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# *Scolicia* and its producer in shallow-marine deposits of the Miocene Chenque Formation (Patagonia, Argentina): functional morphology and implications for understanding burrowing behavior

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## ABSTRACT

*Scolicia* is one of the most conspicuous trace fossils in lower shoreface deposits of the Miocene Chenque Formation of Patagonia, Argentina. This ichnotaxon consists of horizontal, sinuous or meandering trace fossils with a laminated backfill and two parallel strings located at the base. Abundant body fossils attributed to *Brisaster iheringi* occur in close association to these trace fossils. The echinoids are very well preserved, and most of the specimens have some areas with their spines attached in life position. In particular, preservation of the subanal tufts of spines, associated to isopores (which are interpreted as being associated to funnel building tube feet), supports the interpretation that these organisms are the producers of *Scolicia* isp. A shaft connecting the burrow with the sediment-water interface was not observed in vertical sections of the excavations, although on bedding plane surfaces, some small circular tube outlets are recognized. However, the great diversity and abundance of ichnofossils co-occurring in these deposits may preclude adequate identification of vertical structures. These deposits provide an excellent opportunity to integrate trace fossil data, body fossil information and observations from modern analogues in order to perform a morpho-functional analysis of *Scolicia*.

## KEYWORDS

Echinoid; Spatangoid; Miocene; shallow marine; *Brisaster*; *Scolicia*

## Introduction

During the Early Cretaceous, the Order Spatangoida appeared, diversifying during the Late Cretaceous and Paleogene-Neogene (Fischer 1966; Kanazawa 1992), and becoming key bioturbators in infaunal communities since then (Bromley 1990). These irregular echinoids live from shallow- to deep-marine areas, reworking the substrate during deposit-feeding activities and locomotion (Thompson and Riddle 2005). Two distinctive trace fossils have been interpreted as produced by the locomotion-feeding activities of these echinoids; *Scolicia* De Quatrefages 1849 since the Late Jurassic, and *Bichordites* Plaziat and Mahmoudi 1988 since the Oligocene (Plaziat and Mahmoudi 1988; Bromley 1990; Uchman 1995; Tchoumatchenco and Uchman 2001; Gibert and Goldring 2007, 2008; Buatois et al. 2016; Belaústegui et al. 2017). These

structures consist of large horizontal sinuous or meandering trace fossils, with a laminated backfill and one (*Bichordites*) or two drains (*Scolicia*) (Plaziat and Mahmoudi 1988; Bromley 1990; Uchman 1995).

Previous studies have addressed the functional significance of some morphological traits of spatangoids and their relation to burrowing behaviour (see Nichols 1959; Kanazawa 1992, 1995; Asgaard and Bromley 2007). For example, Kanazawa (1992) studied the test shape of different spatangoid species and how they constrain burrowing activities, finding that the test profile is apparently related to a specific habitat. Similarly, Walker and Gagnon (2014) discussed the role of spines for locomotion in *Brisaster fragilis* and in *B. latifrons*. Nichols (1959) and Asgaard and Bromley (2007) noticed that most infaunal spatangoid echinoids had a subanal fasciole around the drain-constructing podia and spines, which helps in the

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production of the pair of drains acting as pumps and controlling the flow of water in the drains.

