHNOLOGY

Ichnofamily: Favreinidae Vialov, 1978

Ichnogenus *Palaxius* Brönnimann and Norton, 1960

Type ichnospecies: Palaxius habanensis Brönnimann and Norton, 1960, p. 838-840, Fig. 4a-e, by original designation.

Remarks: *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). For the moment, this ichnogenus contains 29 known ichnospecies from the Early Carboniferous to Pleistocene (Senowbari-Daryan et al. 2017, Gischler et al. 2017), including the new ichnospecies described in this paper.

***Palaxius chosmalalensis* n. isp.**

Fig. 3a-f

1992 *Palaxius decemlunulatus* (Paréjas): Senowbari-Daryan and Kuss, 138–140, p., Figs. 4, 5, Pl. 3-5.

2014 *Palaxius* isp.: Motaharian, Aghanabati, Ahmadi and Meisami, 297, p., Fig. 3G.

Diagnosis: Microcoprolite with circular to oval cross section, without ventral groove, and with ten internal, hook-shaped canals. In cross-section, the pattern of the canals is 2-3:3-2. Canals 1/1' and 4/4' show a specular orientation, facing with their concave sides ~35° down and out of the symmetry plane. Canals 2/2' and 3/3' face with their concave sides towards the center of the coprolite. Canals 5/5' are oriented with their concave faces ~25° down and out of the symmetry plane and are located below the symmetry center (centroid).

Etymology: Named after the geographic occurrence of this ichnospecies in the Chos Malal area.

Type locality: Puerta Curacó Section (37°22'57.48"S, 69°56'0.00"W), Neuquén province, Argentina (Figs. 1 and 2)

Type level: At approximately 110 m from the base of the Mulichinco Formation, *Olcostephanus* (*O.*) *atherstoni* Zone (lower Valanginian) (Fig. 2).

Holotype: Specimen in figure 3a, from the Middle Member of the Mulichinco Formation, CPBA-23720.

Paratypes: Nine specimens from the Middle Member of the Mulichinco Formation (Figs. 3 and 4), CPBA-23720- 23721.

Dimensions in transverse section: Diameter: 1100-1500 µm; Canal length: 150-300 µm; Canal width: 56-70 µm.

Description: Microcoprolite with circular to oval outline in cross-section, without ventral groove. It has a diameter of

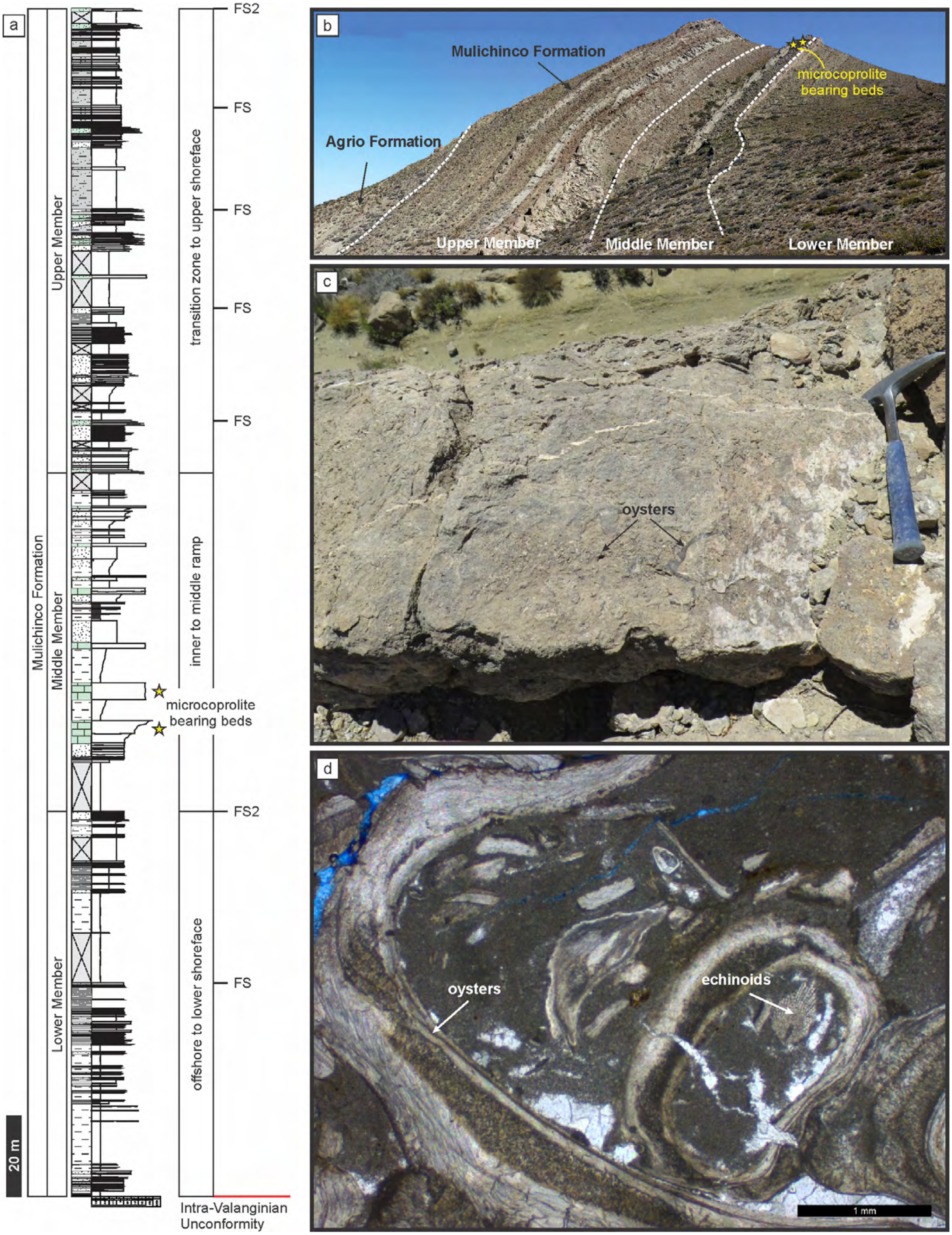


Figure 2. a) Litholog of the Mulichinco Formation at Puerta Curacó section, showing lithostratigraphic units, paleoenvironmental interpretations, and location of the described microcoprolites. Abbreviations: (FS) flooding surface, (FS2) second-order flooding surface; b) General view of the Mulichinco Formation at Puerta Curacó, showing boundaries within the three informal members defined by Schwarz (1999); c-d) Macroscopic and microscopic view of the oyster-dominated biostromes.

