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# Analysis of *Asteriacites* von Schlotheim 1820 from Mulichinco Formation (Lower Cretaceous, Neuquén Basin) and ichnotaxonomic implications

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## ABSTRACT

The last review of *Asteriacites* (Knaust and Neumann 2016) dismissed sculpture as an ichnotaxobase for this ichnogenus and used simple morphometric parameters to differentiate the ichnospecies, reducing them to three: *A. lumbricalis*, *A. stelliformis*, and *A. quinquefolius*. In this work, ichnotaxonomic tools are discussed through the analysis of trace fossils assigned to this ichnogenus from the Mulichinco Formation (Valanginian) of the Neuquén Basin, northern Patagonia. New *Asteriacites*-bearing levels from different localities are described, and specimens that were previously assigned to *A. lumbricalis* are reassigned to *A. stelliformis*. Taking into account this material and previous works where *Asteriacites* were analysed, we observed that some problems arise in the ichnospecific assignment when applying the methodology of Knaust and Neumann (2016). Therefore, in this work, three simple criteria were incorporated to facilitate the ichnospecific assignment through this morphometric approach. It is also noted that the specimens with epirelief preservation are challenging to identify because the delineation of the edge of the trace, necessary for the morphometric analysis, depends on the used methodology. Additionally, examples of previous works are analysed, allowing discussion of proposed ichnospecific ichnotaxobases and the relevance of sculpture.

**Keywords:** Valanginian, ichnotaxonomy, morphometric analysis, Asteroidea, ornamentation.

## RESUMEN

*Análisis de* Asteriacites *von Schlotheim 1820 de la Formación Mulichinco (Cretácico Inferior, Cuenca Neuquina) y las implicancias icnotaxonómicas.*
La última revisión de *Asteriacites* (Knaust y Neumann, 2016) descartó a la ornamentación como icnotaxobase para este icnogénero y diferenció las icnoespecies en base a parámetros morfométricos simples, reduciendo las válidas a tres: *A. lumbricalis*, *A. stelliformis* y *A. quinquefolius*. En este trabajo se discuten las herramientas icnotaxonómicas a través del análisis de trazas fósiles pertenecientes al icnogénero provenientes de la Formación Mulichinco (Valanginiano) de la Cuenca Neuquina, en Patagonia septentrional. Se describen nuevos niveles de *Asteriacites* de distintas localidades y *Asteriacites* previamente asignadas a *A. lumbricalis* son reasignadas a *A. stelliformis*. Teniendo en cuenta trabajos previos donde se analizan especímenes del icnogénero, surgieron algunos problemas al momento de asignar icnoespecificamente al aplicar la metodología de Knaust y Neumann (2016). Por lo tanto, se han incorporado tres criterios simples para facilitar la asignación icnoespecífica a través de un enfoque morfométrico. También se observa la dificultad de la asignación icnotaxonómica en los ejemplares preservados en epirrelieve negativo debido a que la delimitación del borde de la traza

fósil, necesaria para el análisis morfométrico, dependerá de la metodología utilizada. A su vez, se analizaron ejemplares de trabajos previos, permitiendo discutir las icnotaxobases icnoespecíficas propuestas y la relevancia de la ornamentación.

**Palabras clave:** Valanginiano, icnotaxonomía, análisis morfométrico, Asteroidea, ornamentación.

## INTRODUCTION

*Asteriacites* von Schlotheim 1820 consists of star-shaped trace fossils generally classified as resting traces (Cubichnia) of ophiuroids or asteroids (e.g., Seilacher 1953, Ishida et al. 2013). This trace fossil is considered to be a shallow burrow produced by the organism´s tube feet (Seilacher 1953, Seilacher 2007). *Asteriacites* has been recorded from Cambrian to recent (e.g., Mikuláš 1992, Mángano et al. 1999, Bell 2004, Cook 2007).

For many decades, the validity of *Asteriacites* was discussed (Seilacher 1953, Osgood 1970, Schlirf 2012) until Knaust and Neumann (2016) rediscovered the type material of *Asteriacites* and put the ichnogenus on a firm foundation. The authors reduced the ichnospecies to three: *Asteriacites lumbricalis* von Schlotheim 1820, *Asteriacites quinquefolius* (Quenstedt 1876) Seilacher 1953, and *Asteriacites stelliformis* (Miller and Dyer 1878) Osgood 1970. They emended the diagnosis of the ichnogenus and its three ichnospecies. The difference between *A. quinquefolius* and *A. stelliformis* was based on the ratio of arm length versus arm width. In the case of *A. lumbricalis*, the authors used the presence of arm imprints distinctly set off from a central disc to differentiate it from the other ichnospecies. They studied the three type specimens and defined *A. quinquefolius* to include specimens with a length/width ratio of the arm imprint of less than 2, while *A. stelliformis* has a length/width ratio of more than 2.

Previously, the diagnoses of ichnospecies of *Asteriacites* were based on the sculpture (striae) observed in the arms (e.g., Seilacher 1953). However, Knaust and Neumann (2016) argued that sculpture is a subordinate value compared with the morphometric data because it has a strong relation with taphonomic circumstances.

In the last few decades, *Asteriacites* specimens have been recorded in Jurassic and Lower Cretaceous shallow-marine successions from the Neuquén Basin (McIlroy et al. 2005, Rodríguez et al. 2007, Fernández et al. 2013, Fernández et al. 2019, Pazos et al. 2019). However, most of the Lower Cretaceous specimens were analysed before Knaust and Neumann (2016) emended the diagnosis. The objective of this work is (1) to analyse the specimens from the Mulichinco Formation (Lower Cretaceous) based on the emended diagnoses; (2) to describe some problems that have arisen during the ichnotaxonomic analysis when applying the morphometric method of Knaust and Neumann (2016) and test if these problems occur in selected specimens worldwide; and (3) to present criteria used to facilitate this analysis under the current diagnoses.

## GEOLOGICAL SETTING

The Neuquén Basin is located in west-central Argentina between 34° and 41° S (Fig. 1a). It represents an epicontinental basin in a back-arc position to the Palaeo-Pacific Andean subduction zone (e.g., Howell et al. 2005, Zapata and Folguera 2005). It contains a thickness of more than 7000 m of marine and continental deposits from Late Triassic to Palaeogene (Fig. 1b) making the Neuquén Basin a unique example when compared with other basins along the Andean chain (Vergani et al. 1995, Legarreta and Uliana 1999, Horton 2018). Most of the Jurassic and Early Cretaceous deposits formed in marine settings while temporarily enhanced subsidence and sea-level fluctuations accentuated the diverse facies and highly fossiliferous units that allow the construction of a robust biostratigraphic framework (Howell et al. 2005, Aguirre-Urreta et al. 2007). The trace fossils analysed here were recorded in marine intervals of the Mulichinco Formation.

The Mulichinco Formation of the Mendoza Group (Weaver 1931) is early to late Valanginian (Aguirre-Urreta and Rawson 1997, 1999, Aguirre-Urreta et al. 2005). According to the position in the basin, this unit presents regional differences, including continental (south) to marine (north) deposits with siliciclastic and mixed siliciclastic–carbonate sedimentation (Schwarz and Howell 2005, Schwarz et al. 2011, 2016).

The present work analyses in detail specific intervals of the Mulichinco Formation logged at Puerta Curaco, Pampa de Tril, Vega de Escalone and Barranca de los Loros localities, located between 37º 11´ 13´´/37º 23´ 1.93´´ S and 69º 47´ 17´´/ 69º 56´ 8.01´´ W (Fig. 1a). Following the stratigraphic scheme proposed by Schwarz et al. (2011), these localities belong to the informally named “Septentrional” area of the unit, where sedimentary deposits are only represented by ma-