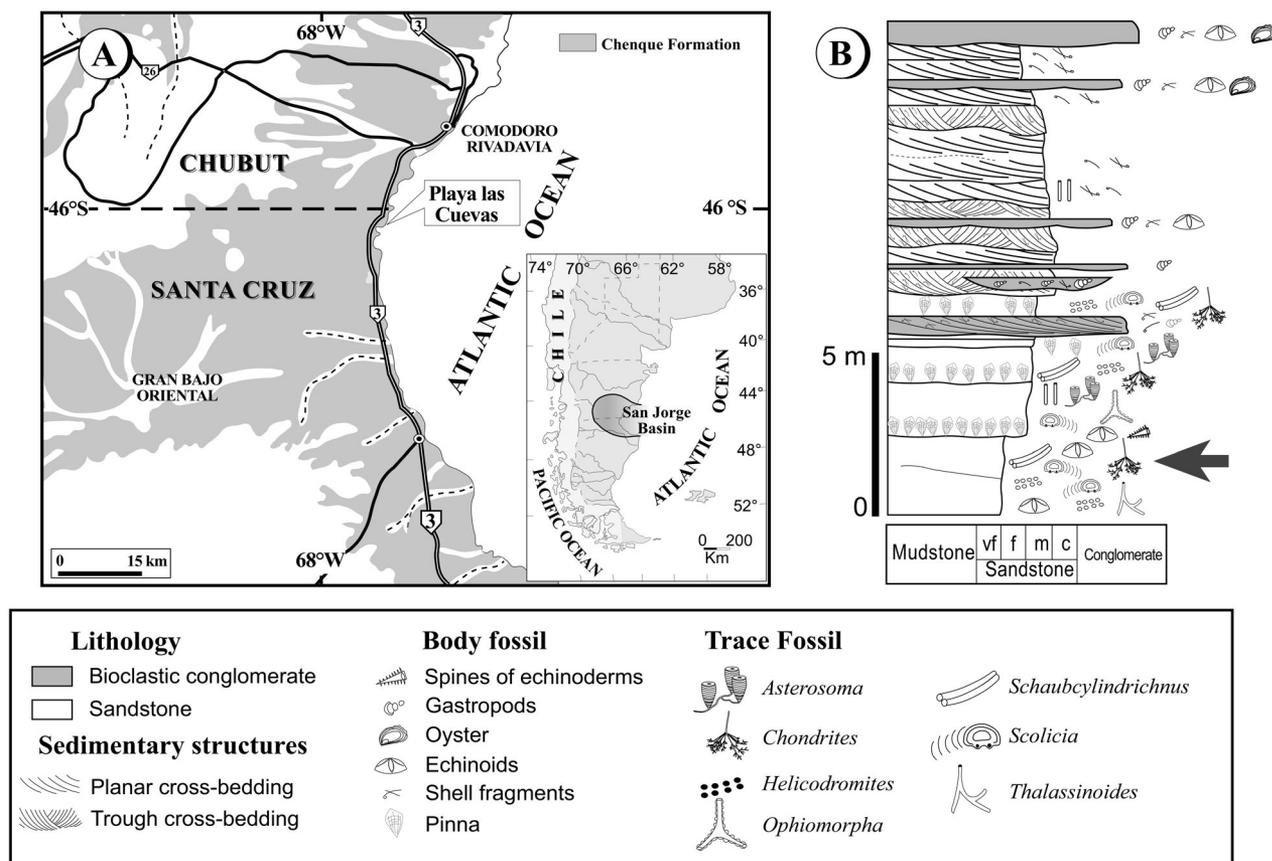
Interestingly, Asgaard and Bromley (2007) also argued that some of the behaviours observed in *in vitro* experiments of spatangoids were a consequence of problems in the designs of the studies (for example, small areas to burrow or insufficient duration of the experiments), and thus, these structures were abnormal. These authors centered their analysis on the schizasterid *Schizaster canaliferus*, which do not possess subanal fasciole, but however construct clear drains at the base of the burrow due to the presence of large podia.

The present study focuses on very well-preserved *Brisaster iheringi* specimens that occur in close association to the trace fossil *Scolicia* isp. in lower shoreface deposits of the Miocene Chenque Formation of Patagonia, Argentina (Bellosi 1987; Buatois et al. 2003; Carmona 2005; Carmona et al. 2008; Parma 2012; Martínez and del Río 2017). As in *Schizaster*, the genus *Brisaster* does not possess a subanal fasciole (Gibbs 1963). Nevertheless, the ciliary current pattern

of the test observed on modern organisms resembles that of the spatangoids that possess that fasciole (Gibbs 1963). Thus, the main objective of the study is to integrate the trace fossil data with the body fossil information in order to perform a morpho-functional analysis of *Scolicia*. Additionally, a brief section including a discussion of some taphonomic observations is also provided.

## Geological setting

Miocene marine deposits of the Chenque Formation are part of the infill of the San Jorge Basin of central Patagonia. This unit crops out in the Chubut and Santa Cruz provinces, Argentina (Figure 1). It consists mainly of shallow-marine deposits bearing abundant and diverse invertebrate body fossils and trace fossils. This formation comprises five shallowing-upward depositional sequences, accumulated during the Leonian (late early Miocene) and Superpatagonian (early middle Miocene) Atlantic transgressions (Bellosi 1987, 1995; Cuitiño et al. 2015). The lower two sequences