1100 to 1500 μm in cross section. Internally, it shows ten canals arranged in two bilaterally symmetric groups of five canals. Each group consists of two "dorsal" canals (canals 1 and 2) and three "ventral" canals (3/3', 4/4' and 5/5'). Canals are hook-shaped and show rounded protuberances in their extremities. Canals are 150 to 300 μm long and 56-70 μm wide. Canals 5/5' are the largest sometimes duplicating in size the other canals. The pattern of the canals observed in cross-section is 2-3:3-2 with the following orientations: canals 1/1' face with their concave sides ~35° down and out of the symmetry plane, canals 2/2' and 3/3' face with their concave sides towards the center of the coprolite, canals 4/4' show a specular orientation to canals 1/1', facing with their concave sides ~35° up and out of the symmetry plane, and finally canals 5/5' are oriented with their concave faces ~25° down and out of the symmetry plane. Canals 5/5’ are displaced downward with respect to the symmetry center (center of the coprolite), being located below it.

Comparison: There are eight other *Palaxius* ichnospecies with ten canals: *P. habanensis* Brönnimann and Norton, *P.dechaochetarius* Palik, *P. colombiensis* Blau, Grün and Senff, *P. malarguensis* Kietzmann, *P. floridanus* Gischler, Blau and Peckmann, *P. decemporatus* Senowbari-Daryan, *P. decemlunulatus* (Paréjas), and *P. caracuraensis* Kietzmann. *P. floridanus*, *P. colombiensis*, *P. malarguensis*, *P. decemporatus*, *P. dechaochetarius*, and *P. caracuraensis* differ clearly in the orientation pattern of the canals (Fig. 5), starting with canals 5/5', which have a different orientation in all of them. *P. caracuraensis* also shows the difference in size of canals 5/5' with respect to the rest of the canals, but it differs in that canals 1/1' and 2/2' are crescent instead of hooked, and that canals 1/1' point towards the center of the coprolite.

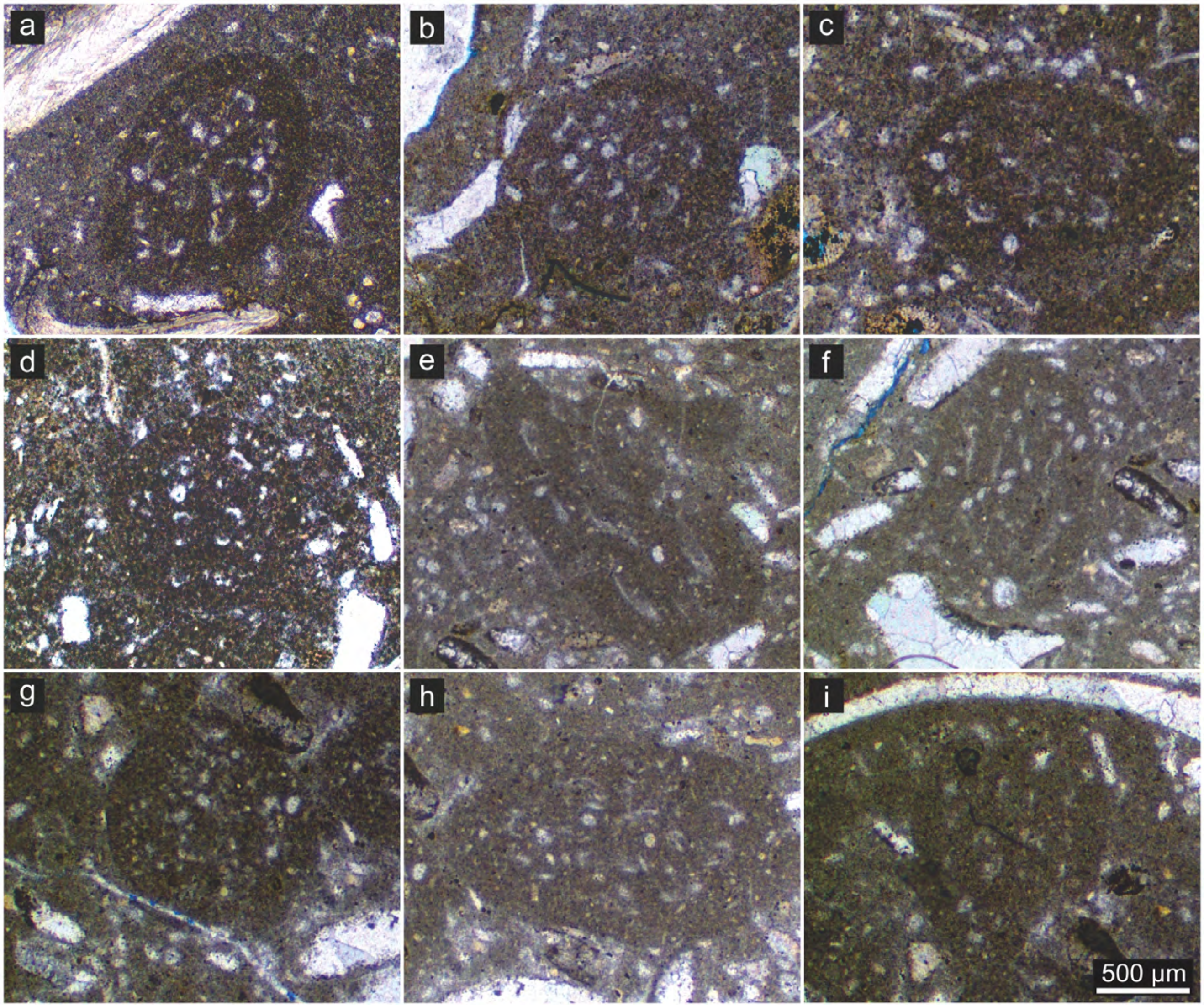


Figure 3. *Palaxius chosmalalensis* n. isp. from oyster-dominated biostromes at Puerta Curacó section, including transversal and oblique sections. a-e) CPBA-23720; f-i) CPBA 23721.

P. habanensis and *P. decemlunulatus* are similar ichnospecies to *P. chosmalalensis* n. isp. It can be separated from *P. habanensis* by the morphology of canals which are crescent-shaped in *P. habanensis* and hook-shaped in *P. chosmalalensis* n. isp., and by the direction of canals 1/1' and 2/2'. In *P. habanensis* canals 1/1' face with their concave sides ~45° down and out of the symmetry plane, and canals 2/2' face towards the symmetry plane instead of the center of the coprolite (Figs. 5 and 6). On the other hand, *P. decemlunulatus* differs in the direction of canals 2/2' and 4/4'. In that ichnospecies canals 2/2' face with their concave sides towards canals 1/1' instead of pointing towards the center of the coprolite, and canals 4/4' face to the center of the coprolite instead of being specular to canals 1/1' (Figs. 5 and 6). That is why the specimens described by Senowbari-Daryan and Kuss (1992) from the Cenomanian of Egypt cannot be assigned to *P. decemlunulatus* (Paréjas) and instead belong to the new ichnospecies described here as *P. chosmalalensis* n. isp.