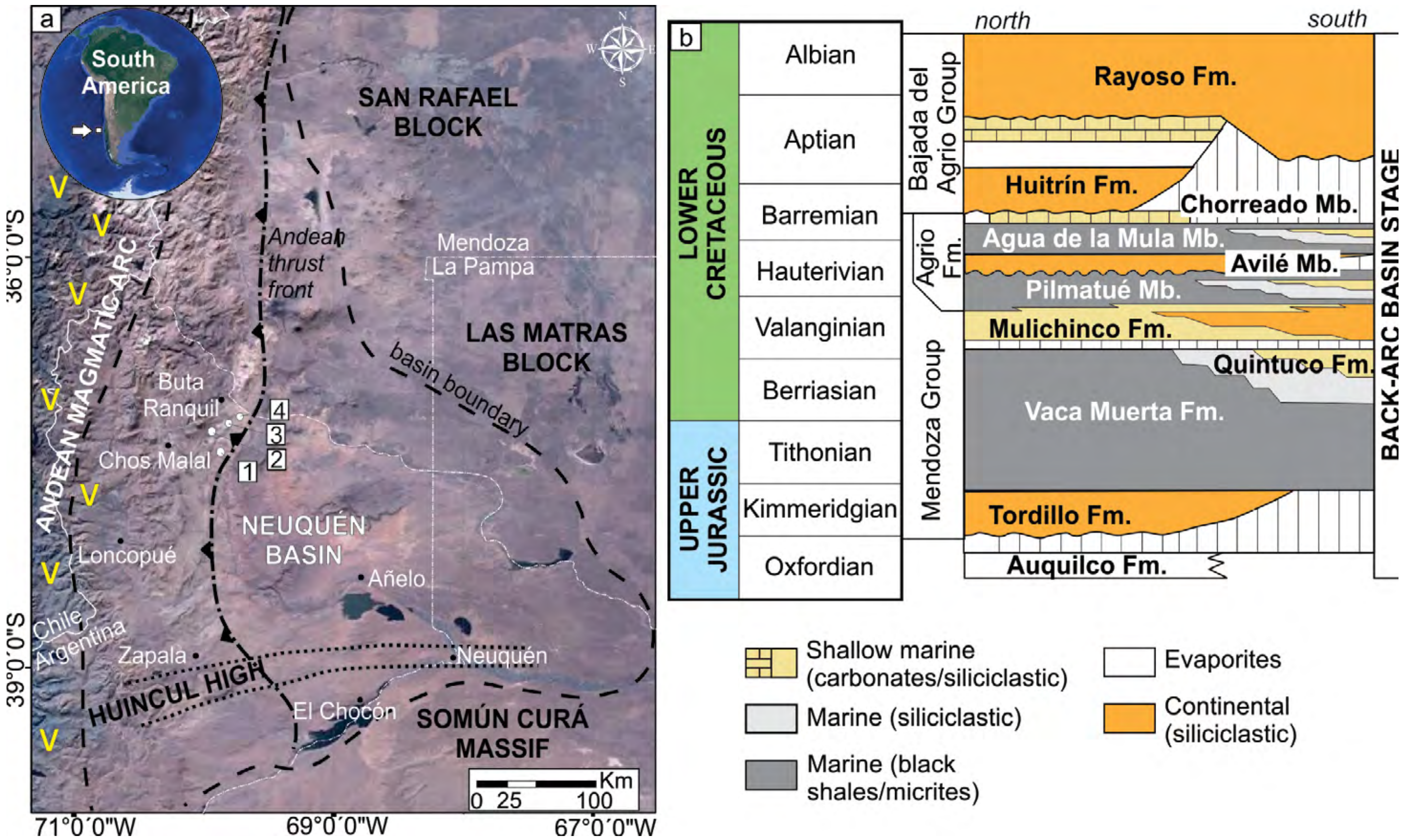


**Figure 1.** a) Satellite image of the Neuquén Basin in northern Patagonia (modified from Naipauer et al. 2015). Studied localities: (1) Puerta Curaco, (2) Pampa de Tril, (3) Vega de Escalone, (4) Barranca de los Loros; b) Upper Jurassic−Lower Cretaceous stratigraphic chart for the Neuquén Basin (modified from Howell et al. 2005). In this work, the analysed specimens come from the Mulichinco Formation of the Mendoza Group.

rine facies with mixed siliciclastic–carbonate sedimentation. The Mulichinco Formation contains body fossils of bivalves, gastropods, nautiloids, ammonoids, decapod crustaceans, and echinoderms, among other invertebrates (e.g., Schwarz 1999, 2003, Aguirre-Urreta 1989, Aguirre-Urreta et al. 2008, Luci and Lazo 2012, Fernández et al. 2014).

## METHODOLOGY

In this study, 35 specimens from the Mulichinco Formation (Neuquén Basin) were analysed. Samples are housed in the Palaeontology Collection of the Department of Geological Sciences, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires under the collection number CPBA. The specimens were analysed following the methodology of Knaust and Neumann (2016). The ratio of arm length versus arm width was calculated from the maximum length (measured from the central point to their tip) and the maximum width (measured at their base). For measurements, a millimetric calibre and the software Adobe Illustrator were used on samples and photographs, respectively. Further specimens from previous works were also measured (through photographs) for the methodological discussion, including material from Ireland, the United States of America, Spain and Japan (Buckman 1992, Rindsberg 1994, Mángano et al. 1999, Wilson and Rigby 2000, Carrasco 2011, Ishida et al. 2019). The ratio of arm length versus arm width from all the specimens (with the exception of those assigned to *Asteriacites lumbricalis*) was plotted in a graphic, where one point represents a single arm imprint, and a set of points represents one specimen.

Subsequently, a line was drawn in the graphic that marks the ratio of arm length versus arm width = 2, i.e., the ratio that separates *A. quinquefolius* from *A. stelliformis*. The area above the line belongs to the values expected for *A. stelliformis* and the area below to those expected for *A. quinquefolius* (see Ichnotaxonomical assignment and methodological discussion). In one previous study, Singh et al. (2017) used a similar graphic to give an ichnospecific assignment to *Asteriacites* specimens. However, they did not detail the procedure. Morphological terms and names follow the discussions in Bertling et al. (2006), Bertling (2007), and Rindsberg (2018).

## *Asteriacites*-BEARING BEDS

Regardless of the locality, *Asteriacites* are present in beds within intervals equivalent to the informally named “Lower Member” and the “Middle Member” (*sensu* Schwarz 2003, Schwarz et al. 2011). In the “Septentrional” area, these intervals are interpreted as mostly comprising offshore to upper shoreface deposits with some tidal influence (e.g., Schwarz 2003, Schwarz et al. 2006, Rodríguez et al. 2007, Schwarz et al. 2011, 2016, Fernández 2013). The logged intervals record mixed siliciclastic—carbonate sedimentation with sandstones that show wave-related structures such as combined-flow and