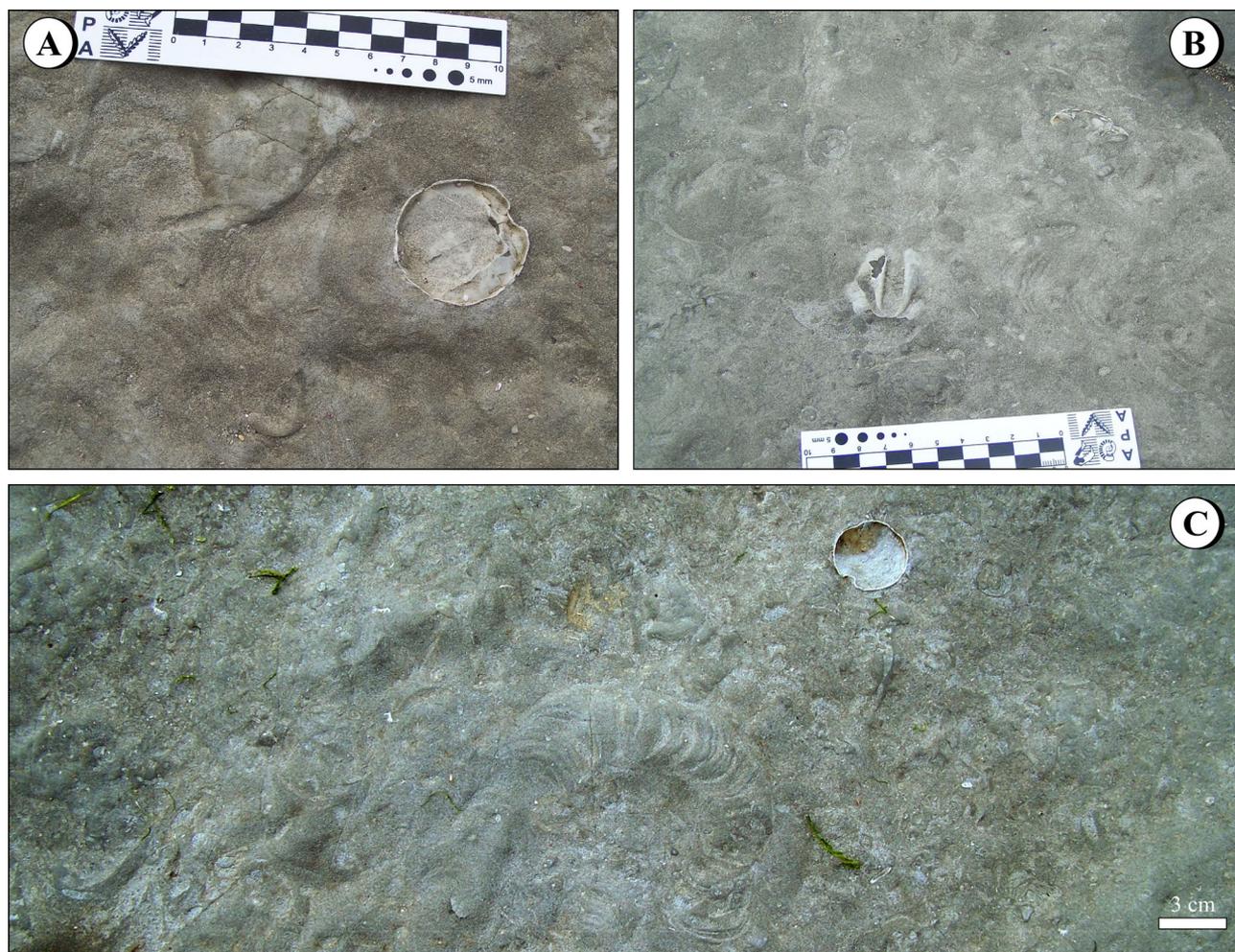
**Figure 1.** A. Map showing the distribution of the Chenque Formation and the location of the studied section at Playa Las Cuevas. B. Schematic representation of the section at the studied locality, integrating the sedimentologic and ichnologic information. Arrow indicates the horizon with *Brisaster iheringi*.

(Leonian) are dominated by sandy, muddy, tuffaceous shoreface deposits and thin-shell beds, with abundant body fossils (specially oysters and other mollusks), and trace fossils, while the upper three sequences (Superpatagonian) are sandier, with less abundant body fossils and ichnofossils, reflecting deposition in restricted, marginal-marine, tide-influenced environments (Bellosi 1987, 1995, 2000; Bellosi and Barreda 1993, Carmona et al. 2008). This study focuses on the section assigned to the Leonian (late early Miocene) transgression located in Playa Las Cuevas (northern Santa Cruz Province, see Figure 1), characterized by very fine-grained glauconitic sandstone, interpreted as deposited in a weakly storm-affected lower shoreface environment (Bellosi 1995; Buatois et al. 2003, Carmona 2005, Carmona et al. 2008). At this locality, occurrence of both vertical and extensive horizontal surfaces (exposed during low tide), allows three dimensional reconstructions of the trace fossils.