Occurrence: The studied specimens of *P. chosmalalensis* n. isp. come from the lowermost *Olcostephanus* (*O.*) *atherstoni* ammonite Zone, indicating the uppermost lower Valanginian. However, this ichnospecies was previously reported from the Upper Cretaceous (Cenomanian) of Egypt as *P. decemlunulatus* (Paréjas) by Senowbari-Daryan and Kuss (1992), and the Middle Jurassic (Bathonian) of the Iranian Zagros Zone as *Palaxius* isp. by Motaharian et al. (2014). Therefore, the stratigraphic range of *P. chosmalalensis* n. isp. should be considered as Bathonian–Cenomanian.

SEDIMENTARY PALEOENVIRONMENT

The studied specimens come from oyster-dominated biostromes from the Middle Member of the Mulichinco Formation at Puerta Curacó. Oyster accumulations form tabular bodies (biostromes *sensu* Kershaw 1994) up to six meters thick. Biostromes are internally complex, built by the amalgamation and accretion of shell beds usually separated by erosive contacts. Shell beds consist of coarse-grained bioclastic fabrics (bioclasts > 2 mm) that form massive or graded floatstones to rudstones and cross-stratified rudstones. Bioclasts are dominated by oysters, but other minor components include former aragonitic bivalves, echinoderms, serpulids (*Parsimonia* sp. and *Sarcinella* sp.), gastropods, benthonic foraminifera and dasycladacean algae. Oysters show occasionally bioerosion, are densely-packed, with low to moderate fragmentation, low abrasion, and general chaotic orientation. Some strata show a poorly-defined orientation coinciding with the foresets of cross-stratified facies. Particles are immersed in a sand-sized pelloidal micritic matrix originating fromthe accumulation of crustacean microcoprolites in plastic state.

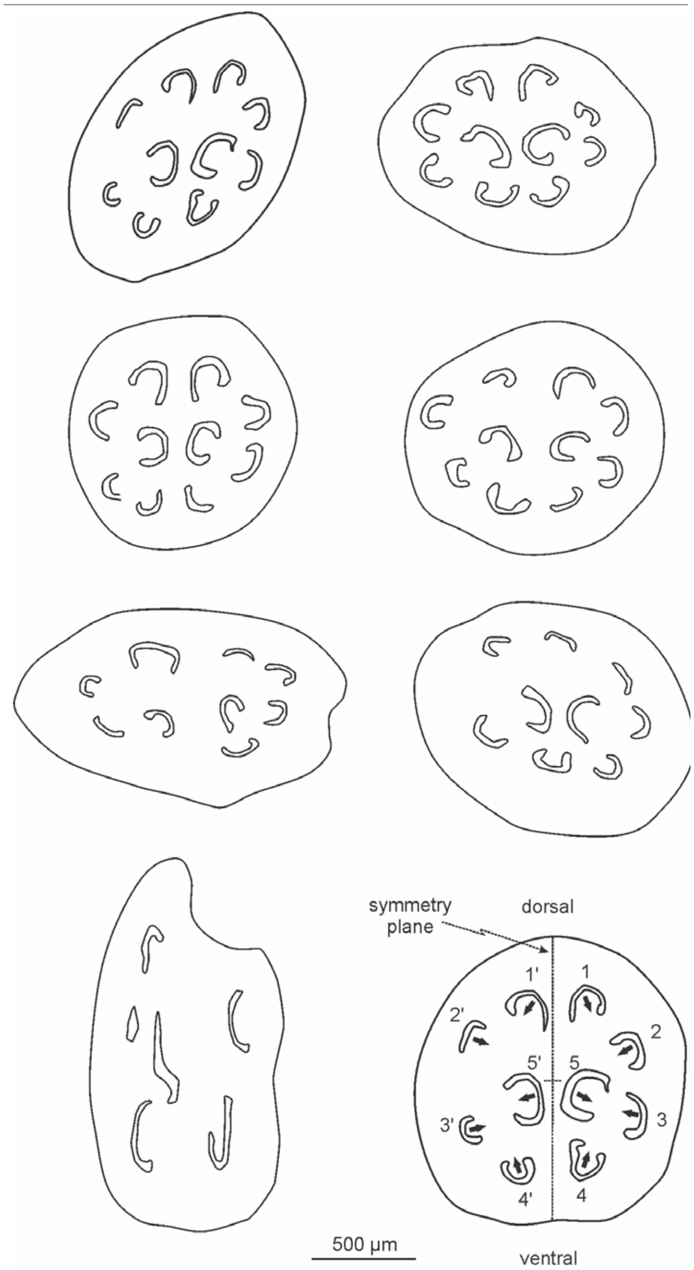


Figure 4. Interpretation schemes of different specimens of *Palaxius chosmalalensis* n. isp. in figure 3. The last scheme (bottom right) corresponds to an idealization that arises from the information of the studied specimens.

Taphonomic features of shell beds, such as moderate fragmentation, dense packing and orientations, as well as graded and cross-stratified deposits, allow us to interpret that oyster biostromes were deposited in a well-oxygenated setting, above the fair-weather wave base in the inner ramp. Cross-stratified deposits are interpreted as accretionary bio-

