

Bivalve trace fossils in an early Miocene discontinuity surface in Patagonia, Argentina: Burrowing behavior and implications for ichnotaxonomy at the firmground–hardground divide

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Abstract

Ichnofossils developed in a firmground at the contact between the middle Eocene–lower Miocene continental Sarmiento Formation and the lower Miocene marine Chenque Formation, in central-eastern Patagonia, Argentina, are assigned to *Gastrochaenolites ornatus* Kelly and Bromley [Kelly, S.R.A., Bromley, R.G., 1984. Ichnological nomenclature of clavate borings. *Palaeontology* 27, 793–807.], and interpreted as dwelling structures of suspension-feeding bivalves. These record the activities of pholadids, most likely belonging to the Pholadinae. Bivalves are usually preserved as casts and external molds within the biogenic structures. The details of the internal ornamentation in *G. ornatus* allow identification of two sets of scratch patterns, permitting comparison with the boring behavior of modern pholadids.

In terms of ichnotaxonomy, when the same organism is able both to excavate and to bore, and the excavation technique is identical to the mechanical perforation technique, the same name should be used. Accordingly, *Gastrochaenolites*, whilst more commonly assigned to bioerosion structures in hard substrates, is herein regarded as available also for bivalve burrows in firm, but unlithified substrates.

The firmground studied here represents a co-planar surface of lowstand erosion and transgressive erosion that produced exhumation of deposits belonging to the Sarmiento Formation, providing appropriate conditions for the development of the *Glossifungites* ichnofacies. Differential erosion of the apertural necks, the heterogeneity of the available casting material, and the wide size range of ichnofossils suggest a complex history of colonization and erosion for this surface.

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1. Introduction

The ichnogenus *Gastrochaenolites* Leymerie, 1842, is interpreted as a dwelling trace fossil produced by sus-

pension-feeding bivalves that commonly live in shallow-marine rockgrounds and hardgrounds (Kelly and Bromley, 1984). It has been mentioned also as occurring in firm substrates (Kelly and Bromley, 1984; Frey and Pemberton, 1984; Pemberton et al., 1992; Mikuláš et al., 2003). This ichnogenus comprises clavate or tear drop-like structures, and the most common forms are circular in cross-section, with a neck-like upper portion (Kelly and Bromley, 1984). *Gastrochaenolites* has been recorded as

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occurring since the Ordovician (Ekdale and Bromley, 2001; Benner et al., 2004), but they are quite rare in Paleozoic strata, and the next oldest *Gastrochaenolites* is of Late Carboniferous age (Taylor and Wilson, 2003).

Although *Gastrochaenolites* is fairly common in Jurassic to Recent rocks, few studies have provided a detailed analysis of this biogenic structure and focused at the same time on the identification of the potential

tracemaker (e.g., Evans, 1968a,b; Pojeta and Palmer, 1976; Kennedy, 1993; Mikuláš et al., 2003; Donovan and Hensley, 2006). Still less common have been attempts to reconstruct bivalve boring/burrowing behavior based on the ornamentation preserved on the walls of the structure (see Seilacher, 1985). This paper documents the occurrence of densely packed *Gastrochaenolites ornatus* Kelly and Bromley, 1984, at the boundary surface between the