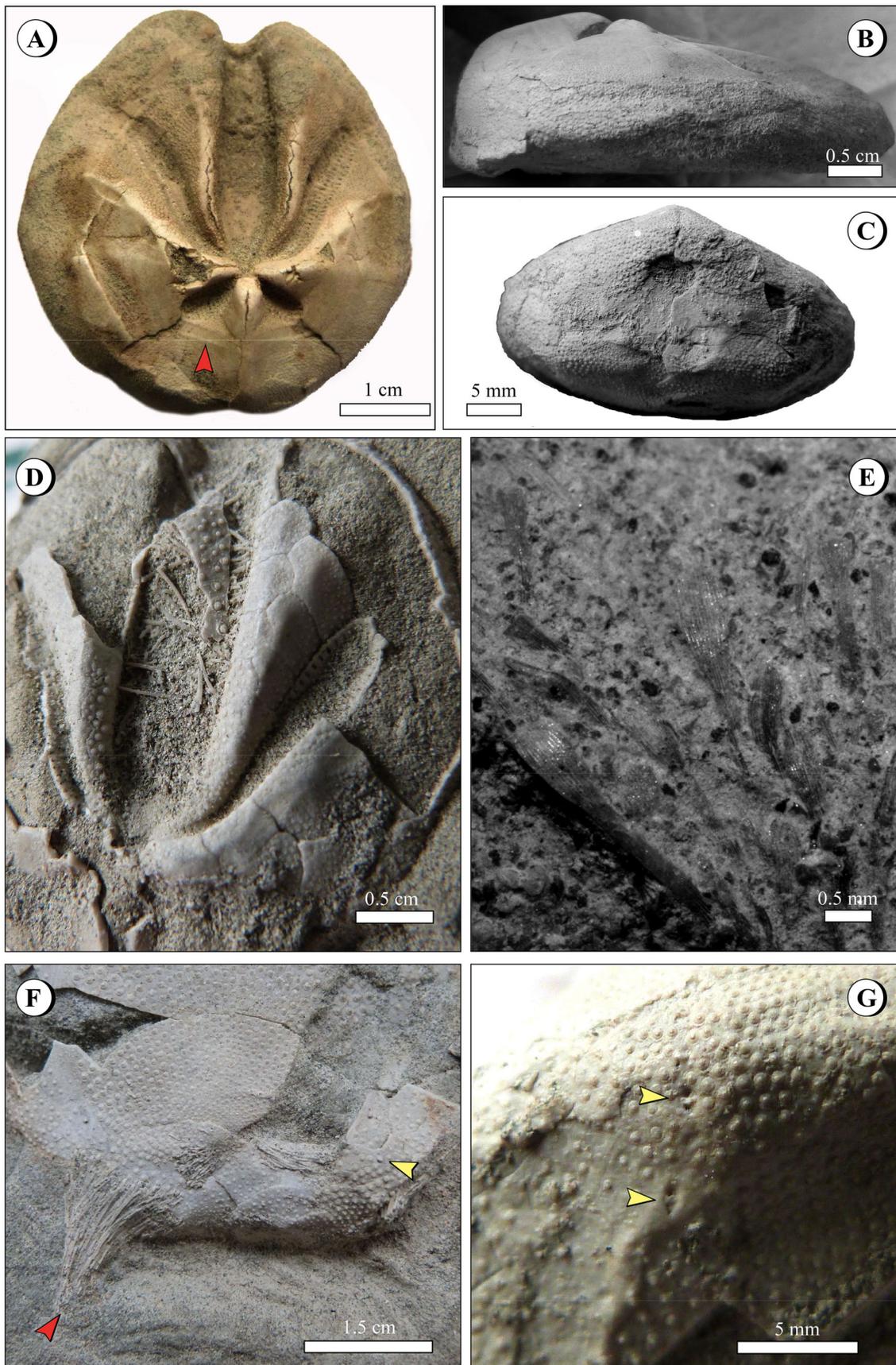
## Studied material

The analyzed deposits correspond predominantly to the abrasion platform, where the echinoids are *in situ* (Figure 2). The relationship of *Brisaster iheringi* and the associated *Scolicia* isp. specimens were analyzed in the field. Ten body fossils were collected for a more detailed morphologic study (Figure 3), and they are housed at the invertebrate collection of the Museo Regional Provincial Padre Jesús Molina (MPM-PI), Río Gallegos, Santa Cruz province, Argentina.