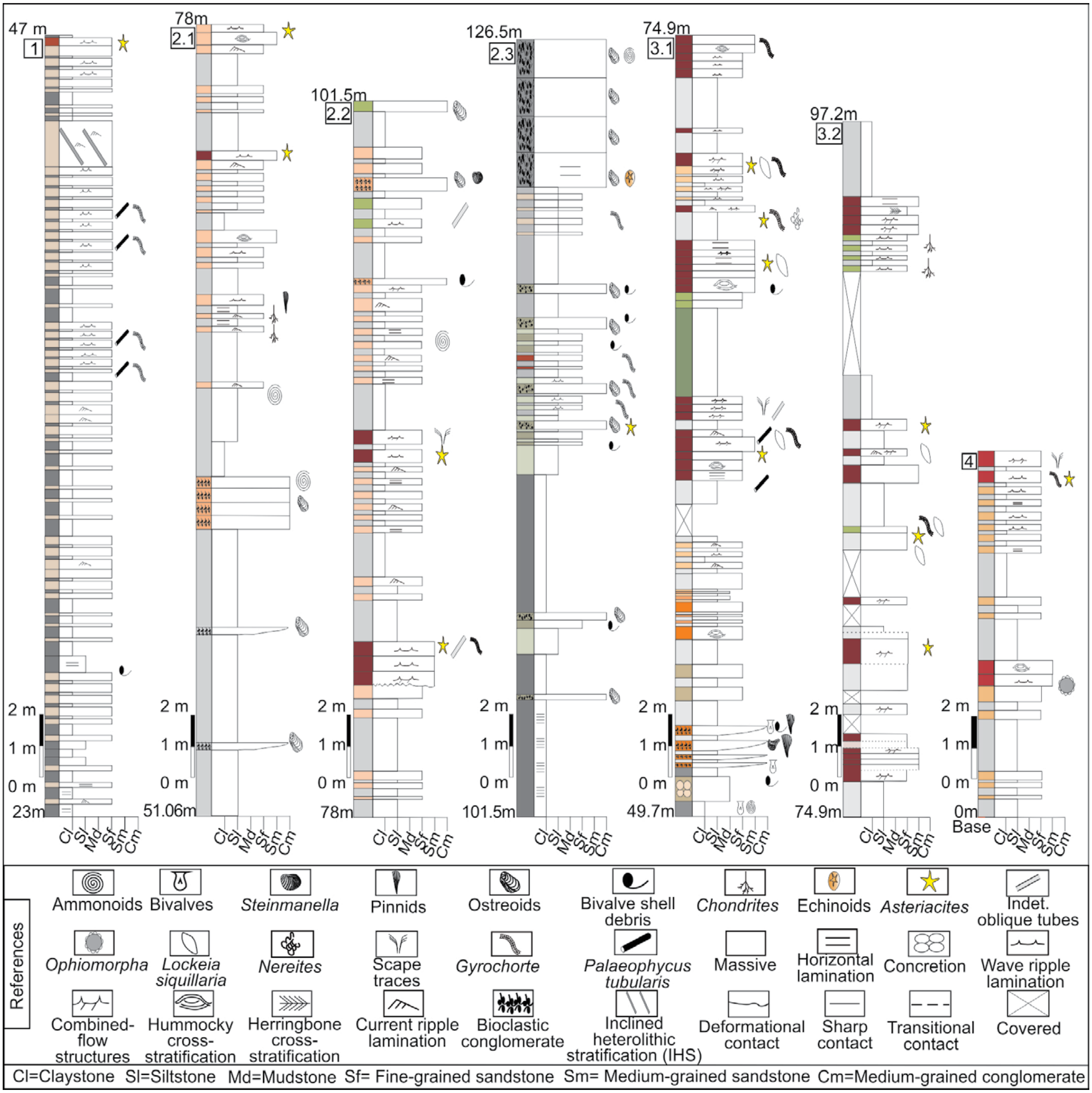


**Figure 2.** Logged intervals where *Asteriacites* specimens were registered with main sedimentological characteristics (modified from Fernández 2013). The studied localities are, from south to north: (1) Puerta Curaco, (2.1-2.3) Pampa de Tril, (3.1-3.3) Vega de Escalone and (4) Barranca de los Loros.

wave ripples as well as hummocky cross-stratification indicating deposition above the storm-wave base (Fig. 2). In Vega de Escalone and Barranca de los Loros, herringbone cross-stratification associated with mud drapes and inclined heterolithic stratification point to tidal currents as another mechanism that controlled sedimentation (Fernández 2013). The detailed facies analysis that includes Pampa de Tril—Barranca de los Loros localities confirms a tide—influenced environment indicating deposition along an irregular paleocoastline affected by wave and tidal processes (Sleveland et al. 2020).

These *Asteriacites* are usually associated with *Gyrochorte comosa* Heer 1865 (Fig. 3a), *Nereites* MacLeay 1839 (Fig. 3b), cf. *Arenicolites* Salter 1857 (Fig. 3c), or cf. *Palaeophycus* Hall 1847 (Fig. 3d) among other trace fossils (e.g., *Lockeia*), as was recorded in previous works (Rodríguez et al. 2007, Fernández 2013, Fernández et al. 2018). In Puerta Curaco, the specimens are present in one sandstone bed dominated by wave-ripple lamination within a heterolithic interval at 47 meters above the contact with the underlying Vaca Muerta Formation; this interval contains inclined heterolithic stratification (Fig. 2, section 1). In Pampa de Tril, the *Asteriacites* are present in five sandstone beds at the top of heterolithic intervals with wave-ripple lamination, combined-flow structures, and hummocky cross-stratification between 74 and 113 meters above the contact with the Vaca Muerta Formation (Fig. 2, section 2). In Vega de Escalone, the *Asteriacites* are present in seven sandstone beds with combined-flow structures within heterolithic intervals between 62 and 88 meters from the base of the Mulichinco Formation (Fig. 2, section 3). In Barranca de los Loros, they are present in one sandstone bed within a heterolithic interval dominated by wave ripple lamination and combined-flow structures at 10 meters above the contact with the underlying Vaca Muerta Formation (Fig. 2, section 4).

In summary, at all localities the *Asteriacites*-bearing beds characterise fair-weather sedimentation under a relatively low-energy regime and correspond to shallow depositional settings interpreted as wave-dominated and tidal-influenced shoreface deposits.

## ICHNOLOGY

### Description of *Asteriacites* from the Mulichinco Formation

Previously, *Asteriacites* specimens in this unit were described in only two sandstone beds at Vega de Escalone (Rodriguez et al. 2007). Here, more stratigraphic levels are introduced from this and the other three localities aforementioned.

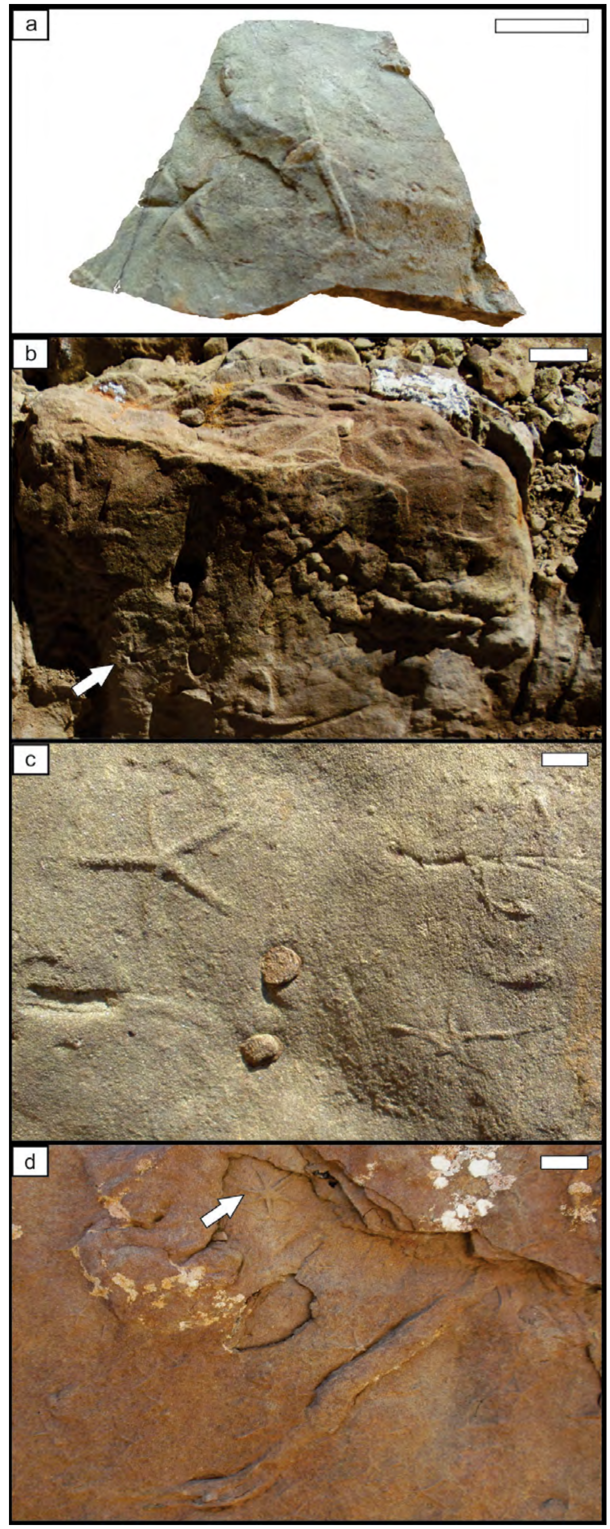


**Figure 3.** Trace fossils associated with *Asteriacites* from Mulichinco Formation. a) *Gyrochorte* in positive epirelief with *Asteriacites stelliformis* in negative epirelief from Vega de Escalone; b) *Nereites* (see Fernández et al. 2018, Fig. 3B) with *Asteriacites lumbricalis* (white arrow) in negative epirelief from Vega de Escalone; c) cf. *Arenicolites* in cross section with *Asteriacites stelliformis* in positive hyporelief from Barranca de los Loros; d) cf. *Palaeophycus* and *Asteriacites lumbricalis* in positive hyporelief from Barranca de los Loros. Scale bar: 1 cm in c, 2 cm in a and d, and 4 cm in b.