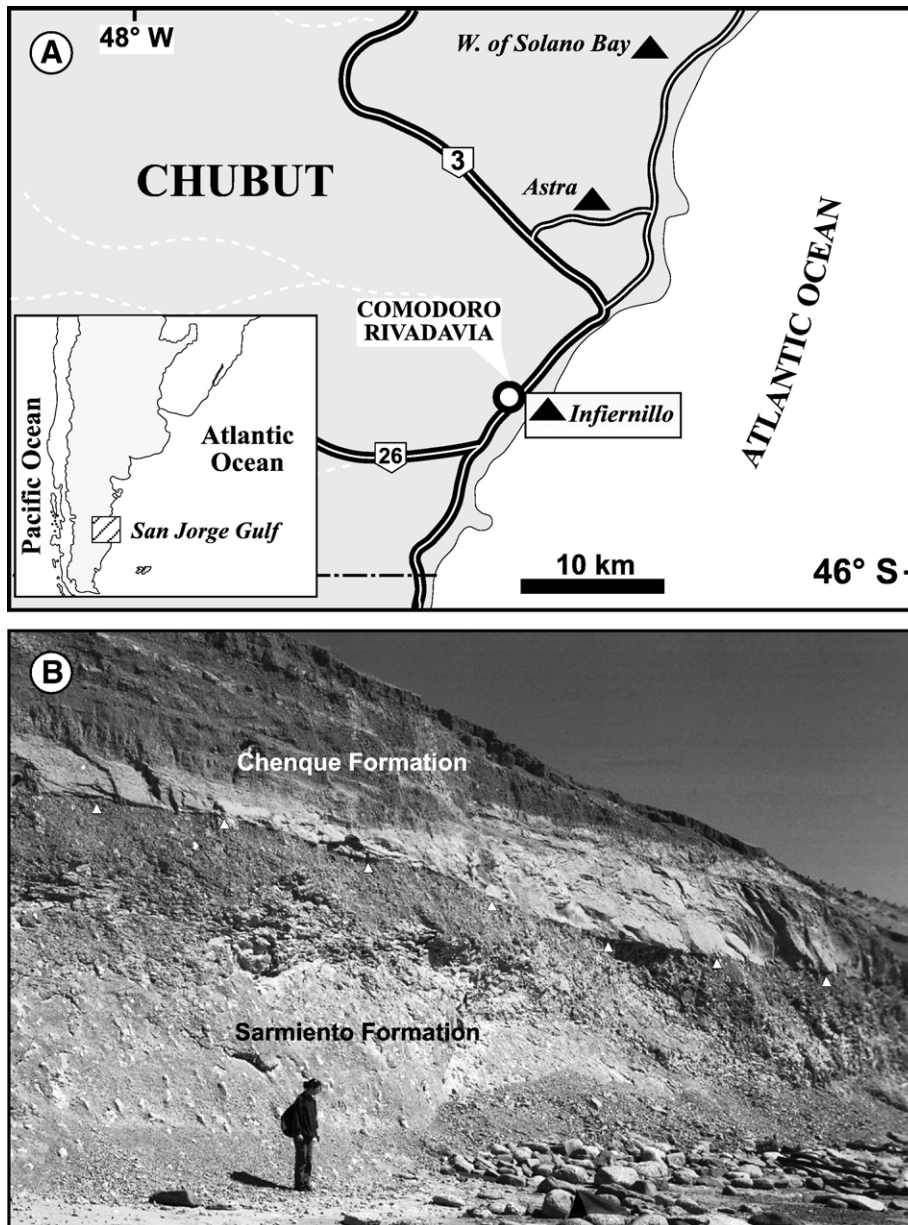


Fig. 1. A — Map of the study area. Localities where the firmground surface was studied are indicated with a black triangle. Infiernillo locality is outlined. B — Outcrop photograph at Infiernillo, showing the sharp contact (indicated with white triangles) between the continental Sarmiento Formation and the marine Chenque Formation. The analyzed ichnofossils come from this transgressive surface.

middle Eocene–lower Miocene continental Sarmiento Formation and the lower Miocene shallow-marine Chenque Formation in southern Argentina. These ichnofossils contain the body fossils of their producers, which are preserved as casts and external molds. Based on the finely preserved bioglyphs on the wall of the burrows and behavioral patterns exhibited by modern boring bivalves in hardgrounds, it is suggested that a similar mechanism was used for excavation in firm-grounds. Because the same behavior is represented in the bivalve dwelling structures in the hard (lithified) and firm (unlithified but stiff) substrates, the ichnogenus *Gastrochaenolites* applies for both borings and burrows in such situations. Cross-cutting relationships among specimens, differential erosion of the apertural neck, and the filling by more than one casting material reveal a palimpsest surface recording a complex history of multiple events of erosion and colonization.

2. Stratigraphy and occurrence

The specimens described here occur in several localities near the city of Comodoro Rivadavia, Chubut Province, Patagonia, Argentina (Fig. 1A), where the Sarmiento and Chenque Formations are well exposed. The Chenque Formation comprises shallow-marine

deposits recording two Atlantic transgressions during the early Miocene (Bellosi, 1995). This formation overlies the continental Sarmiento Formation (middle Eocene–early Miocene), which is characterized by fluvial and lacustrine deposits with common development of paleosols (Spalletti and Mazzoni, 1979; Bellosi, 1995) (Fig. 2). The boundary surface between both formations records the first transgressive episode (Leonense) that took place in the early Miocene. After the development of an omission surface, deposition of the Sequences I and II (*sensu* Bellosi, 1995) took place in the Golfo de San Jorge, central Patagonia. Although bivalve structures are relatively common in all the outcrops recording this transgressive surface, the best-preserved examples occur at Infiernillo (Fig. 1B). In all the localities, cross-section views along cliff outcrops are good, but there is limited exposure of bedding planes.