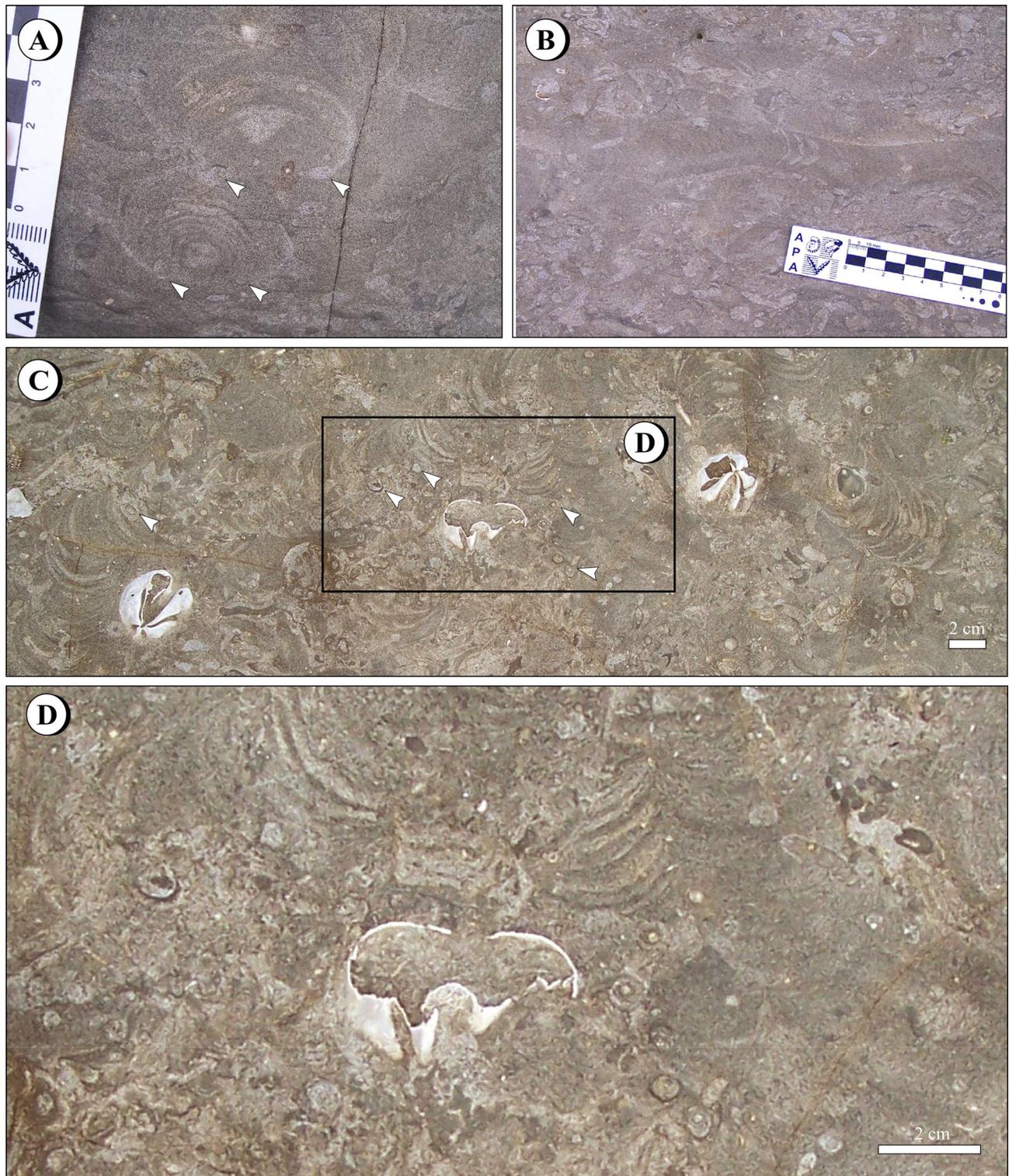
Abundant trace fossils co-occur in these levels (e.g. *Helichodromites mobilis*, *Thalassinoides suevicus*, *Teichichnus rectus*, *T. zigzag*, *Planolites montanus*, *Phycosiphon incertum*, *Nereites missouriensis*, *Asterosoma* isp., *Chondrites* isp.), showing a great abundance and diversity and forming a very complex tiering pattern (Buatois et al. 2003; Carmona 2005; Carmona et al. 2008, 2012).



**Figure 2.** Upper bedding plane views with several specimens of *Scolicia* isp. and their producers. Note in A that the echinoid is preserved at the end of the burrow. Scales are in cm.



**Figure 3.** Specimens of *Brisaster iheringi*. **A.** Dorsal view. The peripetalous fasciole is indicated with a red arrow head (MPM-PI 19288). **B.** Lateral view showing the wedge-shaped morphology of the test (MPM-PI 19288). **C.** Posterior view (MPM-PI 19282). **D.** Dorsal view showing spines preserved within the anterior ambulacrum (MPM-PI 19286). **E.** Spatulate spines of the plastron (MPM-PI 19281). **F.** Ventral view. Yellow arrow head showing the position of the isopores. Red arrow head indicating a tuft of long spines preserved in situ (MPM-PI 19285). **G.** Detail of the isopores (yellow arrow heads) (MPM-PI 19288).



**Figure 4.** *Scolicia* isp. A-B. Cross-section of *Scolicia* isp. specimens, showing the laminated backfill, and the paired strings (white arrow heads in A). C. Upper bedding plane view with several specimens of *Scolicia* isp. associated with their producers. White arrow heads indicate possible openings of the shafts that connected the excavation with the sediment surface. D. Close up of C.

#### **Characterization of *Brisaster iheringhi***

The studied specimens correspond to *Brisaster iheringhi* (de Loriol 1902). Martínez and del Río (2017) provided a revised description of this species from the

same locality (Figure 3). This genus is a member of the Family Schizasteridae, and ranges from the Late Cretaceous to the Holocene (Smith and Kroh 2011). It has been recorded in areas with soft fine-grained

sediments, from relatively shallow- to deep-marine environments (up to 1820 m according to Gibbs 1963).