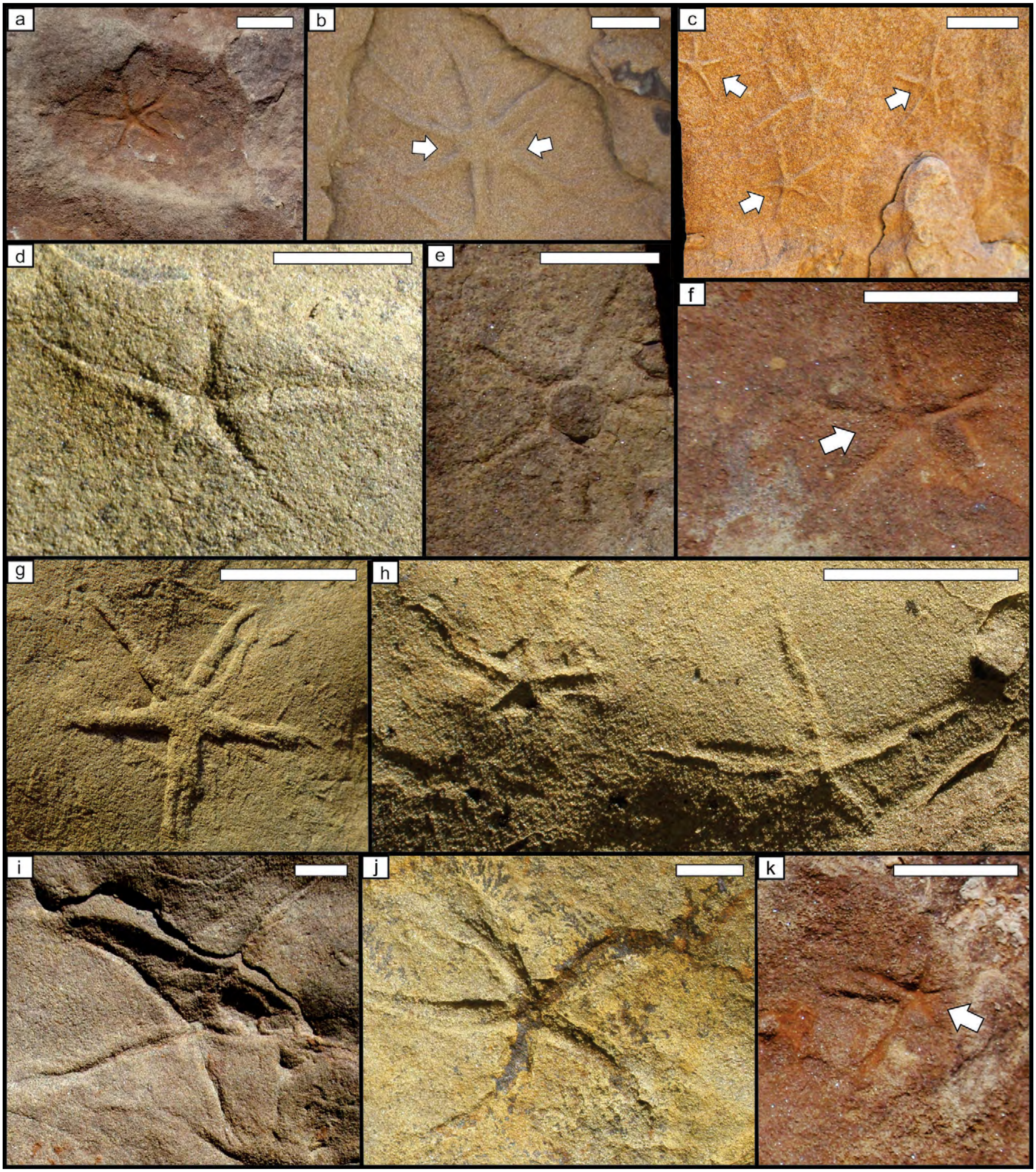


**Figure 4.** Examples of *Asteriacites* of Mulichinco Formation from Neuquén Basin. a) *A. lumbricalis* in negative epirelief from Puerta Curaco (specimen 25); b) *A. lumbricalis* in positive hyporelief from Barranca de los Loros (specimen 10, see white arrow; the lateral repetition was disregarded); c) *A. lumbricalis* in positive hyporelief from Vega de Escalone (upper left: specimen 18, down left: specimen 19 and right: 20, see white arrows; other poorly preserved specimens were disregarded); d) *A. stelliformis* in negative epirelief from Pampa de Tril (specimen 17); e) *A. lumbricalis* in negative epirelief from Pampa de Tril (specimen 9); f) *A. stelliformis* in negative epirelief from Puerta Curaco (specimen 26; see white arrow); g) *A. stelliformis* in positive hyporelief from Pampa de Tril (specimen 3; the lateral repetition was disregarded); h) *Asteriacites* in negative epirelief from Pampa de Tril. Right: *A. stelliformis* in (specimen 23). Left: *Asteriacites* isp. Indeterminate (specimen 22); i) *A. stelliformis* in negative epirelief from Pampa de Tril (specimen 2); j) *A. lumbricalis* in positive hyporelief from Barranca de los Loros (specimen 1; CPBA 20446); k) *A. stelliformis* in negative epirelief from Puerta Curaco (specimen 27). Scale bar: 2 cm.

The specimens are star-shaped trace fossils with five or less radiating arm imprints (Fig. 4). Some present a distinctive central disc with slender arms having rounded or slightly pointed tips (e.g., Fig. 5a). Most of these samples show straight arms. Other specimens have an undifferentiated centre and arms with rounded or slightly pointed tips (e.g., Fig. 5b). Some of these specimens present striae on both sides of the arm. The striation is perpendicular to the arm axis (e.g., Fig. 5c), and one sample presents V-shaped to irregular striae (e.g., Fig. 5d). Most specimens are small: the maximum diameter is about 30 mm (e.g., Fig. 5b). The length of the arms is between 3.9 and 27 mm, and the width of the arms is between

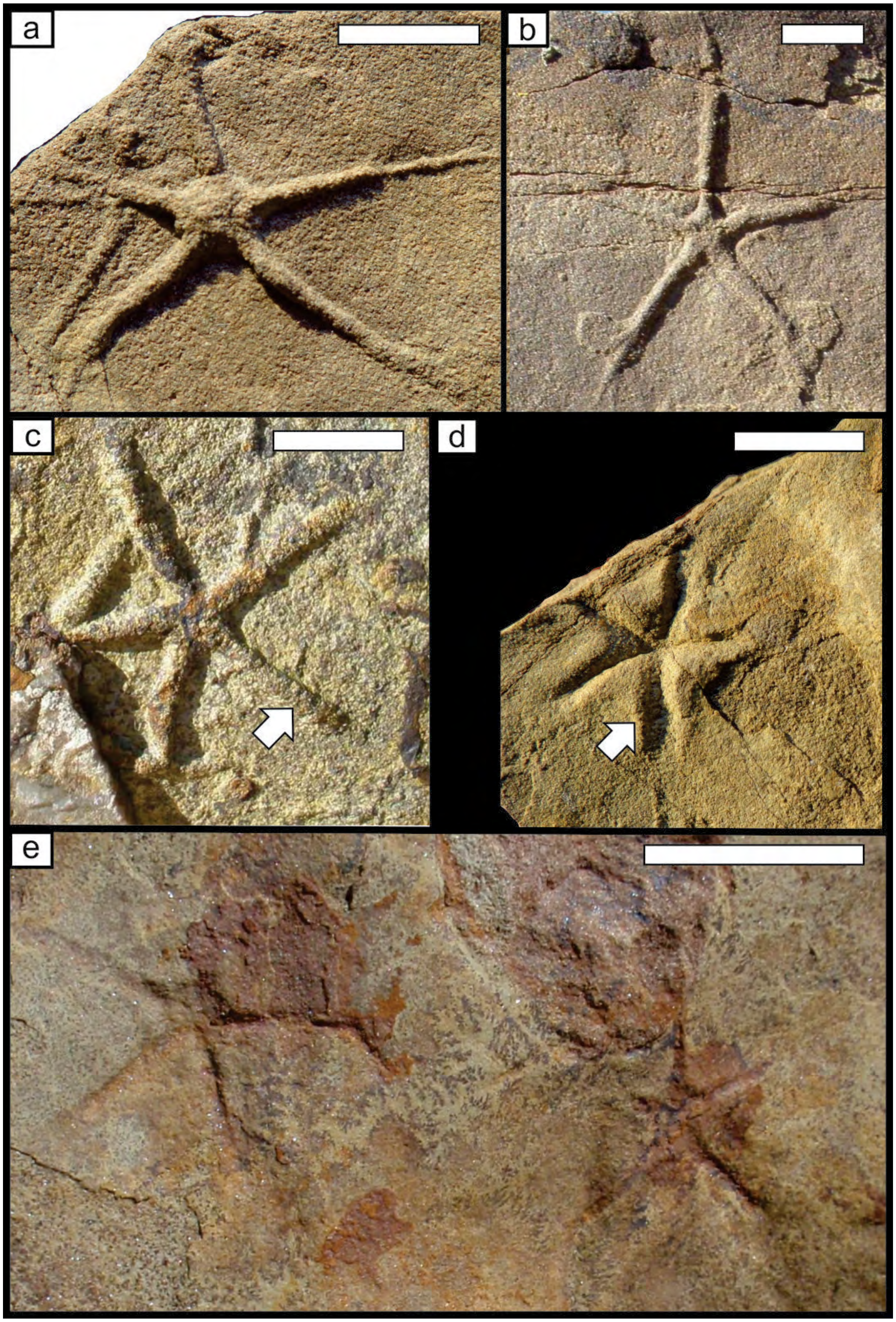


**Figure 5.** Examples of the studied specimens with the characteristics described in the text. a) Specimen with a distinctive central disc and slender arms with rounded or slightly pointed tips. *A. lumbricalis* in positive hyporelief from Pampa de Tril (CPBA 20447.2: specimen 14); b) Specimen with an undifferentiated center and arms with rounded or slightly pointed tips. *A. stelliformis* in positive hyporelief from Pampa de Tril (photograph taken in the field; specimen 4); c) Specimen with striae on both sides of the arm. The striae are perpendicular on the arm (see white arrow). *A. stelliformis* in positive hyporelief from Pampa de Tril (photograph taken in the field; specimen 5); d) Specimen with V-shaped to irregular striae (see white arrow). *A. stelliformis* in negative epirelief from Pampa de Tril (CPBA 20448; specimen 15); e) *A. lumbricalis* in negative epirelief from Pampa de Tril (photograph taken in the field; specimen 7 and 8). Scale bar: 2 cm

0.41 and 3.8 mm. Some specimens are preserved as epirelief (e.g., Fig. 5e), and others present hyporelief preservation (e.g., Fig. 5d).