3. Studied material

Bivalve ichnofossils at Infiernillo extensively cover the transgressive surface and display a distinctive pattern of distribution as clusters (Fig. 3). This occurrence seems to mimic pholadid colonies in modern environments with vast numbers of individuals closely spaced and partially in contact (Evans, 1968a; Savazzi, 1999). The lithologic

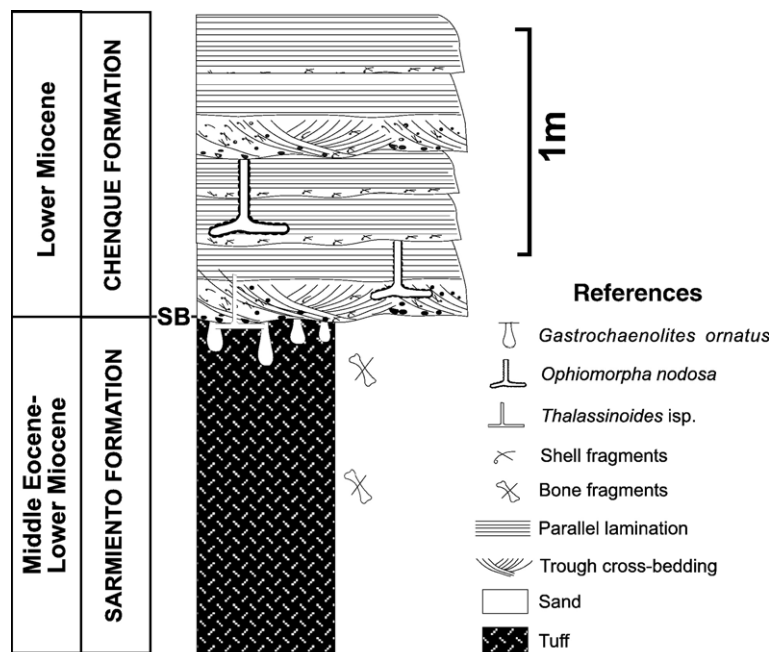


Fig. 2. Stratigraphic section encompassing the boundary surface between the Sarmiento and Chenque formations. The Sarmiento Formation (middle Eocene–early Miocene) is composed of tuffaceous sediments deposited in fluvial and lacustrine environments, whereas the overlying Chenque Formation (early Miocene) is dominantly sandy and deposited in shallow-marine environments.