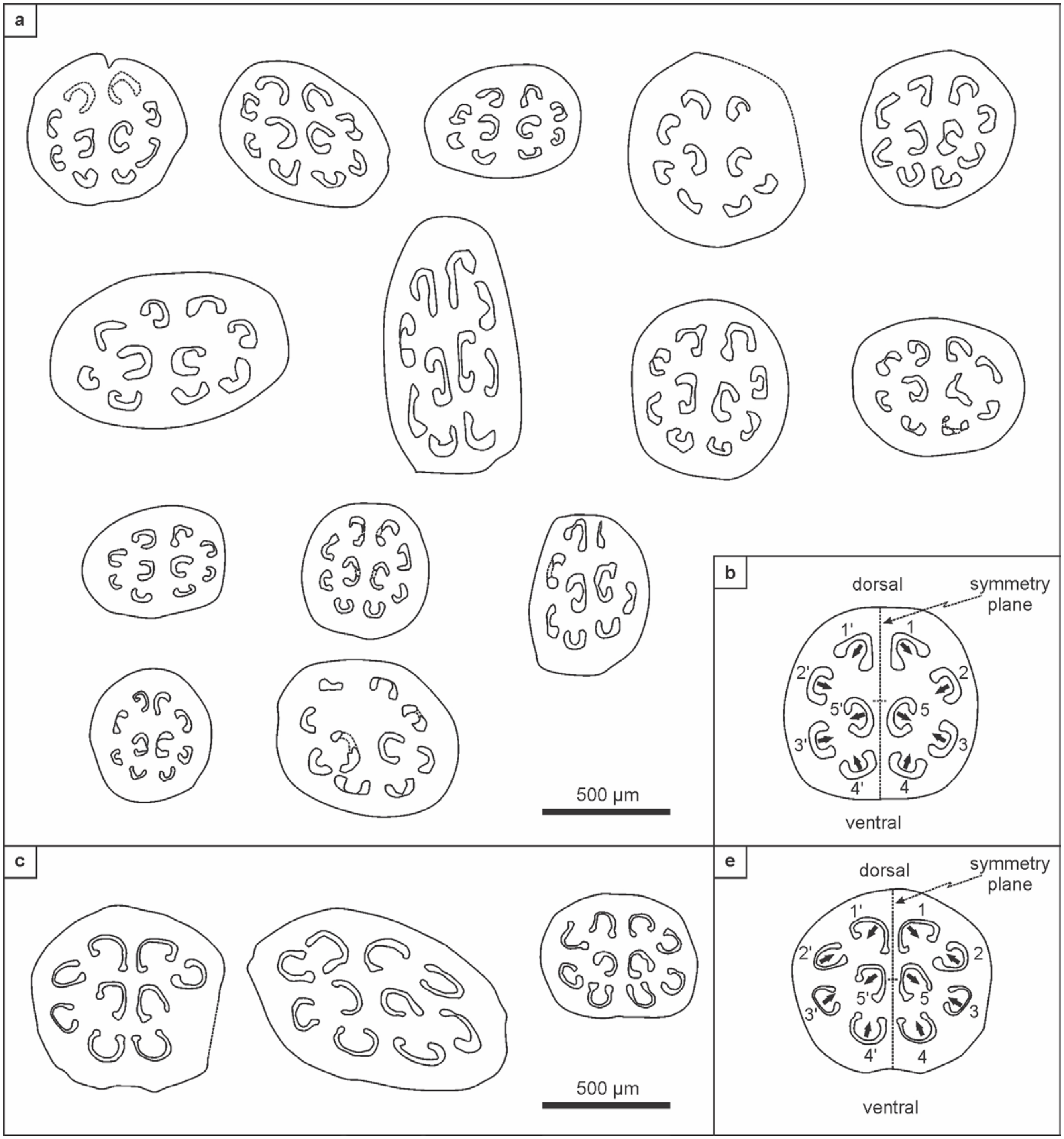
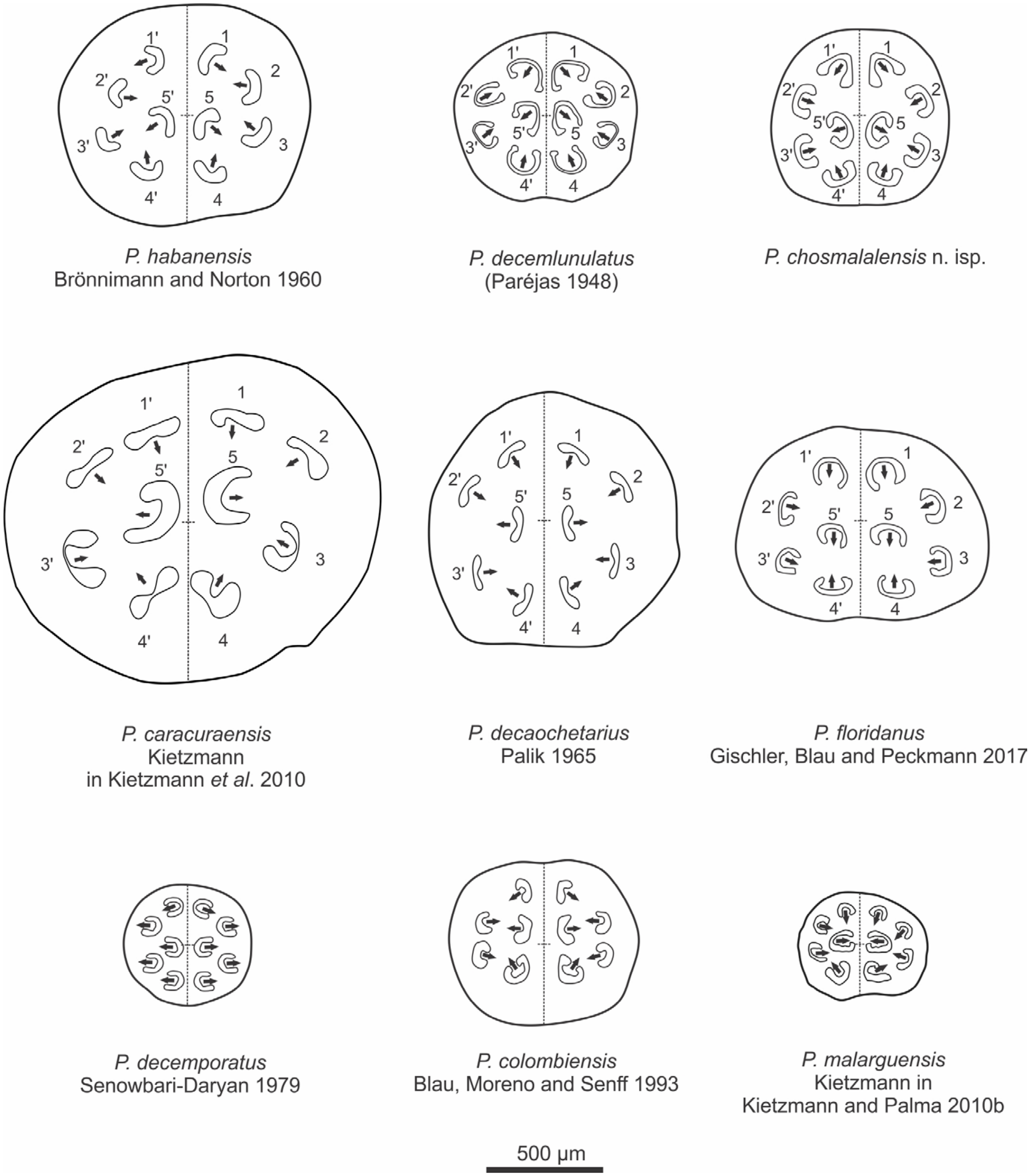


Figure 5. a) Redrawn specimens of *Palaxius* from the Cenomanian of Egypt from microphotographs illustrated in Senowbari-Daryan and Kuss (1992) as *Palaxius decemlunulatus*; b) Idealized scheme that arises from the redraw of the *Palaxius* specimens described by Senowbari-Daryan and Kuss (1992). The type of canals, their arrangement and orientation are the same as that of the described specimens of *Palaxius chosmalalensis* n. isp.; c) *Palaxius decemlunulatus* from the Oligocene of Turkey redrawn after original figure of Paréjas (1948); d) Idealized scheme that arises from the redraw of *Palaxius decemlunulatus* (Paréjas). The similarity of both species is remarkable, but they differ in the orientation of the canals 2/2' and 4/4', and the position of canal 5/5' with respect to the center of the coprolite, which are displaced downward in the new ichnospecies.

clastic bars, and massive and graded floatstone/rudstones as lateral facies of the biostromes, reworked and accumulated by storms. These facies interpretations agree with previous authors (e.g., Schwarz 1999, Schwarz and Howell 2005), which interpret low-energy facies of an epeiric carbonate ramp, where sediment starvation and high stressed marine conditions, favored low-diversity accumulation of oysters.

