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Taphonomy of decapod-bearing concretions and their associated trace fossils from the Agrio Formation (Lower Cretaceous, Neuquén Basin), with paleobiological implications for axiid shrimps

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ABSTRACT

A total of 22 concretions containing 37 decapod crustacean specimens belonging to the family Axiidae, from the Hauterivian (Lower Cretaceous) of the Agrio Formation in the Neuquén Basin, were studied. The decapods were assigned to *Protaxius* sp., which likely had a fossorial life habit. In this work we attempt to determine, through taphonomic analysis, if the specimens fossilized within their burrows or outside them in order to interpret paleobiological aspects of the studied taxon. Several taphonomic criteria of the specimens and concretions, known from the literature, were applied and their utility discussed, including anatomical disposition, completeness of specimens, orientation and alignment, dispersion of exoskeletal elements in the concretion, preservation of both chelae, sedimentary fabric of the concretion, position within the concretion, and shape of the concretions. The relative importance of these criteria was discussed especially in those concretions with conflicting evidence pointing to either fossilization within or outside burrow systems. In the studied case, the specimens preserved in eight concretions were interpreted as fossilized within their burrows while two represent preservation outside burrow systems, on the sediment-water interface. The remaining concretions were difficult to interpret and taphonomic information was insufficient to conclude; however, the completeness and articulation of the specimens suggest preservation within burrow systems. The preservation of several specimens within the same burrow suggests a gregarious behavior, spending most of their lives in their galleries, and molting in special chambers without external disturbances.

Keywords: *Protaxius* sp., fossorial life habit, burrows, gregariousness, Hauterivian.

RESUMEN

Tafonomía de concreciones portadoras de decápodos y sus trazas fósiles asociadas de la Formación Agrio (Cretácico Inferior, Cuenca Neuquina) con implicancias paleobiológicas para camarones de la Familia Axiidae.
Se estudiaron 22 concreciones portadoras de 37 ejemplares de crustáceos decápodos de la Familia Axiidae procedentes del Hauteriviano (Cretácico Inferior) de la Formación Agrio, Cuenca Neuquina. Los decápodos fueron asignados a *Protaxius* sp., interpretados como de hábito de vida fosorial. Se buscó determinar si los camarones fosilizaron dentro de sus sistemas de galerías o fuera de ellas a fin de realizar inferencias paleobiológicas. Se aplicó una lista de criterios tafonómicos basada en la literatura consistente en la disposición anatómica, completitud, orientación, alineación, dispersión dentro de la concreción, preservación de ambas quelas, fábrica sedimentaria de la concreción, posición dentro de la concreción y forma de las concreciones. Se ponderó la importancia de

estos criterios a fin de definir el sitio de formación de la concreción para aquellas concreciones con evidencias contradictorias. En el caso de estudio, los individuos preservados en ocho concreciones se determinaron como fosilizados dentro de las galerías, y dos lo hicieron por fuera, en la interfase agua-sedimento. Para las restantes concreciones, la información fue insuficiente para definir con certeza el sitio de fosilización aunque la completitud y articulación de los especímenes sugieren preservación confinada y protegida. La ocurrencia de varios individuos juntos dentro de las galerías indicaría un comportamiento gregario, pasando gran parte del tiempo dentro de las excavaciones y mudando en cámaras especiales, protegidos de disturbios externos.

Palabras clave: *Protaxius* sp., hábito fosorial, excavaciones, gregarismo, Hauteriviano.

INTRODUCTION

The group of decapods formerly named as “thalassinideans” (now Infraorders Axiidea and Gebiidea) are well known by their fossorial habit (Dworschak et al. 2012) and their ability to produce several trace fossils belonging to *Ophiomorpha* Lundgren, 1891, *Thalassinoides* Ehrenberg, 1944, *Psilonichnus* Fürsich, 1981, *Spongeliomorpha* Saporta, 1887, *Gyrolithes* Saporta, 1884, *Macanopsis* Macsotay, 1967, and *Skolithos* Haldeman, 1840 (e.g. Frey et al. 1984, Dworschak and Rodrigues 1997, Nesbitt and Campbell 2002, Gingras et al. 2008, de Gibert et al. 2012, Ter and Buckeridge 2012). Even though the abundance of these traces is high in the fossil record, the direct association of one trace fossil with one particular decapod producer is generally absent and thus subject of interpretation (Hyžný 2011). Fossil remains may indeed appear preserved within the burrows (Waage 1968, Sellwood 1971, Mourik et al. 2005, Fraaije et al. 2006, Neto de Carvalho et al. 2007, Schweitzer et al. 2007, Hyžný 2011, Hyžný and Klompmaker 2015), but this appear to be pretty uncommon, besides it is thought that there is a reporting bias (Hyžný and Summesberger 2019). Many occurrences involve the association of body fossils with trace fossils, but the remains are not preserved right within their burrows as mentioned by Pickett et al. (1971), Feldmann et al. (1995), Kato (1996), Compton (2001), Schweitzer et al. (2006), and Hyžný and Klompmaker (2015), and thus these cases are also subject to interpretation.

Feldmann et al. (2012) have stated that there is not always unequivocal evidence to support all the published occurrences of decapods within burrows and proposed some criteria to recognize such cases. These criteria can be added to those previously proposed by Bromley and Aasgard (1972), Tsujita (2003), and Bishop and Williams (2005).

Decapod-bearing concretions may provide interesting paleobiological information of fossil decapods, such as molting and feeding behaviors, gregariousness and population densities. The present work is centered on 22 decapod-bearing concretions from the Agrio Formation (Lower Cretaceous, Neuquén Basin, west-central Argentina). The studied shrimp specimens have been identified as *Protaxius* sp. (Beurlen, 1930, Infraorder Axiidea, Family Axiidae), on the basis of the features of pereiopods and pleon but are left in open nomenclature waiting for a thorough taxonomic revision. Although extant representatives of the family Axiidae have burrow-dwelling habits and some of their burrows have been studied by *in situ* resin casting (Pemberton et al.1976, Nash et al. 1984, Dworschak and Ott 1993), no direct associations of fossils and traces of this family have been found hitherto.

The aims of this paper are threefold: to discuss the applicability and predictive strength of the criteria proposed previously to identify preservation within burrow systems, to recognize those concretions that correspond to burrows systems or alternatively preservation out of them following these criteria, and, finally, with the latter information, to infer paleobiological aspects of these fossorial shrimps.

GEOLOGICAL SETTING AND DECAPOD-BEARING BEDS

The Neuquén Basin, located in west-central Argentina, has been interpreted as a back-arc basin (Digregorio et al. 1984, Legarreta and Uliana 1991, 1996, Ramos 1999). It has a thick sedimentary record of latest Triassic-Paleogene continental and marine clastic, carbonate, and evaporitic deposits (Yrigoyen 1991, Gulisano and Gutiérrez Pleimling 1994, Howell et al. 2005).

The Agrio Formation of Valanginian to latest Hauterivian age (Aguirre-Urreta et al. 2007, 2015, 2017) is composed of three members: the Lower or Pilmatué Member, the Middle or Avilé Member and the Upper or Agua de la Mula Member (Leanza et al. 2005). The Pilmatué and Agua de la Mula members are characterized by a thick shale succession of a mixed siliciclastic-carbonate marine ramp environment, with interstratified thin shell beds and sandstones (Spalletti et al. 2011). The Avilé Member corresponds to continental facies, composed mainly of fluvial and eolian sandstones, interpreted as an interruption of the marine sedimentation in the basin (Veiga et al. 2011).