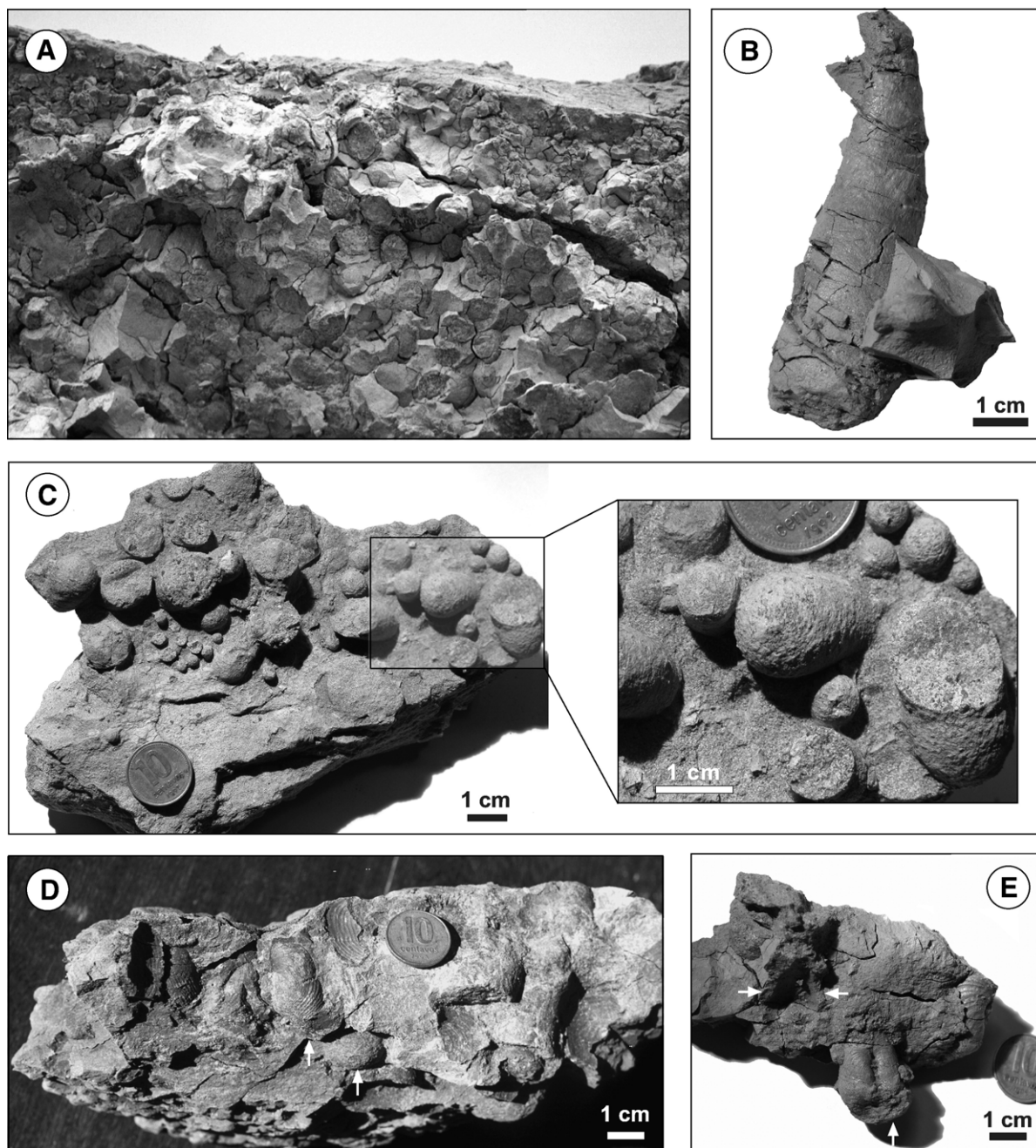


Fig. 3. Bivalve trace fossils. A — General view of the boundary surface (seen from below). Note the abundance of *Gastrochaenolites* at this level. B — One of the largest specimen found. C — Basal view showing specimens with different sizes. The photograph in the right is a closer view of the ichnofossils showing the scratch traces on their surfaces. D and E — Lateral view of the specimens. Note the excellent preservation of the cast (and in some cases external molds) of the bivalves. Some ichnofossils are indicated with arrows.

contrast between the host rock (i.e., fine-grained tuffaceous sandstone of the Sarmiento Formation) and the casting material (i.e., poorly sorted granular and pebbly sandstone of the Chenque Formation) allows easy

visualization of the structures. More than two hundred specimens were collected. Specimens are housed at the collections of the Centro Austral de Investigaciones Científicas (CADIC), Ushuaia, Argentina.

3.1. The ichnofossils

These ichnofossils display a circular outline in transverse cross-sections and basal views (Figs. 3A, C and 4), and have a diagnostic clavate to tear drop-like morphology in lateral views (Fig. 3B and E). In the majority of cases, the cast and external mold of the bivalve tracemaker are preserved within the biogenic structure (Figs. 3D–E and 5). The infilling material is variable in grain size, from fine-grained to coarse-grained pebbly sandstone. Typically it is composed of very poorly sorted, medium-grained pebbly sandstone with abundant chips eroded from the Sarmiento Formation, plus larger clasts of variable composition and bioclasts (Fig. 6). In some cases, the presence of a thin, greenish silt layer is present along the boundary between the bivalve and the excavation wall, further enhancing the preservation of external morphologic features of the shells and the delicate ornamentation of the wall of the biogenic structures (Fig. 6A).

In basal and lateral views (Figs. 4 and 7), the wall exhibits fine sculptures or bioglyphs (*sensu* Bromley

et al., 1984). Two preferred orientations are present: horizontal (parallel to the stratification) and oblique. In general, bioglyphs follow a concentric, more or less continuous pattern around the basal bulb (Fig. 7A–B and D). Another common feature is the presence of a small, shallow depression in the basal part of some internal casts, which is usually displaced from the center of the structures (Fig. 4A–B and E).

The ichnofossils range from small structures (0.5 cm in basal diameter) to robust excavations (3.3 cm in basal diameter). In general, it is difficult to measure the total length of the specimens due to common erosion of their upper parts (apertures and necks). The most complete specimen reaches 7.5 cm long (Fig. 3B).