The test of these specimens has a wedge-shaped type (following the classification by Kanazawa 1992), with the posterior face truncated (Smith and Kroh 2011) (Figure 3A–B). The periproct opens slightly above the ambitus in these specimens (Figure 3C). The anterior ambulacrum is wide and deeply sunken (Figure 3A). The petals are also well developed and sunken. The anterior pair is long, whereas the posterior one is shorter, being this a characteristic of this genus (Gibbs 1963). In the studied specimens, only the peripetalous fasciole was clearly observed (Figure 3A), which pass around the distal ends of the petals (Smith and Kroh 2011). According to Gibbs (1963) and Smith and Kroh (2011), the genus *Brisaster* displays the lateroanal fasciole completely developed only in very young organisms, disappearing partially or completely in adults of some species. Most of the body fossils analyzed here were found in life position, and many of them have their spines *in situ* (Figure 3D–F). These specimens are 42–54 mm wide and 42–49 mm long. As the body fossils are not collapsed due to sediment infill, their outlines are considered to roughly represent the original form of the echinoids. In one complete specimen, height is 19.57 mm (Figure 3A–C).

Three types of spines were recognized. On the aboral area, they were mostly preserved within the sunken ambulacrum (Figure 3D), although the morphology of these spines could not be clearly observed. In the oral area, spatulate spines were identified in some specimens (Figure 3E). Most of these spines have their tips oriented to the front of the organism. A third type of spines was observed in one specimen (Figure 3F), forming a tuft of long and thin spines located in the area of the subanal tube feet. In addition, isopores are recognized in the subanal area (Figure 3F–G), in association with the tuft of long spines in the posterior region of *Brisaster iheringi*.

### Characterization of *Scolicia* isp.

Specimens of *Scolicia* isp. comprise horizontal, sinuous or meandering trace fossils with a bilobate backfill and two parallel strings located at the base. These structures are preserved as full relief (Figure 4). The backfill is composed of alternate sandy and muddy laminae. In cross section, the outline of the burrow is typically oval to somewhat squarish (Figure 4A), being 42–55 mm wide and 20–22 mm high. The strings are

7–8 mm wide and are interpreted as the traces of the drains. The region between these drains is flat to slightly concave upward, and no pit was observed in the basal part of the trace fossils (Figure 4A and B). The sediment of the strings is lighter in colour than in the rest of the structure (Figure 4A). Although no clear shaft connecting the burrow with the sediment water-interface was observed, in some specimens vertical tubes with clear fill and concentric muddy linings were observed cutting the middle upper part of *Scolicia* (Figure 4C). Studied specimens were not assigned to any defined ichnospecies of *Scolicia* as they are distinguished by characters present on their bases, which are only observed in hypichnial preservations.

## Discussion

### Integration of trace fossil and body fossil information

Analysis and integration of the observations from the trace fossils and the body fossils studied here, in addition to the information obtained from studies on modern spatangoids, allow refining the morphologic interpretation of *Scolicia* isp. in relation to the morphology of its producer, *Brisaster iheringi*.

The general morphology and size of the trace fossils assigned to *Scolicia* isp. perfectly fit with the test profile and dimensions of the studied *Brisaster iheringi* specimens. As previously mentioned, Kanazawa (1992) analyzed the test shape of different spatangoid species, evaluating the way they condition the burrowing behaviour of these organisms, and how they are related to specific habitats. This author indicated that this group has morphologically distinct spines on the test surface, with different functions, which are arranged in the same basic way in all spatangoids (Kanazawa 1992). However, he also stated that as spatangoids show a wide variety of test shapes, it is expected that this condition will provide the spines with different positions and directions of movements (Kanazawa 1992). When analyzing particularly the wedge-shaped type of test, he studied specimens of *Brisaster latifrons* and *Spatangus lacunosus*, which live by excavating only up to 5 cm deep in soft muddy bottoms, and considered that this type of test shape is more effective for locomotion in soft cohesive mud (Kanazawa 1992). Previous studies (e.g. McNamara and Philip 1980; Smith 1984) have already observed that the wedge-test shape makes burrowing easier in fine-grained substrates. The fact that the deposits of Playa Las Cuevas host a great abundance of *Brisaster*