The studied decapod-bearing concretions proceed from the Pilmatué Member at Agua de la Mula locality, 80 km south of Chos Malal (Neuquén Province) (Fig. 1). In this area, the Pilmatué Member overlies the continental to marginal marine Mulichinco Formation (Schwarz et al. 2011) by means of an important second-order transgressive surface of regional extent (Spalletti et al. 2011). This rapid flooding episode was followed by a prolonged period of high relative sea level. Thus, the Pilmatué Member corresponds to a basal second-order transgressive systems tract followed by a highstand systems tract. Along with the underlying Mulichinco Formation, which is a second-order lowstand systems tract, forms a complete second-order depositional sequence (Schwarz et al. 2011). Lithofacies in the Pilmatué Member are arranged in shallowing-upward successions, where sediments are preserved as regressive deposits, including high-frequency transgressive-regressive cycles (see Spalletti et al. 2011, Pazos et al. 2020).

The Agrio Formation has a rich and abundant fossil content represented by macroinvertebrates (bivalves, gastropods, nautiloids, ammonites, corals, decapods, echinoderms, and serpulids), trace-fossil assemblages, and scarce vertebrate remains including ichthyosaurs, plesiosaurs, and elasmobranchs and pycnodontid fishes (Lazo et al. 2005, 2018, Aguirre-Urreta et al. 2011, Fernández and Pazos 2012, 2013, Pazos et al. 2012, O'Gorman et al. 2015, Fernández et al. 2019a, b, Gouiric-Cavalli et al. 2018, 2019). In this unit, trace fossils assignable to crustaceans and belonging to *Ophiomorpha nodosa* Lundgren, 1891, *Ophiomorpha* isp., *Thalassinoides suevicus* Rieth, 1932, *Thalassinoides* isp., and *Trypanites* isp., have been recognized (Aguirre-Urreta 1989, Lazo et al. 2005, Fernández and Pazos 2012), as well as decapod body fossils including representatives of the Infraorders Axiidea, Glypheidea, Astacidea and Achelata, which have been studied mostly from a taxonomic perspective, but there have been also some paleoecological and taphonomic approaches, but none of them linking body to trace fossils (Aguirre-Urreta 1989, 2003, Aguirre-Urreta et al. 2008, 2012, Andrada 2018). Particularly, *Protaxius* sp. has been found associated (i.e., in the same beds) with *Thalassinoides* isp. (Aguirre-Urreta 2003, Lazo et al. 2005).

The studied concretions were recorded in an 8 m-thick succession placed in the upper third of the Pilmatué Member in association with ammonoids of the *Hoplitocrioceras genti-*

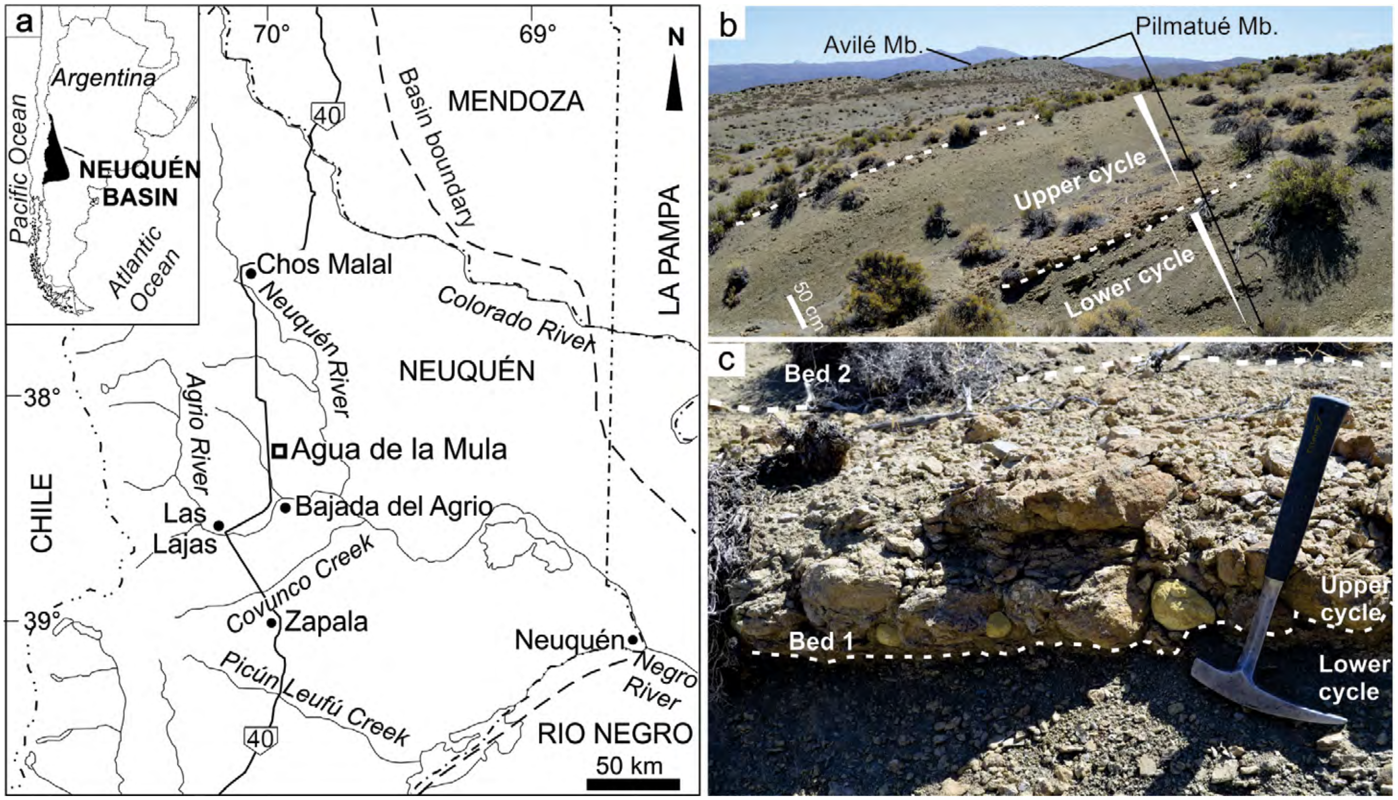

Figure 1. a) Schematic map of the Neuquén Basin showing the studied locality, Agua de la Mula; b) Field picture towards the west of the studied succession in the Pilmatué Member, also showing outcrops of the base of the Avilé Member, both belonging to the Agrio Formation, Agua de la Mula Locality; note transgressive-regressive cycles 1 and 2 (lower and upper cycles); c) Detail of bed 1 containing reworked decapod-bearing concretions (marked in yellow) and the overlying bed 2 containing in situ decapod-bearing concretions.

lii Zone of early Hauterivian age, which is in turn correlated with the lower part of the *Lyticoceras nodosoplicatum* Zone of the Mediterranean Province (see Aguirre-Urreta and Rawson 2001, Aguirre-Urreta et al. 2007). This succession is composed of two stacked transgressive-regressive cycles. Each one represents a shallowing-upward high-frequency cycle (Figs. 1 and 2). The lower cycle is 6 m-thick and is composed by dark grey shales, bioturbated greenish siltstones, and very fine sandstones (Fig. 1b-c) including the presence of sparse shrimp-bearing concretions and concretionary tubes of *Thalassinoides* isp., although no samples were collected from this level. The upper cycle is 2 m-thick and has, at its base, a 26 cm-thick tabular shell bed with erosive base and carbonate mud matrix. This shell bed is composed of densely packed bivalve shells and contains reworked decapod-bearing concretions (bed 1) from which 19 were collected and studied (Fig. 1b-c). Even though these concretions were affected by reworking, they can be regarded as parautochthonous and not allochthonous, given the small scale of the transgressive-regressive cycle and also because of the presence of *in situ* concretions in cycles 1 and 2 (bed 2). Overlaying this shell bed there is a succession of shales, siltstones and fine-grained sandstones that completes the upper cycle. Three additional decapod-bearing concretions were sampled here (bed 2). Each transgressive-regressive cycle represents a shallowing-upward succession from proximal offshore to inner shelf settings (see Schwarz et al. 2018). The reworked concretions resulted from erosive processes that took place during the initial transgressive phase of the transgressive-regressive cycle 2 (upper cycle).