3.2. The tracemakers

Because the producers are preserved within their domiciles, there is little doubt that the biogenic structures represent dwelling structures (domichnia) of bivalves. The original valves of the tracemakers were dissolved, and only the internal casts and external molds are

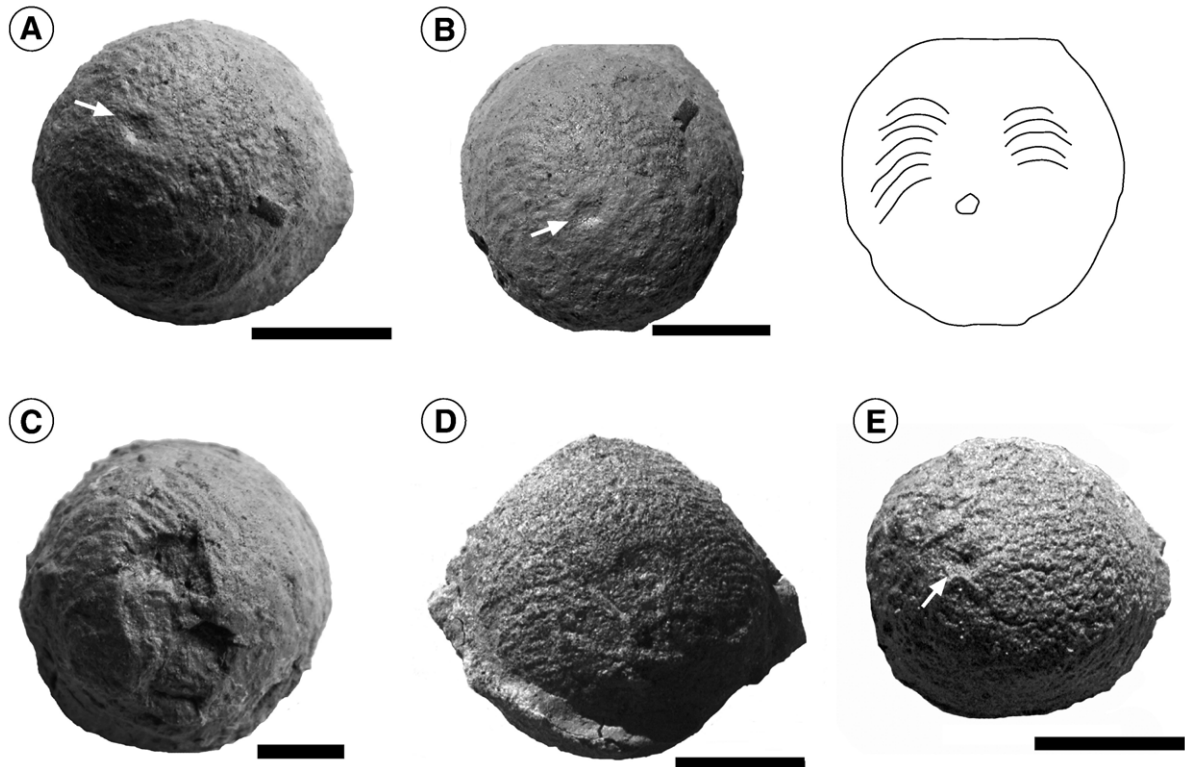


Fig. 4. Basal view of the ichnofossils. A and B correspond to different views of the same specimen. The white arrows in A, B and E indicate the basal depression commonly found in the casts of these structures. In B, specimen and schematic drawing show the divergent arrangement of the scratches from the central part of the ichnofossils. This arrangement is also visible in D. Scale bars are 1 cm long.