From these conclusions, we infer that microcoprolites



P. habanensis
Brönnimann and Norton 1960

P. decemlunulatus
(Paréjas 1948)

P. chosmalalensis n. isp.

P. caracuraensis
Kietzmann
in Kietzmann *et al*. 2010

P. decaochetarius
Palik 1965

P. floridanus
Gischler, Blau and Peckmann 2017

P. decemporatus
Senowbari-Daryan 1979

P. colombiensis
Blau, Moreno and Senff 1993

P. malarguensis
Kietzmann in
Kietzmann and Palma 2010b

Figure 6. Comparison of transversal sections of *Palaxius* ichnospecies with ten canals.

probably come from protected areas where the crustaceans where able to proliferate and colonize the substrate. The presence of callianassid crustaceans must have been important, given the abundance of *Palaxius* type fecal pellets. In fact, monospecific suites of *Thalassinoides* are mentioned for this interval by Wesolowski et al. (2018). Pellets were probably transported by tides and storms to the high-energy outer inner shelf, where they were concentrated generating pelletoidal muds.

DISCUSSION

Paleoenvironmental considerations

The new ichnospecies *Palaxius chosmalalensis* is reported so far from the Middle Jurassic of Iran, the Lower Cretaceous of Argentina, and the Upper Cretaceous of Egypt. The specimen described by Motaharian et al. (2014) for the Bathonian of the Zagros Zone comes from the Lower Shaley Unit of the Surmeh Formation (Kaftar section). This unit corresponds to calciturbidite slope facies related to an extensive shallow carbonate platform, which contains mostly platform-derived components including ooids, intraclasts/lithoclasts, peloids, echinoderms, brachiopods, bivalves, foraminifers, and sponge spicules (Jalilian 2010, Lasemi and Jalilian 2010). The specimens from the Mulichinco Formation in the Neuquén Basin were found in oyster dominated biostromes interpreted as inner ramp bioclastic bars. Finally, the specimens described by Senowbari-Daryan and Kuss (1992) come from the upper Cenomanian of Egypt (Galala Formation), that represents shallow mixed siliciclastic-carbonate ramp sequence, associated with ammonites, peloids, calcareous algae (*Halimeda* and *Dissocladella*), as well as ooids, gastropods, echinoderms, serpulids, phosphate grains, steinkerns of gastropods, and other crustacean microcoprolites: *Favreina radiata*, *Fundalutum dakhalensis* (*Palaxius caucaensis*?, see Kietzmann and Palma 2014), and *Palaxius* isp.

From the three available records it can be assumed that the producer of *Palaxius chosmalalensis* n. isp. was a crustacean that inhabited shallow and protected waters, probably the subtidal zone (lagoon) or intertidal zone. Becker and Chamberlain (2006) considered callianassid shrimps as producers of *Palaxius* ichnofossils. Crescentic canals were found in pellets of modern callianassids (Moore 1932, Powell 1974, Pryor 1975), and the association of *Palaxius* with callianassid body fossils was also reported by Peckmann et al. (2007). However, crustacean body fossils from the Mulichinco Formation include scarce lobsters represented by astacideans (*Eryma* and *Hoploparia*) and palinurids (*Meyerella*) (Aguirre Urreta et al. 2008). Although it cannot rule out the presence of callianassids, it is possible that the ichnogenus *Palaxius* was produced by other groups of shrimps or lobsters that inhabited shallow protected waters of the carbonate ramp.

Criteria for the classification of *Palaxius* ichnospecies

The diagnostic features for the classification of crustacean microcoprolites were established by Brönnimann (1955, 1972). At the present time 12 ichnogenera were defined based on (a) type of canal system, (b) morphology of the canals, and (c) presence or absence of a ventral cap. In the case of *Palaxius*, the number and arrangement of the canals are used to differentiate between ichnospecies (Molinari Paganelli et al. 1986, Senowbari-Daryan and Kube 2003). So far 29 ichnospecies of *Palaxius* are known, of which nine ichnospecies have ten canals (Fig. 6).

The arrangement of the canals and the orientation of each canal with respect to the symmetry plane are frequently used for the description and diagnosis of ichnospecies (i.e. Senowbari-Daryan and Kube 2003). However, as the number of species increases, these criteria must be improved. One of the distinguishing features of *P. chosmalalensis* n. isp. is the position of canal 5/5’ with respect to the center of the coprolite (centroid), which are displaced downward. This feature is also observed in the specimens from the Cenomanian of Egypt (Senowbari-Daryan and Kuss 1992) described as *P. decemlunulatus*, but not in the specimens of *P. decemlunulatus* described by Paréjas (1948) (Fig. 5). Also, the Cenomanian specimens of Egypt differ from *P. decemlunulatus* in the orientation of the canals 2/2’ and 4/4’. For this reason, the Egyptian specimens cannot be assigned to P. decemlunulatus, as already noted by Gischler et al. (2017). The redraw and review of the specimens published by Senowbari-Daryan and Kuss (1992) (Fig. 5) show a similar pattern (arrangement 2-3:3-2, position of canal with respect to the centroid of the coprolite, and canals orientation) to the one found in the specimens from the Valanginian of the Neuquén basin. Consequently, it should be assigned to *P. chosmalalensis* n. isp.

The orientation of the canals is another important feature that is generally used as diagnostic: if the canal faces inward or outwards from the coprolite, if it faces towards the center or if it faces at a determined canal. For example, canals 5/5’ in *P. habanensis*, *P. decemlunulatus* and *P. chosmalalensis* n. isp. face outwards from the coprolite and towards canals 3/3’ and 4/4’. However, the angle with respect to the horizontal plane that crosses the centroid is ~45° in *P. habanensis* and *P. decemlunulatus*, and ~25°in *P. chosmalalensis* (Fig. 6). For this reason, we propose the use of numerical criteria for the diagnosis of the ichnospecies of the genus *Palaxius* (Fig. 7). In addition to the number and arrangement of the canals we suggest including the position of canals with respect to the center of the coprolite (centroid), and the angle respect to the horizontal plane that crosses the centroid.