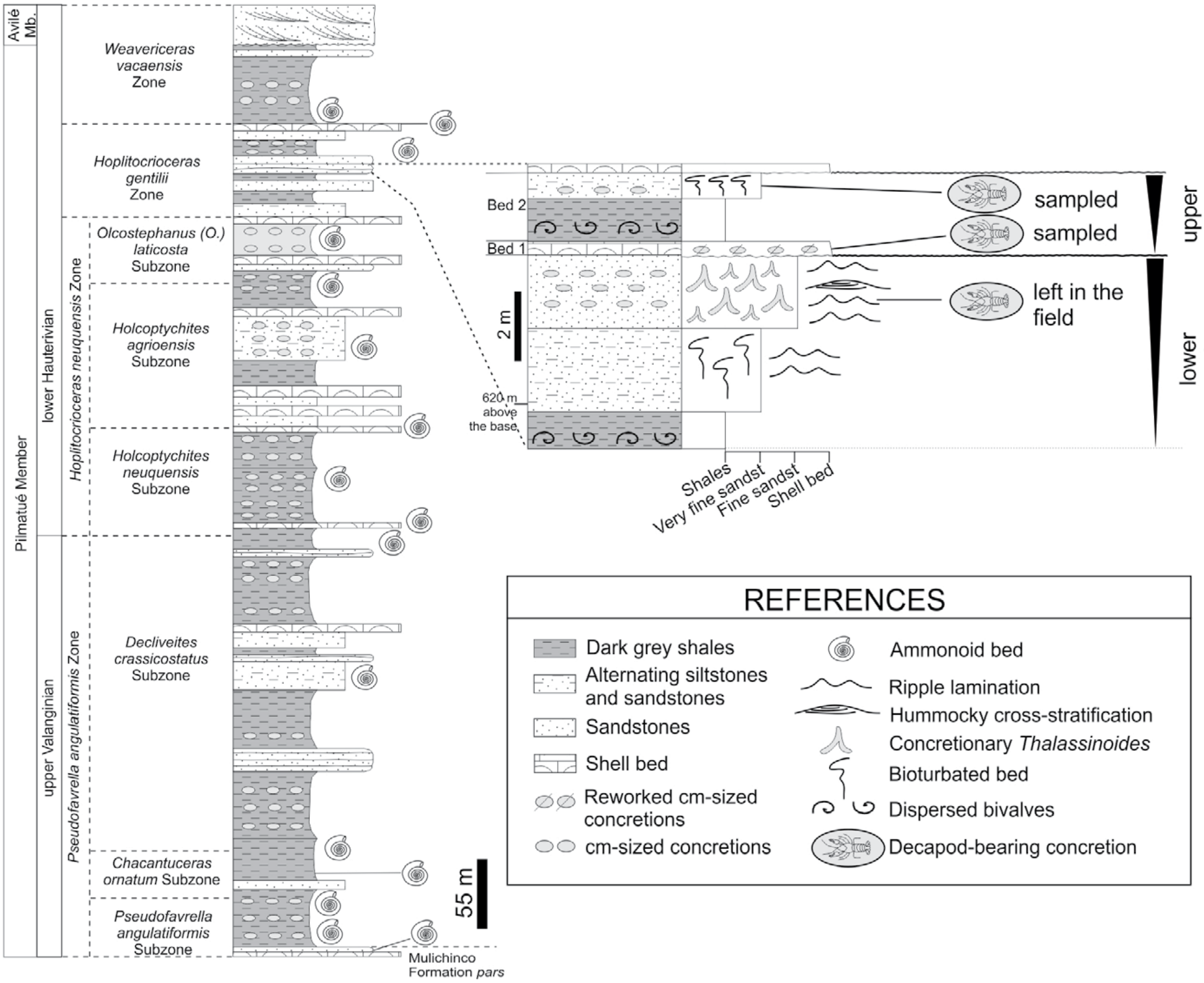

Figure 2. Stratigraphic column of the Pilmatué Member of the Agrio Formation in the studied locality showing ages and ammonoid zonation, and detail of the sedimentary interval containing the studied decapod-bearing concretions. Stratigraphic column modified from Lazo et al. (2005), ages from Aguirre-Urreta and Rawson (2001) and Aguirre-Urreta et al. (2007, 2015, 2017).

MATERIAL AND METHODS

Studied material includes 37 specimens of *Protaxius* sp. preserved in 22 concretions from the Pilmatué Member of the Agrio Formation. A detailed sedimentary log of the 8-m-thick succession was performed in the field taking into account lithology, sedimentary structures, contacts, geometry, and trace fossil and body fossil content including associated ammonoids. These concretions were selected randomly in the field and are housed in the Paleontological Collection of the Facultad de Ciencias Exactas y Naturales of the Universidad de Buenos Aires under the acronym CPBA. Each catalogue number refers to a given concretion, while suffix number indicates each specimen preserved in a given concretion. Two thin sections have been done to describe the sedimentary fabric of the concretions and the composition and features of the decapod cuticle microstructure. Observations about taphonomic characters of the specimens and sedimentological features of the concretions were done and compared with previous records of crustaceans associated to or preserved within burrows and concretions. Anatomical terminology follows that of Dworschak et al. (2012). The types of preservation regarding completeness follow the classification of Bishop and Williams (2005) modified by Hyžný and Klompmaker (2015). Criteria previously described in the literature for recognition of preservation within burrow systems (Bromley and Aasgard 1972, Tsujita 2003, Bishop and Williams 2005, Feldmann et al. 2012) are analyzed and discussed with the purpose of recognizing whether the studied decapods were preserved or not in the burrow systems and the relative importance of each of these criteria. The characteristics of the studied specimens that relate them to burrow systems according to different authors are listed in Table 1. Evidence connected with these criteria are considered positive when support the preservation within burrow systems, while they are considered negative if they point to preservation outside burrows. In those cases where some criteria do not apply to the studied specimens or sufficient information is not available to infer a positive or negative state, they are registered as not applicable (N/A). The criterion “burrow/concretion relationship” (Bromley and Aasgard 1972) has not been evaluated, because they need the preservation of the burrow complex in close contact with the concretions. The criterion “size of the concretion in relation to the size of the enclosed specimens” (Feldmann et al. 2012) is discussed in the next section. Finally, comparisons have been made with the published ecological and paleobiological information of related families in the infraorder Axiidea.

TAPHONOMIC ANALYSIS OF THE CRITERIA USED TO IDENTIFY PRESERVATION WITHIN OR OUTSIDE THE BURROW SYSTEMS

Here, the different criteria proposed in the literature will be analyzed for the studied specimens from the Agrio Formation.

General preservation

Remarks: The studied specimens are well preserved in terms of completeness (*sensu* Hyžný and Klompmaker 2015), i.e. most of them are disassociation units (n = 18, 48.7 %) and nearly complete body fossils (n = 10, 27 %), although some of them are preserved as isolated elements (n = 9, 24.3 %). In the first case, although a slight distance between pereiopods and carapace of the cephalothorax can be noted, they practically preserve their original anatomical relationship. In the case of the specimens that preserved the carapace and pleon, the former is detached and without alignment with the latter. Also, some specimens do not preserve these two tagmata. When thin sections are observed, the microstructure of different elements reveals an endocuticle laminated and well preserved.

Interpretation: The distance between different elements is interpreted as product of decay of the thin membrane that connects them. Specimens where pleon and carapace are detached and without alignment have been interpreted as exuviae, while those which do not preserved these two tagmata cannot be interpreted as exuviae or corpses based in their disposition. The recognition of the endocuticle is indicative that these elements are corpses.