*iheringi* in life position suggests that the original sediment was richer in mud. The very fine-grained silty sandstone displays high glauconitic content (Bellosi 1987), being the final product of complete biogenic reworking. Kanazawa (1992) also observed in aquaria that wedge-shaped spatangoids, such as *Brisaster latifrons*, move through the fine substrate using a repeated upward-downward rocking motion, generating cracks on the sediment surface when the burrowing organisms are 20 mm below the surface. In this context, Asgaard and Bromley (2007) suggested that this rocking motion is an unnatural behaviour, being produced by insufficient experiment duration and sediment depth. In the same vein, Walker and Gagnon (2014) recorded the movement of *Brisaster fragilis* in an aquarium, concluding that at least for this species, a “dig and move” motion was involved, and not the oblique rocking motion usually related to wedge-shaped echinoids. In addition, Asgaard and Bromley (2007) also suggested that the rocking movement should leave some imprints on the trace fossils, such as irregularity in the menisci of the backfilled burrows, which were not observed in the material they studied. They also questioned the inferences by Nichols (1959) when recording the activity of the spines and the oral penicillate podia of *Echinocardium chordatum* in aquaria. Nichols (1959) observed that the spines and podia in the oral zone cleared a crescent-shaped area in the glass-bottomed tank, and represented this behaviour drawing a cavity or hole below the mouth of the echinoid (see Figures 16 and 17 in Nichols 1959). Asgaard and Bromley (2007) concluded that this cavity is not formed when the echinoids are burrowing under natural conditions, as structures representing this suboral cavity are not recorded in the trace fossils. Observations in *Scolicia* isp. from the Chenque Formation support the previous conclusions by Asgaard and Bromley (2007), as there are not evident irregularities in the individual menisci of the backfill, and no hollows were observed at the base of these burrows (although in this last case, the action of compaction during fossilization cannot be discarded) (Figure 4A–B).

A key morphologic characteristic of the ichnogenus *Scolicia* is the parallel strings located at the base of this trace fossil. In relation to this, Asgaard and Bromley (2007) emphasized that drain construction is essential for removing water used in respiration away from the organisms. It has been commonly assumed that the construction of these drains requires the presence of fascioles (in particular the subanal fasciole located beneath the anal opening), two tufts of spines

and two groups of special podia (Asgard and Bromley 2007). However, schizasterids do not have a subanal fasciole, but present two groups of subanal podia which are able to build and maintain the drains at the base of the excavation (Asgard and Bromley 2007). Likewise, Gibbs (1963) analyzed modern specimens of *Brisaster* and indicated that the absence of the subanal fasciole in this genus seems to be associated to its shallow burrowing habit and that, despite this absence, the pattern observed in the ciliary current of the test is similar to that found in Spatangids with that fasciole. In modern *Brisaster* specimens, the construction of the sanitary drains involves the action of the tuft of slender and prolonged spines, and the sanitary tube-building tube-feet, which are very extensible and have a terminal disk similar in morphology to the funnel-building tube-feet (Gibbs 1963). Smith (1980) indicated that the subanal tube-feet collect particles at the posterior wall of the burrow and carry them to the proximity of the subanal tuft of spines, where they are incorporated into the walls of the drains. In laboratory studies on modern *Schizaster canaliferus*, Schinner (1993) observed that the tufts of spines form the drains by rotating in a circular way. Hence, the two strings found in *Scolicia* isp. are interpreted as the fossilized sanitary drains used to extrude used respiration water from the burrows (Figure 4B). Modern drains are lined with mucus (Nichols 1959), and thus the lighter colour observed in the strings of *Scolicia* isp. most likely reflects early diagenetic processes (such as precipitation of carbonate cement), which must have favoured their preservation and prevented their compaction (Bromley and Asgaard 1975, Asgaard and Bromley 2007).

Smith (1980) mentioned that the adoption of a buried mode of life in irregular echinoids was accompanied by a marked diversification and specialization of the tube feet, and also of the associated pores that connect them with the internal ampulla. In this context, this author emphasized that knowing the significance of pore morphology in modern echinoids can help to elucidate the tube feet in fossil counterparts. Asgaard and Bromley (2007) recognized the presence of two sets of partitioned isopores and constricted unipores in *Schizaster canaliferus* in the subanal area. Both types of pores have been also associated to funnel-building tube feet in modern species (Smith 1980). In the specimens of *Brisaster iheringi* studied here, very well-preserved isopores were observed at the posterior end of the test, in close relation to the tufts of spines (Figure 3F), and undoubtedly were associated to funnel-building tube feet.

In modern excavations, another common structure is a respiratory funnel that connects the sediment surface with the burrow (Schinner 1993). This funnel is constructed by specialized tube feet located in the more adapical part of ambulacrum III (Smith 1984), which lined the shaft with mucus, while the peripetalous fasciole drives the water flow within the burrow (Schinner 1993). Additionally, a tuft of spines also contributes to the maintenance of the lower part of the shaft (Smith 1984). In modern experiments, these shafts are easily recognized and studied, although in fossil excavations, identification of this structure is extremely uncommon. One remarkable exception is the material described by Bromley and Asgaard (1975), who recorded *Echinocardium cordatum* burrows with very good preservation of the drains and vertical funnels. These authors have recognized cemented shafts and deeply conical structures leading down to the backfilled burrows (Bromley and Asgaard 1975). In our case, the presence of a shaft in *Scolicia* sp. is not so clear. Nevertheless, close examination of the middle part of the backfill of one specimen presents some small, circular tube outlets that seems to be following the course of the excavation, and that may correspond to successive shafts constructed while the organism was moving (see Figure 4C–D, compare with figure 20 in Bromley and Asgaard 1975). Absence of a clear shaft could be also a consequence of the great abundance of ichnofossils co-occurring in these deposits, which may preclude the identification or preservation of these delicate vertical structures.