## Ichnotaxonomical assignment and methodological discussion

In figure 6, the arm length versus arm width was plotted for each arm in each specimen (20), except those who are assigned to *Asteriacites lumbricalis*. Most of the specimens present a ratio greater than 2 (Table 1, Supplementary material). Although this morphometric method proposed for ichnospecific assignment is easy to use, some questions arose when these materials were studied and we compared with further specimens from previous works. The main problem that we observe was when on the same sample, the arms presented different measurement. Therefore, in this work, three simple criteria were defined: (1) when a specimen only preserves two arm imprints, an ichnospecific assignment cannot be made due to a lack of information; (2) with three or more arm imprints, the area with at least three points will be decisive for the ichnospecific assignment; (3) when one point is crossed by the line equal to 2, this point is disregarded.

The specimens that present a differentiated central disc, the diagnostic character of *Asteriacites lumbricalis*, were directly assigned to this ichnospecies. Concerning the other specimens, also following the diagnosis modified by Knaust and Neumann (2016), they belong to *A. stelliformis* because they present a ratio of arm length *versus* arm width between 2.59 and 24.21 (Fig. 6a). One specimen (specimen number 22, Fig. 4h left) cannot be assigned to an ichnospecies due to criterion number 1.

Previously, all the specimens known from Mulichinco Formation were assigned to *A. lumbricalis* (Rodríguez et al. 2007, Fernández 2013). However, in this work, most of the studied specimens are reassigned to *A. stelliformis*. The specimens that remain assigned to *A. lumbricalis* present a ratio of arm length versus width between 3.99 and 15.67 (Table 1, Supplementary material).

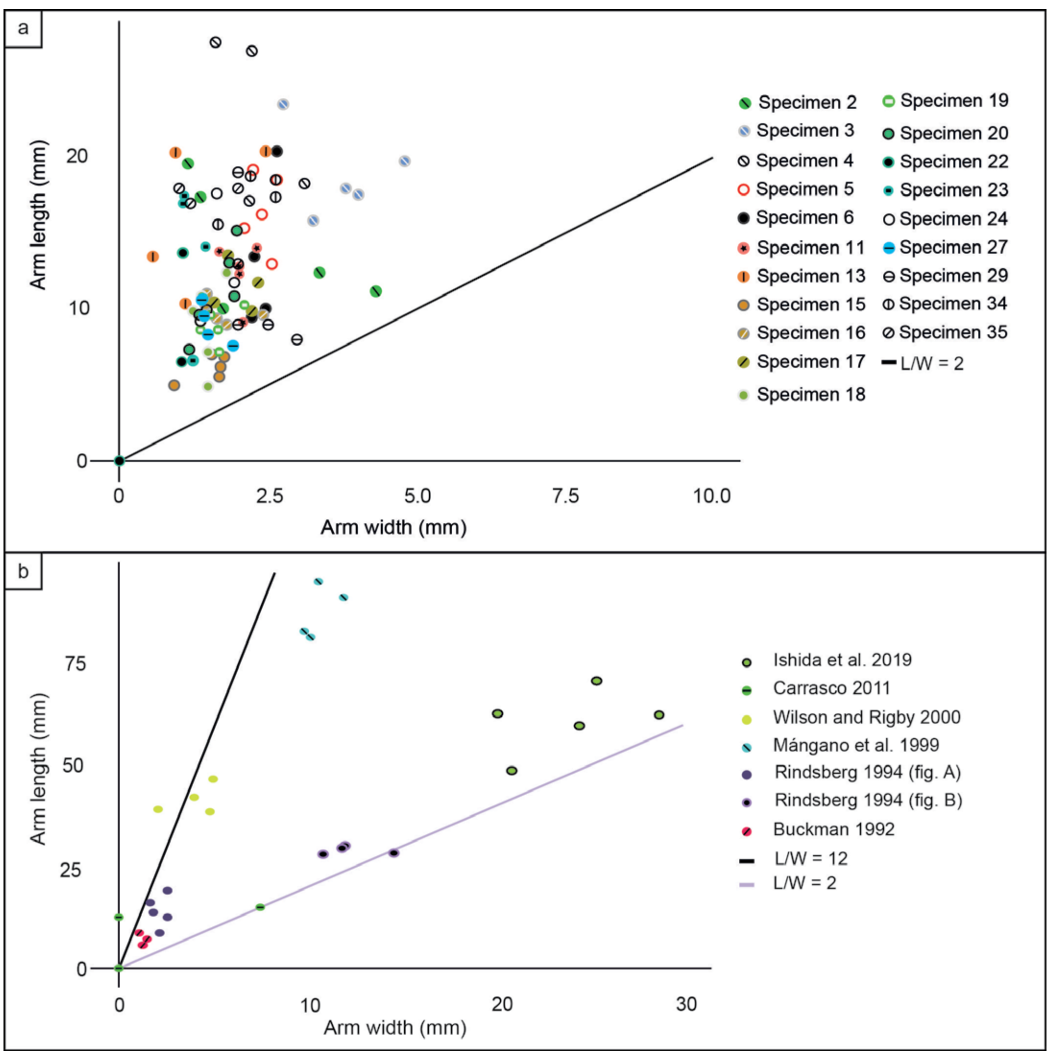


**Figure 6.** Morphometric analysis of length and width of the arm of *Asteriacites* specimens studied in this work (see Table 1, Supplementary material). a) Morphometric analysis of the specimens (20) from Mulichinco Formation (Neuquén Basin) except those assignable to *A. lumbricalis* (*sensu* Knaust and Neumann 2016). Specimen 22 could not be assigned to an ichnospecies; it only presents two arms; b) Morphometric analysis of specimens from previous works as mentioned in the text. Each colour represents one specimen and each point, one arm. L/W is the ratio of arm length versus width. L/W = 2 represents the limit between *A. quinquefolius* and *A. stelliformis* according to Knaust and Neumann (2016), while L/W = 12 is not diagnostic but typical of *A. lumbricalis*.

As mentioned before, three criteria were created to facilitate the ichnospecific assignation of the specimens from the Mulichinco Formation. Information from previous works that analysed *Asteriacites* samples under the diagnosis of Knaust and Neumann (2016) was also considered to establish these criteria (Singh et al. 2017, Fernández et al. 2019). For example, we believe that Singh et al. (2017) assigned specimens to *Asteriacites quinquefolius* from the Carboniferous Po Formation (Himalaya) using a criterion similar to what we here call criterion 2, but they did not make their method explicit. Fernández et al. (2019) analysed two specimens from Agrio Formation (Neuquén Basin): one was assigned to *A. stelliformis*, and the other was tentatively assigned to *A. stelliformis* or *A. quinquefolius* because it presents two arms with an arm length versus arm width ratio between 2.11 and 2.24 and three arms with an arm length versus arm width ratio between 1.80 and 1.96. It was also noted that the sculpture resembles that of *A. quinquefolius* (Fernández et al. 2019). However, in this work, this specimen is assigned to *A. quinquefolius* under the previously mentioned criterion 2. Rindsberg (1994) studied *Asteriacites* from the Upper Mississippian Hartselle Sandstone of Alabama (USA) and assigned them to *A. stelliformis* ("*A. stelliforme*" in Rindsberg 1994). From the two samples figured in that work, one (Rindsberg 1994; plate 1, fig. A) presents an arm length versus arm width ratio greater than 2, while the other sample (Rindsberg 1994; plate 1, fig. B) presents three arms with a ratio greater than 2 and one arm in which the ratio is less than 2 (Fig. 6b). In these examples, following the criterion 2, we confirm the assignment of both samples to *A. stelliformis*.