Configuration of the remains

Remarks: Although the studied specimens are not in an outstretched position as proposed by Tsujita (2003), in those shrimps preserving several segments and tagmata (i.e., near complete body fossils), as explained previously, they keep an anatomical original disposition. In concretions preserving more than one individual, all of them are oriented in the same antero-posterior axis, and almost all of them are coincident in the dorso-ventral axis (except specimens in the concretion CPBA Nº 23643) (Fig. 3). This is similar to the observation of Tsujita (2003) in relation to the so-called end-to-end configuration of different individuals. Propodi preserved in concretion CPBA N° 23656, are in different dorso-ventral orientation and planes.

Interpretation: The fact that the studied specimens show an anatomical original disposition of tagmata points to fossili-

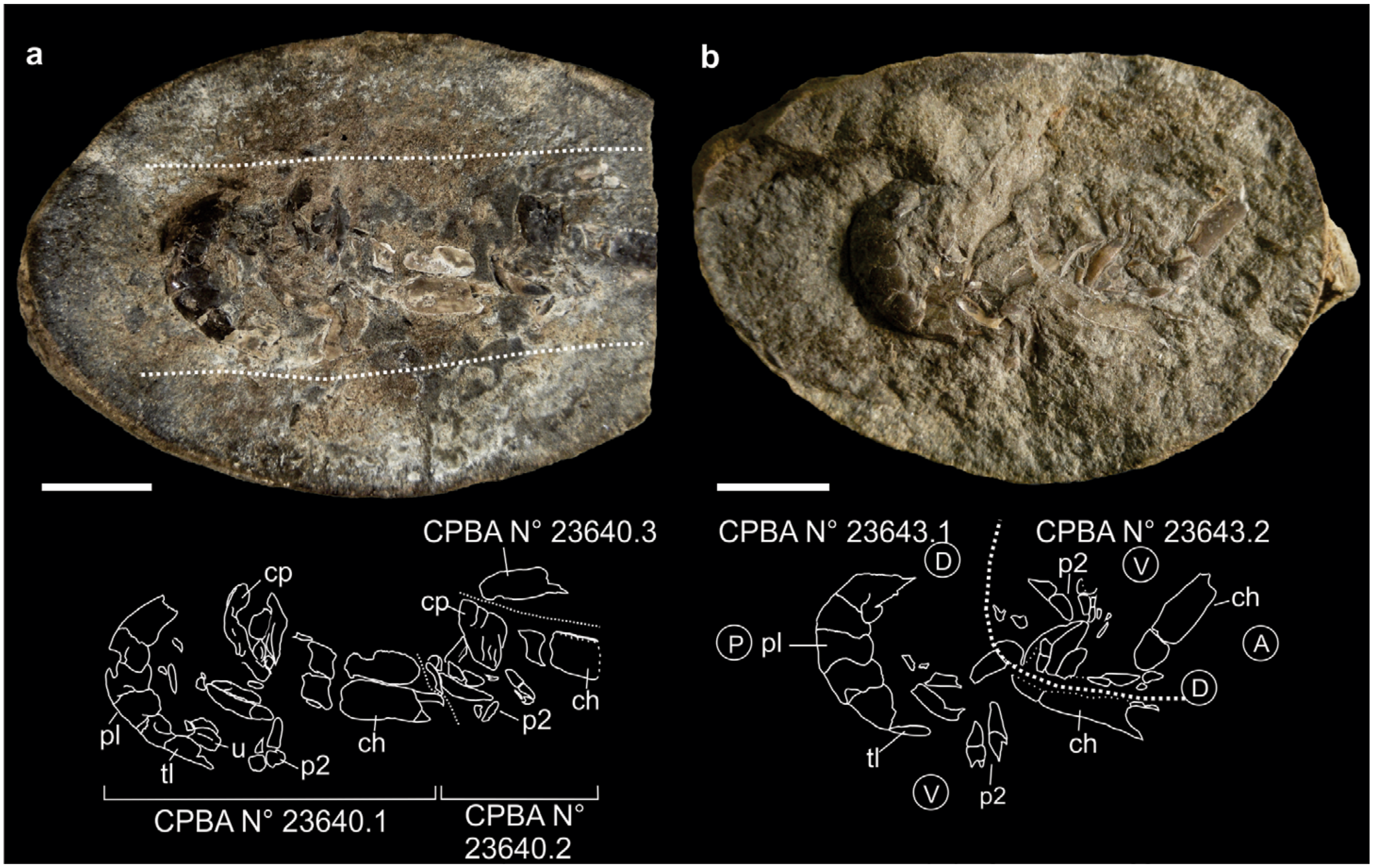

Figure 3. Disposition of the remains in concretions with more than one specimen. a) Concretion CPBA Nº 23640 preserving three aligned specimens, with the same antero-posterior and dorso-ventral arrangement; b) Concretion CPBA Nº 23643 with two specimens with antero-posterior axis coincident, but opposite dorso-ventral arrangement. Abbreviations: A, anterior, ch, cheliped, cp, carapace, D, dorsal, P, posterior, p2, second pereiopod, pl, pleon, tl, telson, u, uropods, V, ventral. Scale bars = 1 cm.

zation within burrows (positive evidence). Even though specimens are not immediately one behind another as in the examples illustrated by Tsujita (2003) and Hyžný (2011), if they had fossilized on the sediment-water interface, they would not have been disposed in that configuration. Only the disposition of propodi preserved in concretion CPBA N° 23656, are considered as negative evidence, because it is opposed to a normal anatomical position (see Fig. 8d).

Disarticulation and dispersion of elements in the concretions

Remarks: Some specimens are preserved as nearly complete body fossils, including isolated pereiopods with various articulated segments, and the disposition of the remains is close to the original anatomical connection in both exuviae and carcass remains (Fig. 4).

Interpretation: The fact that some specimens are preserved as nearly complete body fossils despite the decay of the membranes that connect different segments is here assumed as an important positive evidence of preservation within burrow systems, because if they had been exposed to physical disturbance (i.e., currents or waves), their parts would not have been preserved articulated. Additionally, if any isolated pereiopod with various elements is preserved, the segments are articulated. All of these conditions indicate that fossilization occurred in a quiet, confined space, probably within burrow systems.

Sedimentary fabric in the margins *vs.* center of the concretion

Remarks: Thin sections from two concretions (CPBA Nº 23650, 23651) show horizontal and ripple cross lamination, which also have been observed in the outer surface of two other concretions (CPBA Nº 23654, 23659) and in the fracture plane of a third one (CPBA Nº 23656). Thin section of concretion CPBA Nº 23650 shows a surface that separates an outer zone with a faint parallel lamination from an inner zone, with some decapod elements and a less defined fabric (Fig. 5) but crossed by ripple cross lamination. Concretion CPBA Nº 23656 shows parallel lamination below, crossing and above

Figure 4. Concretion CPBA N° 23659 showing lack of dispersion of the specimen remains, even though tagmata are detached. Note that the specimen is probably an exuvia in Lobster Open Molt Position *sensu* Bishop (1986). Scale bar = 1 cm.

the propodi preserved in it, while CPBA Nº 23659 shows it at the same level to that of the specimen. Conversely, lamination observed in the outer surface of concretion CPBA Nº 23654 is located above the plane in which the specimens are lying. For the remaining concretions, without recognizable sedimentary structures or any internal recognizable boundary, the massive fabric observed would be consistent with a burrow fill.

Interpretation: The presence of specimens crossed by ripple cross lamination, is a strong negative evidence (preservation outside burrows) according to Tsujita (2003), because lamination forms on the sediment-water interface, while the common fabric in the burrow infillings has no preferential orientation. In particular, the concretion CPBA Nº23654 is rather equivocal and may be due to preservation inside or outside burrows. The massive fabric present in the remaining concretions may point either to preservation inside or outside the burrows.

Association with burrow systems in the field

Remarks: In the field, concretionary tubes belonging to *Thalassinoides* isp. have been recorded along with decapod-bearing concretions of cycle 1 (Figs. 1 and 2).

Interpretation: The close association of body and trace fossils is a positive evidence of fossilization within the burrow systems following criteria of Feldmann et al. (2012).