CONCLUSIONS

A new ichnospecies of crustacean microcoprolites, *Palaxius chosmalalensis* n. isp., is described from the lower Valanginian (lowermost *Olcostephanus* (*O.*) *atherstoni* ammoni-

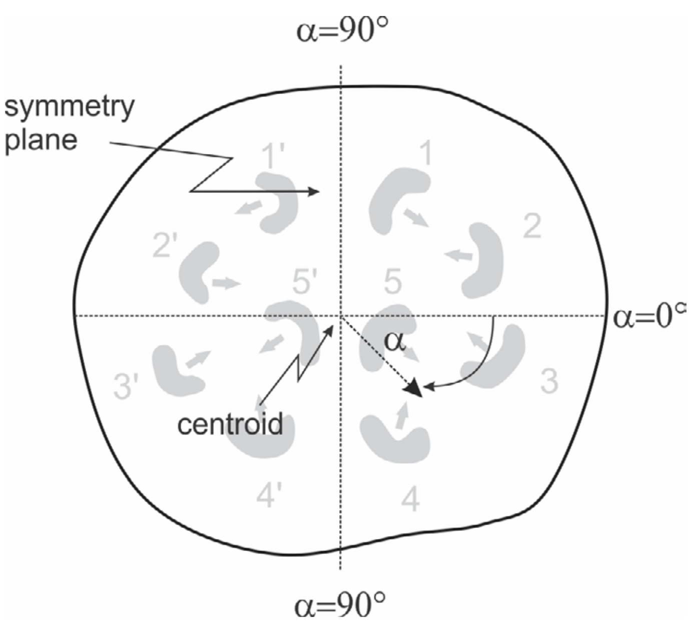


Figure 7. Features and proposed measures for the classification of *Palaxius* at ichnospecies level.

te Zone) in the Neuquén Basin. Other specimens from the Middle Jurassic of Iran and the Upper Cretaceous of Egypt are included within this new ichnospecies.

It is interpreted that the producer of *Palaxius chosmalalensis* n. isp. was a crustacean that inhabited shallow protected waters of inner ramp settings. Although it cannot be ruled out the presence of callianassids, the Mulichinco Formation includes so far body fossils of astacidean and palinurid lobsters, which can be potential producers of this coprolite.

We propose the use of numerical criteria for the diagnosis of the ichnospecies of the genus *Palaxius*. In addition to the number and arrangement of the canals we suggest including the position of canals with respect to the center of the coprolite (centroid), and the angle with respect to the horizontal plane that crosses the centroid.

ACKNOWLEDGMENTS

This research has been done under the framework of the PICT-2016-3762 project supported by Agencia Nacional de Promoción Científica y Tecnológica. We appreciate the collaboration in the field work of Mariano Penin. We are grateful to the guest editors Graciela S. Bressan and Diana E. Fernández for inviting us to participate in this special issue on ichnology, as well as for the suggestions made. We thank Joachim Blau and Felix Schlagintweit for constructive comments to improve the original manuscript.

REFERENCES

Aguirre-Urreta, M.B., Casadio, S., Cichowolski, M., Lazo, D.G. and Rodríguez, D. 2008. Afinidades paleobiográficas de los invertebrados cretácicos de la Cuenca Neuquina, Argentina. Ameghiniana 45(3): 591-612.

Arregui, C., Carbone, O. and Leanza, H.A. 2011. Contexto tectosedimentario. In: Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C., and Vallés J.M. (eds.), Geología y Recursos Naturales de la Provincia del Neuquén. Asociación Geológica Argentina: 29-36, Buenos Aires.

Becker, M.A. and Chamberlain, J.A. Jr. 2006. Anomuran Microcoprolites from the Lowermost Navesink Formation (Maastrichtian), Monmouth County, New Jersey. Ichnos 13: 1-9.

Blau, J., Grün, B. and Senff, M. 1993. Crustaceen-Koprolithen aus der Trias der westlichen Tethys (Lienzer Dolomiten, Österreich; Pragser Dolomiten, Italien) und vom Gondwana-Westrand (oberes Magdalental, Kolumbien, Südamerika). Paläontologische Zeitschrift 67: 193-214.

Blau, J., Rosas, S. and Senff, M. 1994. *Favreina peruviensis* n. sp., ein Crustaceen-Mikrokoprolith aus dem Lias von Peru. Paläontologische Zeitschrift 68: 521-527.

Blau, J., Moreno, M., and Senff, M. 1995. *Palaxius caucaensis* n. sp., a crustacean microcoprolite from the basal Nogales Formation (Campanian to Maastrichtian) of Colombia. Micropaleontology 41(1): 85-88.

Brönnimann, P. 1955. Microfossils *incertae sedis* from the Upper Jurassic and Lower Cretaceous of Cuba. Micropaleontology 1(1): 28-51.

Brönnimann, P. 1972. Remarks on the classification of fossil Anomuran coprolites. Paläontologische Zeitschrift 46: 99-103.

Brönnimann, P. and Norton, P. 1960. On the classification of fossil fecal pellets and description of new forms from Cuba, Guatemala and Libya. Eclogae Geologicae Helvetiae 53: 832-842.

Buchanan, A.S., Kietzmann, D.A. and Palma, R.M. 2017. Evolución paleoambiental de la Formación Remoredo (Jurásico Inferior) en el depocentro Malargüe, Cuenca Neuquina Surmendocina. Revista de la Asociación Geológica Argentina 74(2): 163-178.

Bujtor, L. 2012. A Valanginian crustacean microcoprolite ichnofauna from the shallow-marine hydrothermal vent site of Zengővárkony (Mecsek Mts., Hungary). Facies 58: 249-260.

D'Elia, L., Muravchik, M., Franzese, J.R. and López, L. 2012. Tectonostratigraphic analysis of the Late Triassic-Early Jurassic syn-rift sequence of the Neuquén Basin in the Sañicó depocentre, Neuquén Province, Argentina. Andean Geology 39(1): 133-157.

D'Elia, L., Bilmes, A., Franzese, J.R., Veiga, G.D., Hernández, M. and Muravchik, M. 2015. Early evolution of the southern margin of the NeuquénBasin, Argentina: Tectono-stratigraphic implications for rift evolution and exploration of hydrocarbon plays. Journal of South American Earth Sciences 64(1): 42-57.

De Romero, L. and Galea-Álvarez, F.A. 1995. Campanian Bolivinoides and microfacies from the La Luna Formation, Venezuela. Marine Micropaleontology 26: 385-404.