## DISCUSSION

### The arm length versus arm width of *A. lumbricalis*

Although the ratio of the arm length versus arm width of *A. lumbricalis* is not a diagnostic character, this ratio in our material differs from the one described by Knaust and Neumann (2016) for the type material of *A. lumbricalis* (ratio of the arm = 12 or 12.5). This is not the first time that a specimen assigned to this ichnospecies after the revision of *Asteriacites* by these authors presents a different ratio than 12 (Feng et al. 2019; ratio = 5−10). Besides the specimens assigned to *A. lumbricalis* from the Mulichinco Formation, other examples assignable to this ichnospecies were measured through photographs. For instance, a specimen from the lower Carboniferous Mullaghmore Sandstone (Ireland) described by Buckman (1992; Fig. 8j) clearly presents the diagnostic character of *A. lumbricalis* (a differentiated central disc with slender arms). However, the ratio of the arm length versus arm width in this specimen ranges from 4.31 to 7.89 (Fig. 6b). Another example is a specimen from the Pennsylvanian of Kansas (USA) described by Mángano et al. (1999; fig 3A) that presents a ratio of the arm between 7.62 and 8.96. Furthermore, some specimens of *Asteriacites lumbricalis* (*sensu* Wilson and Rigby 2000) from the Lower Triassic Thaynes Formation (USA) present a well-differentiated central disc (Wilson and Rigby 2000, Fig. 3), but the ratio of the arm is between 7.94 and 18.32 (Fig. 6b). Even though Knaust and Neumann (2016) did not present the ratio of the arm length versus arm width as a diagnostic character, the ratio of 12 or 12.5 of the type material of *Asteriacites lumbricalis* mentioned by the authors is not typical of this ichnospecies.

### Preservational features and their ichnotaxonomical implications

Knaust and Neumann (2016) did not explain the type of preservation of the holotypes of *A. stelliformis* and *A. quinquefolius*. However, from the photographs published in their work (and the cited references), it can be interpreted that they are preserved respectively as positive hyporelief and positive epirelief (negative in the centre). Specimens from the Mulichinco Formation are preserved as negative epirelief or positive hyporelief. In the first case, some problems arose when the length and width of the arm were measured because the edge of the arm is poorly differentiated. Here, the problem was resolved by calculating the mean of the measurements to obtain a more reliable result. This problem has also been described in other works. For example, it was briefly mentioned by Fernández et al. (2019), where the authors used photogrammetry to define the edge of the arm. In any case, it became clear that there is a problem in measuring the ratio of the length *versus* width of the arms in *Asteriacites* specimens that have negative epirelief preservation (in surface impressions or shallow undertraces). In these cases, the delineation of the trace boundary lies with the researcher and will depend on the methodology used, a problem well understood in vertebrate ichnology (Sarjeant 1975; page 285) but not that commonly considered in invertebrate ichnology. Probably, the lack of a defined edge in specimens preserved as negative epirelief implies that the use of morphometric characteristics proposed by Knaust and Neumann (2016) is not as useful nor as objective as these authors intended.

## Sculpture as an ichnotaxobase for *Asteriacites*

Knaust and Neumann (2016) concluded that sculpture only has a subordinate value compared with the morphometric parameter because it has an affinity with taphonomic circumstances and preservation pathways. However, we have observed that the specimens with epirelief preservation tend to present the edge of the arm more poorly differentiated than with hyporelief preservation. Moreover, the authors decided that the ichnotaxobases applied at ichnospecies level were morphology, morphometric parameters, and ornamentation (Knaust and Neumann 2016, Fig. 3) but in the emended diagnoses, they only included morphometric parameters and morphology of the trace fossil. As a consequence, they reduced the number of ichnospecies of *Asteriacites* from five to three ichnospecies. Carrasco (2017) briefly criticised this decision.

Carrasco (2011) created the ichnospecies *Asteriacites obtusus* and described the holotype as having a length (= radius, *sensu* Carrasco 2011) of the arm equal to 15 and a width of the arm equal to 7.50 (Carrasco 2011: Table 1). Therefore, the ratio of the arm length *versus* arm width of this specimen is equal to 2. Following the diagnosis modified by Knaust and Neumann (2016), this specimen cannot be classified in any ichnospecies. Nevertheless, these authors determined that *A. obtusus* is a junior synonym of *A. quinquefolius*. Even though Knaust and Neumann (2016) considered that sculpture is a subordinate value, Carrasco (2017) disagreed about the synonymisation and pointed out that *A. obtusus* does not present the tube foot bioglyphs that characterise *A. quinquefolius*. This is an example of the continuing controversy over the ichnotaxonomic value of sculpture for *Asteriacites*.

Here, the ratio of arm length versus arm width of one specimen (paratype of *A. obtusus* Carrasco, now known as *A. quinquefolius*) from Carrasco (2011, Fig. 2) was calculated, but only three arms could be measured. The ratio of the length *versus* width of the arm from this specimen is between 1.58 and 2.14 (Fig. 6b). Following criterion 2, this specimen cannot be classified in any ichnospecies. The assignation of this and other samples with the same problem could be solved modifying the diagnosis of *A. stelliformis* from an arm length versus arm width ratio of more than 2 to a ratio equal and greater than 2.

In a classic study, Seilacher (1953) conducted aquarium studies with asteroids and ophiuroids and concluded that the striae observed in their shallow burrows result from the movement of the tube feet. The author stated that structures assignable to *A. lumbricalis* are produced by ophiuroids, which can generate transverse (perpendicular to the arm axis) and more regular striae. In contrast, *A. quinquefolius* is produced by asteroids, which make a “shaggy” (sic. “zottig” in German) and less regular ornamentation with their tube feet. With this result, Seilacher (1953) differentiated *A. lumbricalis* from *A. quinquefolius*. Later, Osgood (1970) studied material from the Ordovician Corryville Formation (Ohio), previously analysed by Miller and Dyer (1878), and noted that these specimens presented “V”-shaped striae.

Osgood (1970) interpreted that this types of striae represent the last movement of the tube feet when the organism leaves the shallow burrow, and the author concluded that these specimens belong to *A. stelliformis*, rejecting the idea of this ichnospecies being a synonym of *A. lumbricalis* (Seilacher 1953). Later works have also supported the idea that the sculpture of these trace fossils indicates the movement of the tube feet and is a direct reflection of the behaviour of the tracemaker (e.g., Rindsberg, 1994; Mángano et al. 1999; Ishida et al. 2013, Ishida et al. 2017). Furthermore, it could be argued that sculpture sometimes presents a higher preservation potential due to its presence in undertraces (e.g., Seilacher 1953, Fernández et al. 2019).

Thus far, not all authors have followed the emended diagnoses of Knaust and Neumann (2016). For example, Ishida et al. (2019) assigned a specimen from Japan with hyporelief preservation to *A. quinquefolius* because the trace fossil presents similar ornamentation to the one described in Seilacher (1953). However, following the diagnosis modified by Knaust and Neumann (2016), it can be assigned to another ichnospecies. This specimen presents a ratio of the arm length versus width between 2.17 and 3.13 (Fig. 6b, Ishida et al. 2019), i.e., the diagnostic ratio of *A. stelliformis*.

Bertling et al. (2006) stated that the sculpture usually plays a subordinate role, and is diagnostic only at the ichnospecies level. However, the authors noted that as knowledge about producers is increasing, ornamentation may become more relevant. Later, Bertling (2007) reiterated that when trace fossils do not differ geometrically and show identical proportions of morphometric parameters, they should be synonymised. Although Rindsberg (2018) did not discuss ornamentation, the author remarked that it is absurd to reject the biological aspects of trace fossils as their behavioural functions, because trace fossils are biogenic structures and morphologically based diagnoses should present inferences about the function and the tracemaker. Therefore, in the case of *Asteriacites*, whose tracemakers are known (e.g., Seilacher 1953; Ishida et al. 2017), it could be argued that ornamentation may have the same or even greater importance than a morphometric parameter to differentiate among the ichnospecies.

# CONCLUSION

In this study, specimens of *Asteriacites* from the Valanginian Mulichinco Formation are described at five new stratigraphic levels from Vega de Escalone and seven stratigraphic levels from three new localities in shallow marine intervals (shoreface) mainly subjected to wave action. This expands the geographical distribution of the asterozoan tracemakers in the "septentrional" area of the unit (*sensu* Schwarz et al. 2011). Previously, all specimens of *Asteriacites* from the Mulichinco Formation were assigned to *A. lumbricalis*. Following the emended diagnoses of Knaust and Neumann (2016), most of the specimens were reassigned to *A. stelliformis*. Furthermore, in this work, we could establish that an arm length versus arm width of 12-12.5 is not typical of *A. lumbricalis*.