Position of specimens in the concretion

Remarks: Most of the analyzed concretions have specimens preserved in the center of the concretion and not near the margins. Only one concretion (CPBA Nº 23650) shows the distal part of the right propodus of one individual (CPBA Nº 23650.1) that can be observed on the outer surface of the concretion.

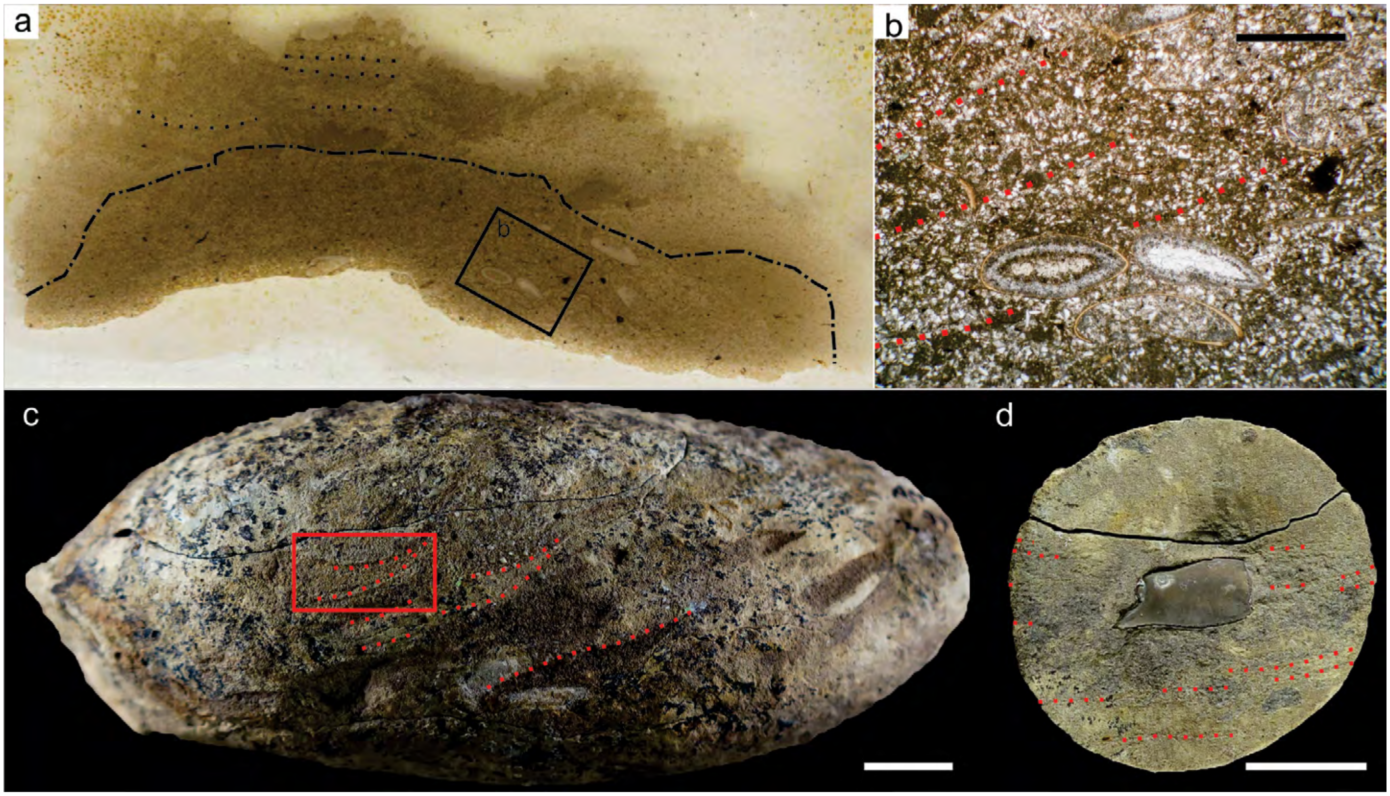

Figure 5. Sedimentary fabric in the margins and the center of the concretions. a) General view of the thin section of the concretion CPBA Nº 23650. Note the difference between the outer zone with a weak lamination and the inner zone with an apparent more chaotic fabric; b) Detailed view of some elements and the ripple cross lamination surrounding them; c) Concretion CPBA Nº 23659 with ripple cross lamination on the surface; d) Cross section of concretion CPBA Nº 23656 showing horizontal lamination at the same level to that of the remains. Scale bars, a-b = 1 mm, c-d = 1 cm.

Interpretation: Presence of specimens in the center of concretions may be considered as negative evidence (preservation outside burrows), while concretion CPBA Nº 23650 can be considered as preserved within burrows (positive evidence).

Shape of the concretions

Remarks: Few of the studied concretions have morphologies such as those proposed by Bromley and Aasgard (1972) and Tsujita (2003) as positive evidences (Table 1). An oblong shape is slightly visible in concretion CPBA Nº 23659, while concretion CPBA Nº 23660 has lobes that could be roughly interpreted as branching (Fig. 6a-c). In contrast, most concretions do not show tubular or branched morphologies, showing instead spherical or discoidal, somewhat flattened or circular in cross section. None of them extend beyond the specimens that they contain (Fig. 6d-h).

Interpretation: The general morphology related to the disposition of the decapods in most of the studied concretions is considered as negative evidence (outside burrows), except some oblong shaped or branching concretions that suggest preservation inside the burrow systems (positive evidence).

Preservation of both chelae

Remarks: Specimens preserved in the concretions CPBA Nº 23641, 23645, 23650, 23652, and 23656 only show preservation of both chelipeds or elements of them, mainly propodi (Fig. 7). The most extreme example was seen in the concretion CPBA Nº 23656, in which the only elements preserved are the left and right propodi (Fig. 7d). In concretions CPBA Nº 23641 and 23650, the propodi are articulated with carpi. Finally, in concretions CPBA Nº 23645 and 23652, one of the chelae is more exposed than the other because the fracture plane is irregular, thus, it is not possible to know if more parts

Figure 6. Shape of concretions. a-b) Concretion CPBA Nº 23659 with oblong shape (positive evidence) in upper and lateral view, respectively; c) Concretion CPBA Nº 23660, with faint lobes which can be interpreted as burrow branching (positive evidence); d-e) Concretion CPBA Nº 23641 with flattened, discoidal shape (negative evidence) in upper and lateral view, respectively; f-g) Concretion CPBA Nº 23654 in external and internal view. The cylindrical shape is coincident with the disposition of the remains, therefore, it is not considered as a positive evidence; h) Concretion CPBA Nº 23653, with spherical shape (negative evidence). Scale bars = 1 cm

Table 1. Criteria described in literature and used to recognize the site of formation of decapod-bearing concretions.

Reference	Criteria	Positive evidence	Negative evidence
Bromley and Aasgard 1972	Shape of the concretions	Regular shape: spheres, sausages or kidney-shaped, with lobes	Irregular or subspherical, uneven boundaries
	Burrow/concretion relationship	Concretions laying within the fill of the fossil traces	Concretions laying outside of the burrows
Tsujita 2003	Shape of the concretions	Oblong, ellipsoidal to cylindrical	Flattened, discoidal
	Configuration of the remains	Outstretched position, chelae forward, pleon more or less extended and tail fan downward or flexed beneath the pleon. If there are more than one specimen, they are aligned and preserved in an end-to-end configuration	Carapace detached and far away from the pleon, remains loosely enrolled
	Dispersion of the remains within the concretion	Little or lack of dispersion	Dispersed remains
	Sedimentary fabric in the margins vs. the center of the concretion	Faint, contorted laminae and bioturbated fabric in the concretion margin; chaotic fabric in the interior of the concretion; sharp contact between them	Horizontal, undulose laminae; strongly bioturbated in all the concretion
Bishop and Williams 2005	Preservation of both chelae	Two chelae preserved together	Isolated chela
Feldmann et al. 2012	Size of the concretion in relation to the size of the enclosed specimens (taxa dependent feature)	Appropriate proportion between the height of the carapace and the diameter of the supposed burrow	Relation between the diameter of the supposed burrow and the height of the carapace less than expected
	Association with burrow networks in the beds	Presence of burrow complexes	Absence of burrow networks
	Position of the specimen in the concretion	In connection with the supposed floor of the burrow	In the center of the structure

of the specimens are preserved within the concretion. Concretion CPBA Nº 23653 preserves only a propodus.