Echevarría, J., Damborenea, S.E. and Manceñido, M.O. 2012. Palaeodemecological analysis of infaunal bivalves "Lebensspuren" from the Mulichinco Formation, Lower Cretaceous, Neuquén Basin, Argentina. Ameghiniana 49(1): 47-59.

Flügel, E. 2004. Microfacies of Carbonate Rocks. Analysis, Interpretation and Application. Springer, p. 976, Berlin-Heidelberg.

Förster, R. and Hillebrandt, A.V. 1984. Das Kimmeridge des Profeta-Jura in Nordchile mit einer *Mecochirus-Favreina*-Vergesellschaftung (Crustacea, Decapoda Ichnogenus). Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 24: 67-84.

Gischler, E., Blau, J. and Peckmann, J. 2017. *Palaxius floridanus* n. isp., a new structured callianassid crustacean microcoprolite from the Pleistocene of south Florida. Journal of Paleontology 91(5): 981-986.

Groeber, P. 1946. Observaciones geológicas a lo largo del meridiano 70. Hoja Chos Malal, Revista de la Asociación Geológica Argentina 1(3): 178-208.

Groeber, P. 1953. Ándico. In: Groeber, P., Stipanicic, P.N., Mingramm, A. (eds.), Geografía de la República Argentina. Sociedad Argentina de Estudios Geográficos GAEA 2: 349-351, Buenos Aires.

Gulisano, C.A. 1981. El Ciclo Cuyano en el norte del Neuquén y sur de Mendoza. 8° Congreso Geológico Argentino, Actas 3: 579-592, San Luis.

Gulisano, C., Gutierrez Pleimling, R. and Digregorio, R.E. 1984. Análisis estratigráfico del intervalo Tithoniano-Valanginiano (Formaciones Vaca Muerta, Quintuco y Mulichinco) en el suroeste de la provincia del Neuquén. 9º Congreso Geologico Argentino, Actas 1: 221–235, San Carlos de Bariloche.

Jáger, V., Molnár, F., Buchs, D. and Koděra, P. 2012. The connection between iron ore formations and "mud-shrimp" colonizations around sunken wood debris and hydrothermal sediments in a Lower Cretaceous continental rift basin, Mecsek Mts., Hungary. Earth-Science Reviews 114(3-4): 250-278.

Jalilian, A.H. 2010. Sequence stratigraphy of the Surmeh Formation (Lower to Upper Jurassic) in the Central Zagros Mountains, southwest Iran. PhD thesis, Tarbiat Moallem University (unpublished), 350 p., Tehran

Kershaw, S. 1994. Classification and geological significance of biostromes. Facies 31: 81-92.

Kietzmann, D.A. and Palma, R.M. 2010a. Primer registro de microcoprolitos de crustáceos de la Cuenca Neuquina: el icnogénero *Palaxius* Palik en el Tithoniano de la Formación Vaca Muerta. Ameghiniana 47(2): 257-261.

Kietzmann, D.A. and Palma, R.M. 2010b. New crustacean microcoprolites from the Lower Cretaceous (middle Berriasian - lower Valanginian) of the Neuquén Basin, southern Mendoza, Argentina. Journal of South American Earth Sciences 30: 58-64.

Kietzmann, D.A. and Palma, R.M. 2014. Early Cretaceous crustacean microcoprolites from Sierra de la Cara Cura, Neuquén Basin, Argentina: Taphonomy, environmental distribution, and stratigraphic correlation. Cretaceous Research 49: 214-228.

Kietzmann, D.A. and Paulin, S. 2019. Cyclostratigraphy of an upper Valanginian- lower Hauterivian mixed siliciclastic-carbonate ramp succession (Pilmatué Member of the Agrio Formation), Loma La Torre Section, Northern Neuquén Basin, Argentina. Cretaceous Research 98: 26-46.

Kietzmann, D.A., Blau, J., Fernández, D.E. and Palma, R.M. 2010. Crustacean microcoprolites from the Upper Jurassic – Lower Cretaceous carbonate ramp deposits of the Neuquén Basin: Systematics and biostratigraphic implications. Acta Paleontologica Polonica 55(2): 73-84.

Kietzmann, D.A., Palma, R.M., Riccardi, A.C., Martín-Chivelet, J. and López-Gómez, J. 2014. Sedimentology and sequence stratigraphy of a Tithonian - Valanginian carbonate ramp (Vaca Muerta Formation): A misunderstood exceptional source rock in the Southern Mendoza area of the Neuquén Basin, Argentina. Sedimentary Geology 302: 64-86.

Kietzmann, D.A., Palma, R.M. and Ferreyra, T.M.A. 2016a. Análisis de facies y asignación estratigráfica de los depósitos fluviales innominados de la Cuenca Neuquina surmendocina. Revista de la Asociación Geológica Argentina 73(1): 104-116.

Kietzmann, D.A., Ambrosio, A., Suriano, J., Alonso, S., González Tomassini, F., Depine, G. and Repol D. 2016b. The Vaca Muerta-Quintuco system (Tithonian – Valanginian) in the Neuquén Basin, Argentina: a view from the outcrops in the Chos Malal fold and thrust belt. American Association of Petroleum Geologists Bulletin 100(5): 743-771.

Lasemi, Y. and Jalilian, H.A. 2010. The Middle Jurassic basinal deposits of the Surmeh Formation in the Central Zagros Mountains, southwest Iran: facies, sequence stratigraphy, and controls. Carbonates and Evaporites 25: 283-295.

Leanza, H.A. 2009. Las principales discordancias del Mesozoico de la Cuenca Neuquina según observaciones de superficie. Revista del Museo Argentino de Ciencias Naturales 11: 145-469

Legarreta, L. and Gulisano, C.A. 1989. Análisis estratigráfico secuencial de la Cuenca Neuquina (Triásico superior- Terciario inferior, Argentina). In: Chebli, G. and Spalletti, L.A. (eds.), Cuencas Sedimentarias Argentina. Serie Correlación Geológica, 6, Universidad Nacional de Tucumán: 221–243, San Miguel de Tucumán.

Legarreta, L. and Uliana, M.A. 1991. Jurassic-Cretaceous marine oscillations and geometry of back-arc basin fill, central Argentine Andes. In: Macdonald D.I.M. (ed.), Sedimentation, tectonics and eustasy: sea level changes at active margins. International Association of Sedimentologists, Special Publication 12: 429-450, Oxford.

Legarreta, L. and Uliana, M.A. 1996. The Jurassic succession in west central Argentina: stratal patterns, sequences, and paleogeographic evolution. Palaeogeography, Palaeoclimatology, Palaeoecology 120(3-4): 303-330.