### **Some additional comments on the taphonomy of *Brisaster iheringi* in the Chenque formation**

Understanding the extraordinary preservation and abundance of *B. iheringi* in life position (several occurring at the end of their excavations, see figure 2A), with the spines attached to their bodies requires a combined sedimentologic, ichnologic and taphonomic analyses. Most authors stated that good preservation of echinoids is commonly related to catastrophic burial or anoxia (Kidwell and Baumiller 1990 and references therein). In this regard, Schäfer (1972) concluded that in shallow-marine environments, irregular echinoids are preserved as complete fossils only when the tests are not displaced after burial. Particularly during storms, large quantities of sediment are deposited, and this has severe effects on the echinoid populations (Smith 1984). In fact, Schäfer (1972) indicated that a rapid cover of 30 cm of

fine-grained sand inhibits *Echinocardium* to escape digging themselves out.

On the other hand, under oxygen deficiency, modern irregular echinoids have been seen actively emerging to the surface (Nichols 1959, Stachowitsch 1984; Schinner 1993, Nebelsick, Schmid, and Stachowitsch 2007). In those cases, Nebelsick, Schmid, and Stachowitsch (2007) recorded that the animals lose their spines within four days after emergence.

Considering the deposits herein studied, we can interpret that most likely the beds with *Brisaster iheringi* represent punctuated minor storm events that may have caused the mortality of these organisms rather than a problem of anoxia. Sporadic storms are recorded by the thin shell beds of Las Cuevas section (Buatois et al. 2003). Evidence of oxygen deficient conditions, such as signs of emergence of *Brisaster iheringi* and encrustation of their test on the surface (Nebelsick, Schmid, and Stachowitsch 2007), were not detected. In addition, indirect evidence, such as the typical decrease in diversity and diameter of trace fossils that occur under lowered oxygen conditions (e.g. Ekdale and Mason 1988; Savrda and Bottjer 1991), are not recorded in these deposits. Therefore, almost certainly during the storm event, the spatangoid population could not escape entombment, and later, when fairweather conditions re-established, these deposits were completely reworked by organisms, erasing any sedimentologic evidence of the previous storm episodes, with the exception of rare stronger storms which accumulated thin shell beds.

Another important observation on modern spatangoids indicates that these organisms tend to excavate along the redox potential discontinuity layer (RPD) (Schinner 1993). In fact, Schinner (1993) observed that burrowing depths of *Schizaster canaliferus* increased with an artificial increase in the depth of the RPD layer. Therefore, if we assumed that this community was buried during a storm event, the RPD layer should have quickly re-established upwards, leaving the organisms in the more anoxic sediments. This situation, in addition to the pile of sediment deposited, may have delayed organic decay, favouring preservation of the articulated spines.

Additional studies have explored the role of other physical parameters on the taphonomy of echinoids. For example, when analyzing the preservation of regular echinoids, Kidwell and Baumiller (1990) showed that temperature has a much more important effect on the preservation of these organisms than oxygen content. These authors observed that in low water temperatures rates of organic decomposition were

slowed. This was also supported by Banno (2008) and Banno, Kamiya, and Kanazawa (2010), who observed that low temperature drastically reduced disarticulation rate of spines in *Schizaster lacunosus* in aquaria. In this regard, further research in the Chenque Formation is needed to evaluate and interpret the influence of water temperature and other parameters on the taphonomy of these spatangoid community.

## Conclusions

*Scolicia* isp. is interpreted as produced by *Brisaster iheringi* in the Miocene Chenque Formation. Integration of body and trace fossil observations, in addition to data from modern analogues, allows interpreting in great detail the burrowing mechanism of these irregular echinoids. Also, detailed trace fossil analysis provides key information that is not consistent with reconstructions of schizasterid behaviour based on modern experiments. *In situ* preservation of spines and pores at the posterior end of *Brisaster iheringi* allow a direct correlation with the ventral morphology of *Scolicia* isp., in particular with the presence of two strings at the base of the structure. The excellent preservation of some specimens of *Brisaster iheringi* at the end of their trace fossils suggests that the organisms were suddenly buried during storms, which prevented the echinoids to escape. Other physical parameters may have also contributed to the good preservation of these echinoids (e.g. water temperature), and deserve further investigation.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

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