Interpretation: Presence of both chelae has been considered as positive evidence (preservation inside burrows) by Bishop and Williams (2005), because if they had been positioned above the sediment-water interface, they would have been separated by simple decay or physical alteration. In contrary, preservation of only one propodus has been considered as preservation outside the burrow systems (negative evidence) by Bishop and Williams (2005). The remains preserved in concretions CPBA Nº 23645 and 23652 are considered as examples of preservation of disarticulated chelae in proximity.

DISCUSSION

Preservation in the burrow systems *vs.* outside, on the sediment-water interface

Concretions analyzed show negative and positive evidence about fossilization in the burrow systems and then the relative importance of each evidence will be evaluated to say, if possible, where the studied shrimps were fossilized.

In relation to the disposition of the remains, the outstretched position, that could be an indicator of a confined space, is a debatable argument. The studied specimens are not strictly extended as the specimens studied by Tsujita (2003), but they are not chaotically distributed in the concretion. Some axiids construct burrows with chambers at different depths, which have a larger diameter than the tunnels between them or the shafts (Pemberton et al. 1976, Dworschak and Ott 1993, Kneer et al. 2013). Then, the outstretched position mentioned by Tsujita (2003) could be developed only in the shafts or tunnels, in which the space is reduced, or when the diameter of the burrow is approximately equal to the size of the burrower. The analyzed shrimps could be interpreted as several specimens which fossilized within a wider part of the burrow, for example a chamber, therefore they are not perfectly aligned, appearing more scattered.

The cross-section diameter of the burrow in relation to the size of the specimens depends on the taxa analyzed, because

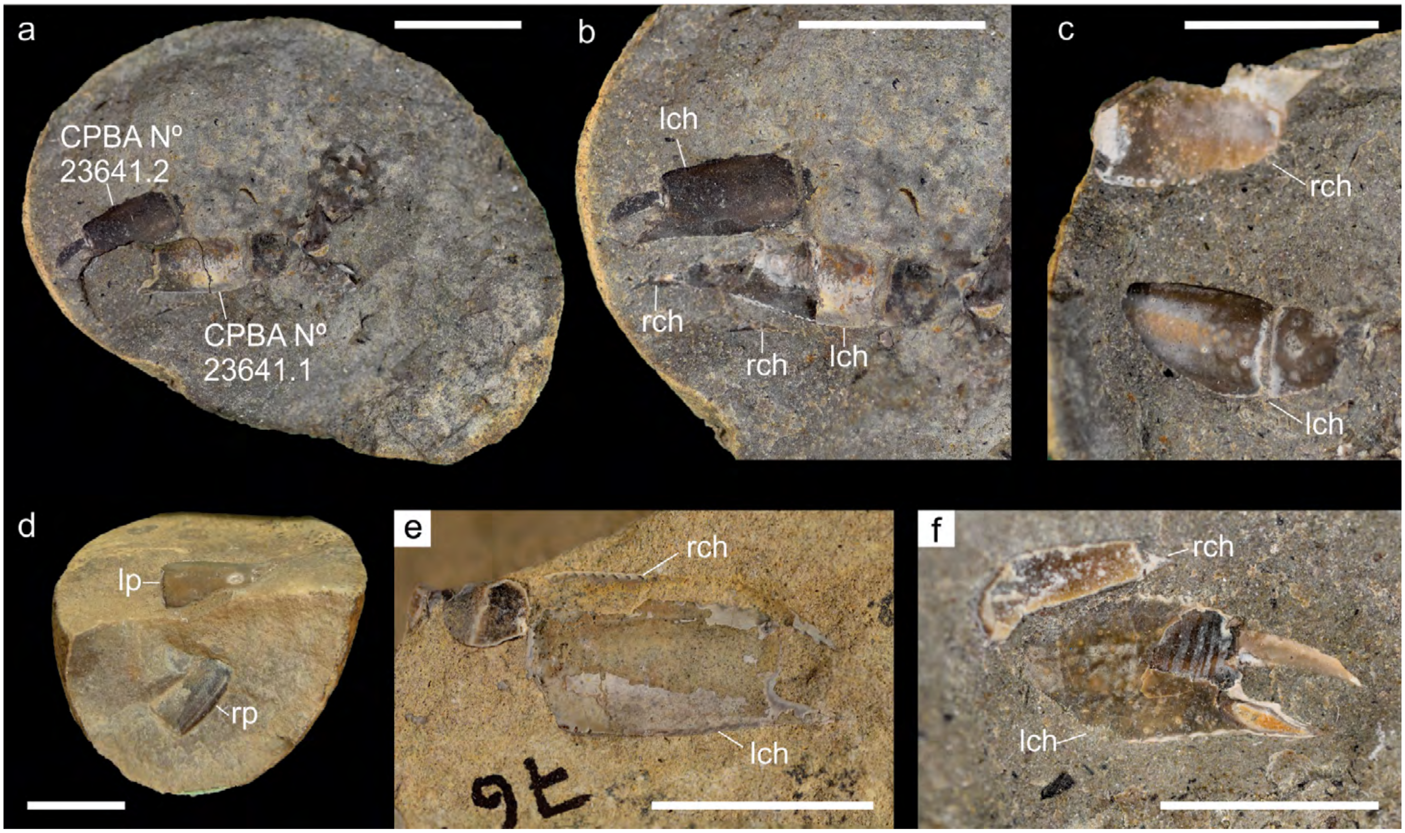

Figure 7. Examples of preservation of both chelae. a-b) CPBA Nº 23641 with two specimens preserved. b. Note that below of the left chela of CPBA Nº 23641.1 there are the inner margins of the right chelae of both specimens, including part of the fixed finger; c) Chelae with propodus and propodus and carpus of CPBA Nº 23650.1; d) CPBA Nº 23656 preserving only the propodus of both chelipeds; e) CPBA Nº 23652 with left cheliped (propodus, carpus and the distal part of the merus) and the mould of the right chela (propodus and dactylus); f) CPBA Nº 23645.1 showing the left chela with propodus and dactylus, and the right chela in section. Abbreviations: lch, left chela; rch, right chela; lp, left propodus; rp, right propodus. Scale bars = 1 cm.

different burrowers have different proportions and the configuration of the galleries is species specific and closely related to the feeding habit (Griffis and Suchanek 1991, Kornienko 2013). In fact, the general burrow diameter in Axiidae is much wider than the animal's cross-section (Dworschak et al. 2012). Therefore, the relation between the size of the concretion and the size of the specimens enclosed within them is a criterion that should be used carefully, taking into account that the diameter is not always constant in all the burrow network, and that the relationship is variable between different species, as was figured by Bromley and Aasgard (1972: Fig. 9).

It is noteworthy that in concretions with more than one specimen preserved, the remains have the same axial orientation (dorso-ventral and antero-posterior) and appear in close proximity to each other, suggesting that they were in a confined space. These individuals are usually of the same or slightly different size. Postmortem orientation by currents or waves is rejected, because the decapod remains would not have resisted transport without disarticulation of carapace and pleon (Allison 1986, Briggs and Kear 1994, Andrada 2018). Moreover, most of the specimens in which the relation between the cephalothorax and the first pleonal somite was observable (CPBA N° 23640.1, 23644.1, 23648.1, 23654.1, 23657, 23659, 23660.1) they showed a Lobster Open Molt Position (Bishop 1986), allowing to interpret these specimens as exuviae. The fact that they were exuviae reinforces the former argument, because if the specimens had molted, the previous split between the pleon and cephalothorax produced during the molting process would have made easier the disarticulation and loss of the tagmata, instead of orienting them. Thus, the disposition of the remains, including the relation of the tagmata and the relation between different specimens, and the lack of dispersion in the concretion are considered as strong evidence of preservation within burrows.