Molinari Paganelli, V., Pichezzi, R. and Tilia Zuccari, A. 1980. I coprolithi di crostacei. Rassegnabibliografica e annotazionitassonomiche. Parte 1: Genere *Favreina*. Bollettino del Servizio geológico d'Italia 100 (1979): 409-454.

Molinari Paganelli, V., Pichezzi, R. and Tilia Zuccari, A. 1986. I coprolithi di crostacei. Rassegna bibliografica e annotazioni tassonomiche. Parte 2: Generi *Helicerina*, *Palaxius, Parafavreina* e *Thoronetia*. Bollettino del Servizio geológico d'Italia 104(1983): 309-344.

Moore, H.B. 1932. The faecal pellets of the Anomura. Proceedings of the Royal Society of Edinburgh 52: 296-308.

Motaharian, A., Aghanabati, A., Ahmadi, V. and Meisami, A. 2014. Crustacean microcoprolites of Middle and Upper Jurassic in Zagros (Southwest Iran). MAGNT 2: 295-304.

Palik, P. 1965. Remains of crustacean excrement from the lower Cretaceous of Hungary. Micropaleontology 11: 98-104.

Paréjas, E. 1948. Sur quelques coprolites de Crustacés. Archives des Sciences 1: 512-520.

Peckmann, J., Senowbari−Daryan, B., Birgel, D. and Goedert, J.L. 2007. The crustacean ichnofossil *Palaxius* associated with callianassid body fossils in an Eocene methane-seep limestone, Humptulips Formation, Olympic Peninsula, Washington. Lethaia 40(3): 273-280.

Powell, R.R. 1974. The functional morphology of the fore-guts of the thalassinid crustaceans, *Callianassa californiensis* and *Upogebia pugettensis*. University of California, Publications in Zoology 102: 1-47.

Pryor, W.A. 1975. Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments. Geological Society of America Bulletin 86: 1244-1254.

Ramos, V.A. 2010. The tectonic regime along the Andes: Present-day and Mesozoic regimes. Geological Journal 45: 2-25.

Ramos, V.A. and Folguera, A. 2005. Tectonic evolution of the Andes of Neuquén: constraints derived from the magmatic arc and Foreland deformation. In: Veiga, G.D., Spalletti, L.A., Howell, J.A. and Schwarz, E. (eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. Geological Society, Special Publication 252: 15-35, London.

Schwarz, E. 1999. Facies sedimentarias y modelo deposicional de la Formación Mulichinco (Valanginiano), Cuenca Neuquina Septentrional. Revista de la Asociación Argentina de Sedimentología 6(1-2): 37-59.

Schwarz, E. and Howell, J.A. 2005. Sedimentary evolution and depositional architecture of a lowstand sequence set: the Lower Cretaceous Mulichinco Formation, Neuquén Basin, Argentina. In: Veiga, G.D., Spalletti, L.A., Howell, J.A. and Schwarz, E. (eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. Geological Society, Special Publication 252: 109-138, London.

Schwarz, E., Spalletti, L.A. and Howell, J.A. 2006. Sedimentary response to a tectonically induced sea-level fall in a shallow back-arc basin: the Mulichinco Formation (Lower Cretaceous), Neuquén Basin, Argentina. Sedimentology 53(1): 55-81.

Schwarz, E., Spalletti, L.A. and Veiga, G.D. 2011. La Formación Mulichinco (Cretácico Temprano) en la Cuenca Neuquina. In: Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C. and Vallés J.M. (eds.), Geología y Recursos Naturales de la Provincia del Neuquén. Asociación Geológica Argentina: 131-144, Buenos Aires.

Schwarz, E., Veiga, G.D., Trentini, G.A. and Spalletti, L.A. 2016. Climatically versus eustatically controlled, sediment-supply-driven cycles: carbonate-siliciclastic, high-frequency sequences in the Valanginian of the Neuquén Basin (Argentina). Journal of Sedimentary Research 86(4): 312-335.

Senowbari-Daryan, B. 1979. Anomuren-Koprolithenaus der Obertrias der Osterhorngruppe (Hintersee/Salzburg, Österreich). Beiträge zu Paläontologie und Mikrofazis obertriadischer Riffe im alpin-mediterranen Raum, 5. Annalen des naturhistorischen Museums Wien 82: 99-107.

Senowbari-Daryan, B. and Kube, B. 2003. The ichnogenus *Palaxius* (crustacean coprolite) and description of P. *hydranensis* n. sp. from the Upper Triassic (Norian part of "Pantokrator" limestone) of Hydra, Greece. Paläontologische Zeitschrift 77: 115-122.

Senowari-Daryan, B. and Kuss, J. 1992. Anomuren-Koprolithen aus der Kreide von Ägypten. Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg 73: 129-157.

Senowbari-Daryan, B. and Stanley, G.D. 1986. Thalassinid anomuran microcoprolites from Upper Triassic carbonate rocks of Central Peru. Lethaia 19(4): 343-354.

Senowbari-Daryan, B., El Rab, A.G., Heindel, K., Gischler, E. and Peckmann, J. 2017. *Palaxius salataensis* Brönnimann, Cros and Zaninetti, 1972, the oldest crustacean microcoprolite from the early Carboniferous of Guangxi, South China. Paläontologische Zeitschrift 91: 299-305.

Stipanicic, P.N. 1969. El avance en los conocimientos del Jurásico argentino a partir del esquema de Groeber. Revista de la Asociación Geológica Argentina 24(4): 367-388.

Vergani, G.D., Tankard, A.J., Belotti, H.J. and Welkink, H.J. 1995. Tectonic evolution and paleogeography of the Neuquén Basin, Argentina. In: Tankard, A.J., Suarez, R., Soruco, H. and Welsink, J. (eds.), Petroleum Basins of South America. AAPG Memoir 62: 383-402, Tulsa.

Vialov, O.S. 1978. Favreinidae (coprolites of Crustacea) from Turonian of the Lower Amudaria. Paleontologiceskijsbornik 15: 58-67.

Wesolowski, L.J.N., Buatois, L.A., Mángano, M.G., Ponce, J.J. and Carmona, N.B. 2017. Trace fossils, sedimentary facies and parasequence architecture from the Lower Cretaceous Mulichinco Formation of Argentina: The role of fair-weather waves in shoreface deposits. Sedimentary Geology 367: 146-163.

Wesolowski, L.J.N., Buatois, L.A., Mángano, M.G., Ponce, J.J. and Carmona, N.B. 2018. Trace fossils, sedimentary facies and parasequence architecture from the Lower Cretaceous Mulichinco Formation of Argentina: The role of fair-weather waves in shoreface deposits. Sedimentary Geology 367: 146-163.