This analysis, together with information from previous works that studied *Asteriacites* samples under the diagnoses of Knaust and Neumann (2016), was considered to establish three simple criteria to aid in morphometric analysis. Criterion number two ("with three or more arm imprints, the area with at least three points will be decisive for the ichnospecific assignment") is the most relevant. Additionally, it is possible that the diagnosis of *A. stelliformis* requires a minor modification.

In the case of specimens preserved as epirelief, the delineation of the edge of the arm, necessary for the morphometric analysis, will depend on the methodology used (e.g., photogrammetry).

Previous researchers have supported the idea that sculpture is a direct reflection of the behaviour of the tracemaker, and morphologically based diagnoses should present inferences about the function and the tracemaker. We argue that sculpture may have more or the same importance than a morphometric parameter as an ichnospecific ichnotaxobase for *Asteriacites*.

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## SUPPLEMENTARY MATERIAL

**Table 1.** Measurements of *Asteriacites* specimens from Mulichinco Formation (specimens 1 to 35) and from previous works (specimens 36 to 40). L/W is the arm length/ arm width ratio following the methodology of Knaust and Neumann (2016).

| SPECIMEN | ARMS | ARM LENGTH (L) | ARM WIDTH (W) | L/W RATIO | LOCALITY (Mulichinco Fm) / COUNTRY | OBSERVATION | ICNOSPECIES AFTER THIS ANALYSIS |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 18,95 | 1,41 | 13,40 | Barranca de los Loros | CPBA 20446 | *A. lumbricalis* |
| | 2 | 22,99 | 1,50 | 15,33 | | | |
| | 3 | 12,39 | 2,66 | 4,66 | | | |
| | 4 | 14,10 | 1,52 | 9,27 | | | |
| | 5 | 20,09 | 2,25 | 8,93 | | | |
| 2 | 1 | 12,41 | 3,36 | 3,69 | Pampa de Tril | Field specimen | *A. stelliformis* |
| | 2 | 11,20 | 4,33 | 2,59 | | | |
| | 3 | 10,08 | 1,75 | 5,76 | | | |
| | 4 | 17,42 | 1,37 | 12,75 | | | |
| | 5 | 19,57 | 1,16 | 16,82 | | | |
| 3 | 1 | 17,98 | 3,81 | 4,72 | Pampa de Tril | CPBA 20447.1 | *A. stelliformis* |
| | 2 | 19,76 | 4,82 | 4,10 | | | |
| | 3 | 23,51 | 2,76 | 8,53 | | | |
| | 4 | 15,87 | 3,27 | 4,86 | | | |
| | 5 | 17,59 | 4,03 | 4,37 | | | |
| 4 | 1 | 27,02 | 2,23 | 12,14 | Pampa de Tril | Field specimen | *A. stelliformis* |
| | 2 | 27,58 | 1,62 | 17,03 | | | |
| | 3 | 17,12 | 2,18 | 7,84 | | | |
| | 4 | 18,31 | 3,12 | 5,87 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 5 | 1 | 19,22 | 2,24 | 8,57 | Pampa de Tril | Field specimen | *A. stelliformis* |
| | 2 | 16,26 | 2,40 | 6,77 | | | |
| | 3 | 15,36 | 2,10 | 7,32 | | | |
| | 4 | 12,99 | 2,57 | 5,06 | | | |
| | 5 | 18,55 | 2,65 | 7,00 | | | |
| 6 | 1 | 20,43 | 2,65 | 7,70 | Pampa de Tril | Field specimen | *A. stelliformis* |
| | 2 | 9,46 | 2,22 | 4,26 | | | |
| | 3 | 0 | 0 | 0,00 | | | |
| | 4 | 13,52 | 2,27 | 5,95 | | | |
| | 5 | 10,04 | 2,47 | 4,07 | | | |
| 7 | 1 | 0 | 0 | 0,00 | Pampa de Tril | Field specimen | *A. lumbricalis* |
| | 2 | 14,43 | 1,76 | 8,19 | | | |
| | 3 | 13,13 | 1,34 | 9,81 | | | |
| | 4 | 16,26 | 1,20 | 13,49 | | | |
| | 5 | 15,17 | 2,39 | 6,34 | | | |
| 8 | 1 | 8,36 | 1,19 | 6,99 | Pampa de Tril | Field specimen | *A. lumbricalis* |
| | 2 | 9,04 | 1,53 | 5,89 | | | |
| | 3 | 11,81 | 1,20 | 9,80 | | | |
| | 4 | 14,13 | 1,56 | 9,06 | | | |
| | 5 | 0 | 0 | 0,00 | | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 9 | 1 | 12,99 | 2,73 | 4,75 | Pampa de Tril | Field specimen | *A. lumbricalis* |
| | 2 | 11,89 | 2,20 | 5,38 | | | |
| | 3 | 17,21 | 3,05 | 5,64 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 10 | 1 | 18,68 | 1,97 | 9,50 | Barranca de los Loros | Field specimen | *A. lumbricalis* |
| | 2 | 16,24 | 1,81 | 8,93 | | | |
| | 3 | 14,42 | 2,08 | 6,94 | | | |
| | 4 | 22,04 | 1,60 | 13,75 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 11 | 1 | 14,08 | 2,31 | 6,10 | Vega de Escalone | Field specimen | *A. stelliformis* |
| | 2 | 12,36 | 2,01 | 6,15 | | | |
| | 3 | 9,19 | 2,08 | 4,42 | | | |
| | 4 | 13,83 | 1,68 | 8,25 | | | |
| | 5 | 12,86 | 2,03 | 6,35 | | | |
| 12 | 1 | 11,57 | 1,62 | 7,12 | Vega de Escalone | Field specimen | *A. lumbricalis* |
| | 2 | 11,23 | 1,32 | 8,50 | | | |
| | 3 | 19,43 | 1,58 | 12,28 | | | |
| | 4 | 9,95 | 1,04 | 9,55 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 13 | 1 | 10,40 | 1,12 | 9,28 | Vega de Escalone | Field specimen | *A. stelliformis* |
| | 2 | 13,49 | 0,55 | 24,21 | | | |
| | 3 | 0 | 0 | 0,00 | | | |
| | 4 | 20,42 | 2,46 | 8,29 | | | |
| | 5 | 20,32 | 0,94 | 21,50 | | | |
| 14 | 1 | 11,70 | 1,91 | 6,13 | Pampa de Tril | CPBA 20447.2 | *A. lumbricalis* |
| | 2 | 21,06 | 1,46 | 14,37 | | | |
| | 3 | 20,25 | 1,29 | 15,67 | | | |
| | 4 | 15,11 | 1,91 | 7,88 | | | |
| | 5 | 10,75 | 1,27 | 8,43 | | | |
| 15 | 1 | 6,21 | 1,69 | 3,66 | Pampa de Tril | CPBA 20448 | *A. stelliformis* |
| | 2 | 5,03 | 0,92 | 5,45 | | | |
| | 3 | 6,90 | 1,77 | 3,89 | | | |
| | 4 | 7,06 | 1,56 | 4,53 | | | |
| | 5 | 5,59 | 1,69 | 3,31 | | | |
| 16 | 1 | 9,68 | 2,42 | 4,01 | Vega de Escalone | CPBA 20468 | *A. stelliformis* |
| | 2 | 10,34 | 1,44 | 7,16 | | | |
| | 3 | 9,03 | 1,80 | 5,01 | | | |
| | 4 | 11,03 | 1,48 | 7,46 | | | |
| | 5 | 9,45 | 1,63 | 5,79 | | | |
| 17 | 1 | 13,59 | 1,83 | 7,43 | Pampa de Tril | Field specimen | *A. stelliformis* |
| | 2 | 9,92 | 2,23 | 4,44 | | | |
| | 3 | 0 | 0 | 0,00 | | | |
| | 4 | 11,79 | 2,34 | 5,04 | | | |
| | 5 | 10,47 | 1,59 | 6,59 | | | |
| 18 | 1 | 12,42 | 1,82 | 6,83 | Vega de Escalone | Field specimen | *A. stelliformis* |
| | 2 | 7,19 | 1,49 | 4,80 | | | |
| | 3 | 9,90 | 1,25 | 7,93 | | | |
| | 4 | 10,84 | 1,39 | 7,78 | | | |
| | 5 | 4,93 | 1,49 | 3,30 | | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 19 | 1 | 7,24 | 1,69 | 4,28 | Vega de Escalone | Field specimen | *A. stelliformis* |
| | 2 | 8,66 | 1,37 | 6,32 | | | |
| | 3 | 8,66 | 1,66 | 5,21 | | | |
| | 4 | 10,29 | 2,11 | 4,88 | | | |
| | 5 | 9,66 | 1,53 | 6,31 | | | |
| 20 | 1 | 7,40 | 1,18 | 6,26 | Vega de Escalone | Field specimen | *A. stelliformis* |
| | 2 | 9,69 | 1,34 | 7,22 | | | |
| | 3 | 15,22 | 1,97 | 7,71 | | | |
| | 4 | 10,86 | 1,93 | 5,63 | | | |
| | 5 | 13,10 | 1,85 | 7,09 | | | |
| 21 | 1 | 11,39 | 1,15 | 9,84 | Vega de Escalone | Field specimen | *A. lumbricalis* |
| | 2 | 12,14 | 0,78 | 15,52 | | | |
| | 3 | 7,29 | 1,83 | 3,99 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 7,07 | 1,30 | 5,43 | | | |
| 22 | 1 | 6,55 | 1,05 | 6,23 | Barranca de los Loros | Field specimen | *Asteriacites* isp. |
| | 2 | 13,70 | 1,07 | 12,79 | | | |
| | 3 | 0 | 0 | 0,00 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 23 | 1 | 14,13 | 1,44 | 9,77 | Barranca de los Loros | Field specimen | *A. stelliformis* |
| | 2 | 17,03 | 1,08 | 15,79 | | | |
| | 3 | 6,65 | 1,24 | 5,36 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 17,46 | 1,08 | 16,13 | | | |
| 24 | 1 | 10,76 | 1,42 | 7,59 | Puerta Curaco | Field specimen | *A. stelliformis* |
| | 2 | 9,22 | 1,36 | 6,79 | | | |
| | 3 | 10,02 | 1,48 | 6,76 | | | |
| | 4 | 17,62 | 1,63 | 10,78 | | | |
| | 5 | 11,76 | 1,93 | 6,09 | | | |
| 25 | 1 | 12,24 | 1,89 | 6,47 | Puerta Curaco | Field specimen | *A. lumbricalis* |
| | 2 | 14,94 | 2,07 | 7,21 | | | |
| | 3 | 9,43 | 2,58 | 3,65 | | | |
| | 4 | 8,17 | 1,19 | 6,82 | | | |
| | 5 | 17,99 | 1,51 | 11,90 | | | |
| 26 | 1 | 4,98 | 0,73 | 6,81 | Puerta Curaco | Field specimen | *A. lumbricalis* |
| | 2 | 3,97 | 0,42 | 9,51 | | | |
| | 3 | 4,28 | 0,87 | 4,94 | | | |
| | 4 | 11,87 | 1,00 | 11,78 | | | |
| | 5 | 8,47 | 1,28 | 6,60 | | | |
| 27 | 1 | 9,54 | 1,42 | 6,72 | Puerta Curaco | Field specimen | *A. stelliformis* |
| | 2 | 7,62 | 1,91 | 3,98 | | | |
| | 3 | 10,62 | 1,39 | 7,65 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 8,34 | 1,49 | 5,59 | | | |