Some representatives of the genus *Protaxius* were found associated with trace fossils in the literature. For instance, *P. isochelus* Woodward, 1876 was found associated with *Thalassinoides* isp. in the Kimmeridgian of Bure, Lorraine, France (Carpentier et al. 2006). In the Neuquén Basin, Aguirre-Urreta (2003) suggested that the preservation of some *Protaxius* sp. from the Agrio Formation would be comparable to those concretions with *Glyphea rosenkrantzii* Van Straelen, 1929 associated with trace fossils from the Toarcian of Neill Klinter Group, in Greenland, analyzed by Bromley and Aasgard (1972).

Regarding the shape of the concretions, Hall and Savrda (2008) have discussed possible relationships between trace fossils and their formation. The morphology of concretions would be a good character to evaluate if the decapods fossilized in their galleries only if the burrow works as a nucleus of mineralization (incidental preservation *sensu* Hall and Savrda 2008), resulting in concretions with the exact extent of the burrow (burrow-casts) or concretions that continues beyond the lining of the trace, including part of the surrounding matrix but preserving the original shape (encased burrow concretions). In contrary, those concretions formed outside the burrows but including part of them passively (collateral preservation *sensu* Hall and Savrda 2008) or inside but with an extended mineralization which hides the limit of the trace fossil, are not useful to evaluate where the fossilization of the decapod took place.

The studied concretions do not show unequivocal evidence indicating that they represent burrow casts. However, two of the studied concretions have morphologies that could represent encased burrow concretions. CPBA Nº 23660 has faint lobes that could have been a point of branching, which normally shows a swelling in *Thalassinoides* (Ehrenberg, 1944), while CPBA Nº 23659 is somewhat tubular-shaped (Fig. 6a-b). The shape of the remaining concretions is more related to the morphology and disposition of the fossil remains than to a burrow, showing spherical or discoidal shapes, flattened to circular in cross section. Therefore, shape seems to be a weak criterion if analyzed alone, with the exception of encased burrow concretions. This criterion was used as positive evidence when connected with other observations, as the direct connection of the concretions with the burrow systems in specimens studied by Bromley and Aasgard (1972) and when there is a boundary between the sedimentary fabric of the margin and the center of the concretion, which allowed to define the lining of the original burrows, in those studied by Tsujita (2003).

Feldmann et al. (2012) have proposed that the position of the fossil remains within the concretion could provide useful information regarding within-burrow preservation. If the margins of the concretion coincide exactly with the burrow, the remains should be placed on one of the sides of it, likely the burrow floor. Nevertheless, if the walls of the burrow do not coincide with the margins of the concretion, a lithological difference should be noted to be able to affirm if the remains are on the floor of the burrow or not. The central position of the remains in the concretion instead of being in contact with the margins of it could be considered as negative evidence to the preservation within burrows *sensu* Feldmann et al. (2012). For Hyžný (2011), the remains of decapods buried alive may be occupying the middle of the burrow filling in the case of vertical shafts. Although there is a possibility of preservation in the middle of the concretion, this is not the case of the studied concretions as they are not vertical shafts.

Regarding the sedimentary fabric, parallel and ripple cross laminations does not form inside burrows, because although the exchange of water is active, it occurs because of the movement of the pleopods and uropods while the shrimps are breathing or feeding (Kornienko 2013), then the presence of any of these structures can be considered as a strong negative criterion. Tidal signature can be recorded in the burrow fill leaving heterolithic lamination, but the characteristics observed in the studied concretions do not fulfill the criteria proposed by Gingras and Zonneveld (2015) for tubular tidalites.

In those cases, with conflicting evidence, as concretion CPBA Nº 23654, which presents lamination above the level at which the specimens are preserved, the evaluation of the following evidence was a valuable tool: 1) disposition of the elements, 2) congruence in orientation of different specimens and 3) the absence of dispersion of the elements. These characteristics are considered as positive evidence pointing to within burrow preservation, even though outer ripple cross lamination was present (see Table 2).

Those specimens whose concretions are thought to have formed outside their burrows (CPBA Nº 23656, 23659), probably underwent a similar taphonomic history as the nephropids studied by Feldmann et al. (2012). The remains placed outside the burrows were covered relatively fast by sediment, and then the concretion was formed in an early diagenetic phase.

Finally, the remaining specimens and their concretions did not preserve strong evidence to distinguish if they have formed within their burrows or not. However, the disposition of the remains, including the relation of the segments of one specimen and the orientation and congruence of different individuals within a concretion, and the dispersion of the rests are strong evidence of preservation in a confined space for the concretions CPBA N° 23640, 23641, 23643, 23644, 23645, 23648, 23654, 23655, and 23660.

On the other hand, the presence of sedimentary structures as parallel or ripple cross lamination crossing the fossil remains is strong evidence of preservation outside the burrow on the sediment-water interface. This situation occurs in concretions CPBA N° 23650, 23651, 23656, and 23659.

The available weaker information in some of the concretions, including positive and negative evidence (Table 2), is

Table 2. Positive and negative evidence in the studied concretions. N/A: Not Applicable.

Concretion CPBA N°	Configuration of the remains		Dispersion within the concretion	Sedimentary fabric in margins vs. center of the concretion	Association with burrow systems	Position of the specimen in the concretion	Shape	Both chelae	Interpretation
	Disposition of tagmata	Congruence between individuals							
23640	+	+	+	+	+	-	-	N/A	Within the burrow
23641	+	+	+	+	+	-	-	+	Within the burrow
23642	+	N/A	+	+	+	-	-	N/A	Insufficient information
23643	+	+	+	+	+	-	-	N/A	Within the burrow
23644	+	+	+	+	+	-	-	N/A	Within the burrow
23645	+	+	+	+	+	-	-	+	Within the burrow
23646	+	N/A	+	+	+	-	-	N/A	Insufficient information
23647	+	N/A	+	+	+	-	-	N/A	Insufficient information
23648	+	+	+	+	+	-	-	N/A	Within the burrow
23649	+	N/A	+	+	+	-	-	N/A	Insufficient information
23650	+	+	+	-	+	+	-	+	Sediment-water interface
23651	+	N/A	+	-	+	-	-	N/A	Sediment-water interface
23652	+	N/A	+	+	+	-	-	+	Insufficient information
23653	N/A	N/A	N/A	+	+	-	-	-	Insufficient information
23654	+	+	+	-	+	-	-	N/A	Within the burrow
23655	+	+	+	+	+	-	-	N/A	Within the burrow
23656	-	N/A	+	-	+	-	-	+	Sediment-water interface
23657	+	N/A	+	+	+	-	-	N/A	Insufficient information
23658	+	N/A	+	+	+	-	-	N/A	Insufficient information
23659	+	N/A	+	-	-	-	+	N/A	Sediment-water interface
23660	+	+	+	+	-	-	+	N/A	Within the burrow
23661	+	N/A	+	+	-	-	-	N/A	Insufficient information

considered insufficient to conclude if the decapods fossilized within their burrows or in the sediment-water interface. However, it does not exclude the possibility of fossilization within the burrows, because the disposition and connection of the preserved segments, their fragility, and the lack of dispersion of them suggest they were in a sheltered place.