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|---|---|---|---|---|---|---|---|
| 28 | 1 | 12,5 | 1,75 | 7,14 | Vega de Escalone | CPBA 20470.1 | *A. lumbricalis* |
| | 2 | 18,5 | 1,5 | 12,33 | | | |
| | 3 | 15,5 | 1,9 | 8,16 | | | |
| | 4 | 15,5 | 1,75 | 8,86 | | | |
| | 5 | 11,5 | 1,75 | 6,57 | | | |
| 29 | 1 | 19 | 2 | 9,50 | Pampa de Tril | CPBA 20469.1 | *A. stelliformis* |
| | 2 | 8 | 3 | 2,67 | | | |
| | 3 | 9 | 2,5 | 3,60 | | | |
| | 4 | 9 | 2 | 4,50 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 30 | 1 | 17 | 1,5 | 11,33 | Pampa de Tril | CPBA 20469.2 | *A. lumbricalis* |
| | 2 | 0 | 0 | 0,00 | | | |
| | 3 | 0 | 0 | 0,00 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 15 | 2 | 7,50 | | | |
| 31 | 1 | 20 | 2 | 10,00 | Pampa de Tril | CPBA 20469.3 | *A. lumbricalis* |
| | 2 | 9 | 1,3 | 6,92 | | | |
| | 3 | 16 | 1,3 | 12,31 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 32 | 1 | 26 | 2 | 13,00 | Vega de Escalone | CPBA 20467 | *A. lumbricalis* |
| | 2 | 28 | 3 | 9,33 | | | |
| | 3 | 28 | 2 | 14,00 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 33 | 1 | 19,21802 | 2,8873 | 6,66 | Puerta Curaco | Field specimen | *A. lumbricalis* |
| | 2 | 15,98545 | 1,748 | 9,14 | | | |
| | 3 | 16,14932 | 1,40863 | 11,46 | | | |
| | 4 | 17,5734 | 1,6358 | 10,74 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 34 | 1 | 18,7995 | 2,216 | 8,48 | Pampa de Tril | Field specimen | *A. stelliformis* |
| | 2 | 15,6452 | 1,672 | 9,36 | | | |
| | 3 | 18,5485 | 2,6414 | 7,02 | | | |
| | 4 | 17,426 | 2,6397 | 6,60 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 35 | 1 | 17 | 1,2 | 14,17 | Vega de Escalone | CPBA 20470.2 | *A. stelliformis* |
| | 2 | 18 | 1 | 18,00 | | | |
| | 3 | 18 | 2 | 9,00 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 13 | 2 | 6,50 | | | |
| 36 | 1 | 70,861 | 25,405 | 2,79 | Japan | Ishida et al. 2019 | |
| | 2 | 59,719 | 24,419 | 2,45 | | | |
| | 3 | 48,618 | 20,838 | 2,33 | | | |
| | 4 | 62,818 | 20,088 | 3,13 | | | |
| | 5 | 62,389 | 28,729 | 2,17 | | | |

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|---|---|---|---|---|---|---|---|
| 37 | 1 | 15 | 7,5 | 2,00 | Spain | Carrasco 2011 | |
| | 2 | 15 | 7,5 | 2,00 | | | |
| | 3 | 12,5 | 0 | 0,00 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 38 | 1 | 5,795 | 1,271 | 4,56 | Ireland | Buckman 1992 | |
| | 2 | 5,652 | 1,31 | 4,31 | | | |
| | 3 | 8,87 | 1,124 | 7,89 | | | |
| | 4 | 0 | 0 | 0,00 | | | |
| | 5 | 7,328 | 1,493 | 4,91 | | | |
| 39 | 1 | 42,22 | 4,061 | 10,40 | United States of America | Wilson and Rigby 2000 | |
| | 2 | 0 | 0 | 0,00 | | | |
| | 3 | 38,49 | 4,847 | 7,94 | | | |
| | 4 | 46,66 | 5,0096 | 9,31 | | | |
| | 5 | 39,17 | 2,138 | 18,32 | | | |
| 40 | 1 | 91,413 | 11,994 | 7,62 | United States of America | Mángano et al. 1999 | |
| | 2 | 95,149 | 10,613 | 8,97 | | | |
| | 3 | 83,03 | 9,878 | 8,41 | | | |
| | 4 | 81,437 | 10,176 | 8,00 | | | |
| | 5 | 0 | 0 | 0,00 | | | |
| 50 | 1 | 8,73 | 2,23 | 3,91 | United States of America | Rindsberg 1994 | |
| | 2 | 12,69 | 2,61 | 4,86 | | | |
| | 3 | 19,26 | 2,59 | 7,44 | | | |
| | 4 | 16,13 | 1,68 | 9,61 | | | |
| | 5 | 13,92 | 1,82 | 7,63 | | | |
| 51 | 1 | 28,02 | 10,86 | 2,58 | United States of America | Rindsberg 1994 | |
| | 2 | 28,43 | 14,61 | 1,95 | | | |
| | 3 | 30,37 | 12,05 | 2,52 | | | |
| | 4 | 29,72 | 11,89 | 2,49 | | | |
| | 5 | 0 | 0 | 0 | | | |
| 52 | 1 | 54,14 | 30 | 1,80 | Agrio Formation Argentina | Fernández et al. 2019 | *A. quinquefolius* |
| | 2 | 57,46 | 29,31 | 1,96 | | | |
| | 3 | 60,67 | 33,24 | 1,83 | | | |
| | 4 | 64,48 | 28,79 | 2,24 | | | |
| | 5 | 61,03 | 28,95 | 2,11 | | | |
| 53 | 1 | 60,40 | 15,15 | 3,98 | Agrio Formation Argentina | Fernández et al. 2019 | |
| | 2 | 51,17 | 12,57 | 4,07 | | | |
| | 3 | 55,59 | 16,65 | 3,34 | | | |
| | 4 | 51,67 | 13,96 | 3,70 | | | |
| | 5 | 60,68 | 14,43 | 4,20 | | | |