Paleobiological implications for fossil axiid decapods

The ecology of extant Axiidae and, in particular, the morphology of their burrows, are not well known because of the difficulty of studying this fossorial and cryptic group. In particular, the burrows of *Axius serratus* Stimpson, 1852 and *Axiopsis* *serratifrons* (A. Milne-Edwards, 1873) are known from *in situ* resin castings. These burrows consist of vertical shafts and several chambers at different depths, which are more than 2.5 m for *A. serratus* and 30 cm in *A. serratifrons* (Pemberton et al. 1976, Dworschak and Ott 1993, Kneer et al. 2013). The number of axiidean shrimps living in a given burrow system is variable. Specimens of *A. serratifrons* live in pairs and male and female of *Neaxius acanthus* (A. Milne-Edwards, 1879) live in the same burrow (Kneer et al. 2008, 2013). This pattern was also observed in the infraorder Astacidea: *Nephrops norvegicus* (Linnaeus 1758) can live in pairs, in some cases two individuals of the same sex (Rice and Chapman 1971). In other axiideans, only one individual inhabits the burrow, as the case of *Neotrypaea japonica* (Ortmann, 1891) and *Corallianassa coutierei* (Nobili, 1904). More than 100 ghost shrimps were extracted from burrows inhabited by *Callichirus major* (Say, 1818), developed in an area with only 10 surface openings (Pryor 1975, Tamaki et al. 1992, Kneer et al. 2008).

The length of time that the shrimps spend inside the burrows is an important factor. In general, it is thought that they spend most of their lives in the burrows; in some cases they get close to the burrow openings at night, and get out only then, as was shown in *A. serratifrons* and *C. longiventris* (A. Milne-Edwards, 1870), but in other cases they do not leave their burrows, as is the case of *N. acanthus* (Kensley 1981, Dworschak and Ott 1993, Kneer et al. 2008). Some species of Callianasoidea (*sensu* Poore et al. 2019) leave their burrows when they are about to die or if they are sick, because they cannot maintain the water current inside the structure, which is necessary for breathing (Rasmussen 1971, Schäfer 1972, Frey et al. 1978).

In the studied case, the presence of more than one exuvia in the same concretion suggests that *Protaxius* sp. molted within special chambers in the burrow systems, probably terminal chambers, distant of external disturbances, which would determine the position of the exuviae in only one direction because the animal can only exit backwards pushing the exuvia forward (Bishop 1986, Hyžný and Klompmaker 2015). Molting within the burrows has been reported by Schäfer (1972) in *Callianassa* Leach, 1814.

Some concretions (e.g., CPBA Nº 23645, 23648, 23654) preserve more than one specimen of different sizes, which would be interpreted as several exuviae of one shrimp. Other concretions have specimens of the same size (e.g., CPBA N° 23640, 23641, 23643, 23660), therefore, they would correspond to several exuviae and/or carcasses of different shrimps inhabiting the same burrow, at the same time, or belonging to different cohorts. This pattern suggests a gregarious behavior (Fig. 8). Extant axiideans are commonly related to antagonistic behavior and living individually or in pairs (Dworschak et al. 2012 and references therein). However, the knowledge of their biology is limited, and some assumptions were done without an empirical basis (Hernáez 2018). Similar to our interpretation, gregariousness was also suggested for

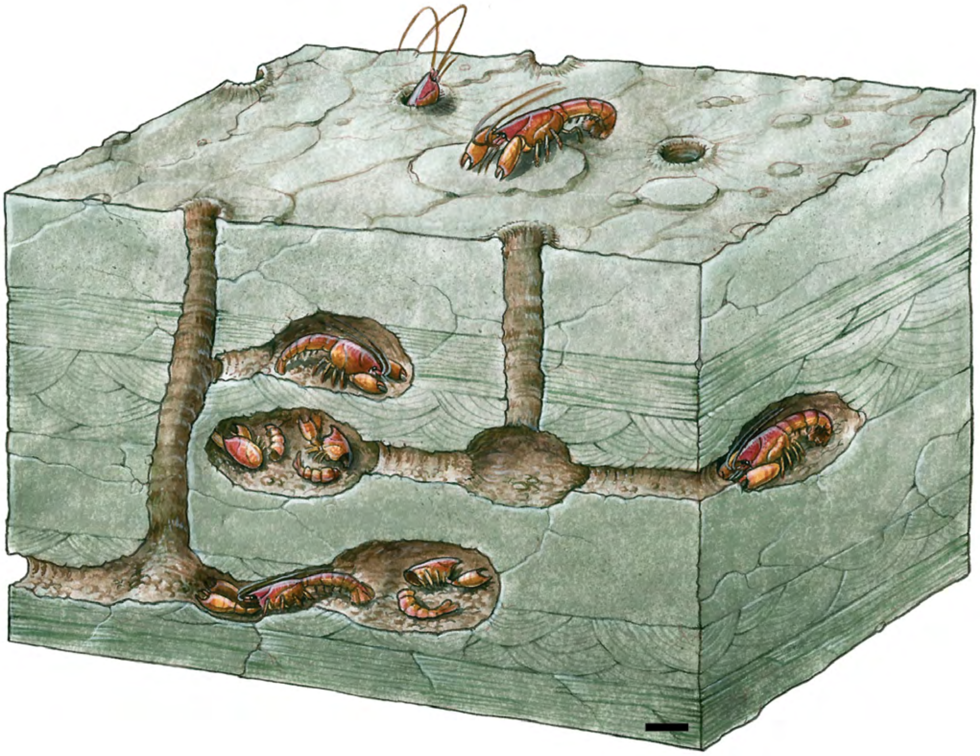

Figure 8. Reconstruction of the paleobiology of *Protaxius* sp. in the proximal offshore to inner shelf setting, Pilmatué Member, Agrio Formation. Several specimens shared their burrows, with chambers at different depths, in which molting took place. Decapods probably lived most of the time within their burrows, spending little time outside them. Lithology is mainly siltstones and fine-grained sandstones massive or with parallel/ripple cross laminations. Depth of the burrow system is not known and is out of vertical scale. Approximate horizontal scale = 2 cm.

other fossil axiideans (Mourik et al. 2005, Hyžný 2011, Hyžný and Summesberger 2019). Mourik et al. (2005) proposed that if death occurred within burrows, living inhabitants could transport those remnants to dead endings of the burrows, in order to not obstruct the tunnels. This idea was mentioned by Bishop and Williams (2005), although it has not been proved (Hyžný and Klompmaker, 2015). On the other hand, Hyžný and Summesberger (2019) interpreted that molts of different individuals were preserved in blind tunnels that were sealed off, supporting the idea of a gregarious community. Studied specimens from the Agrio Formation coincide with the latter interpretation in Callianassidae, although more extensive research is needed in relation with the biology of fossil and extant axiids to avoid inaccurate extrapolations.

The environment inhabited by *Protaxius* sp. was placed in the proximal offshore to inner shelf settings, with relative low energy demonstrated by associated fine-grained facies (Fig. 8).

CONCLUSIONS

The affirmation that fossorial decapod crustaceans in concretions represent preservation within their burrows is not always certain and it is not easy to affirm without supporting evidence. Here, we analyzed specimens from the Agrio Formation taking into account a number of criteria proposed previously by different authors. The studied specimens and their respective concretions did not have direct evidence such as preservation of part of the burrow or direct association of body with trace fossils in the bearing-beds. As seen above, if only one criterion is evaluated, it cannot lead to a definite conclusion. Two statements are derived from that: a) in fossorial decapod fossil material showing equivocal evidence of being preserved within their burrows, the most correct form to approximate to the site of fossilization seems to be the use of several criteria, and b) these criteria have different relative importance, and the combination of the strongest allows for a more precise interpretation.

We propose here that the disposition of the segments, orientation of the individuals and lack of dispersion in a concretion are important criteria for indication of preservation within burrows, and, on the other hand, presence of sedimentary structures as a strong indicator of preservation outside burrows on the sediment-water interface, especially when these structures are at the same level of the body fossils.

The distribution patterns of shrimps seen in the studied concretions indicates the presence of special chambers for molting, while the presence of exuviae of different individuals point to a gregarious life habit for *Protaxius* sp.

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