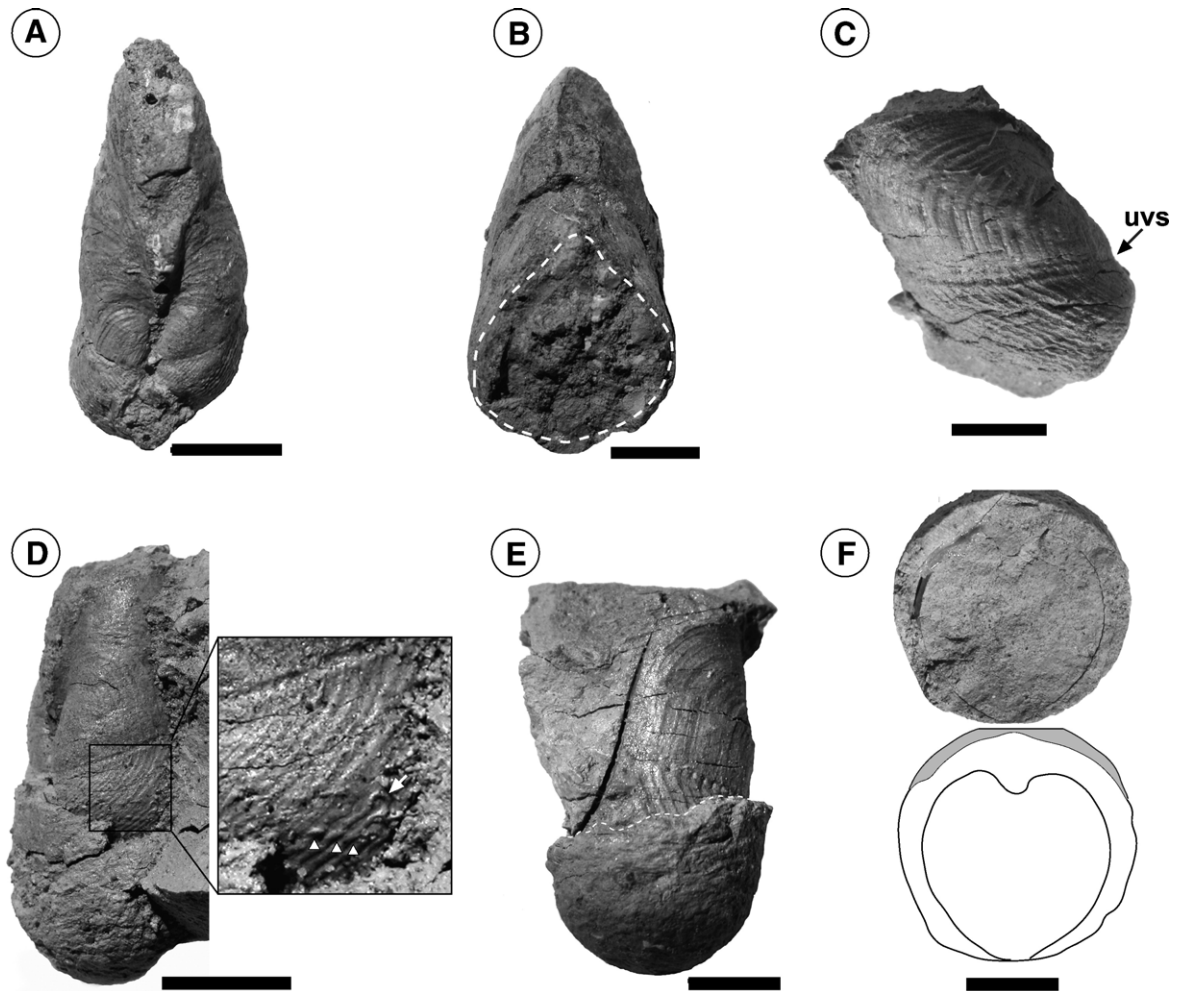


Fig. 5. A, B and C — Dorsal, ventral and lateral view of the internal molds of the bivalves. In C the arrow indicates the weak umbonal–ventral sulcus (*uvs*) that characterizes all the analyzed specimens. D and E — Internal molds with preservation of the basal portions of the ichnofossils. In D, the closer view of the specimens shows evidence of the presence of an encruster (arrow) and the morphology of the bivalve spines (white triangles). F. Photograph and schematic drawing of the cross section of one specimen. In these figures the limit of the internal mold of the bivalve can be clearly identified. Scale bar is 1 cm long.

preserved within the structures. Casts and external molds are elongate in outline (Fig. 5A–B) with a wide size range (2.0–5.2 mm in length and 1.1–2.5 mm in height). The casts show clearly the morphology of the valve exterior and also record the local presence of encrusting serpulids (Fig. 5D). The valves have an anterior and posterior area separated by an umbonal–ventral sulcus (Fig. 5C–E). The anterior part exhibits small protuberances recording the presence of short spines (Fig. 5D).

Based on morphologic features, these bivalves are assigned to the family Pholadidae. Identification at the subfamily level is more difficult, because it is primarily based on morphologic features that are not generally preserved in fossil material. For example, the callum is a structure that closes the pedal gape in adults of the

Martesiinae and Jouannetinae and is absent in Pholadinae. However, the presence of this character is obscure, particularly if they are preserved as casts. This is a preservational bias related to the process of passive infilling of the shell mold after the shell dissolved; the infill may protrude beyond the valves at the anterior part passing through the gape and producing a structure that may resemble a callum (Cox et al. in Moore, 1969). The presence or absence of a callum is difficult to evaluate on the basis of cast material. This structure is apparently absent in the studied specimens (Fig. 5B). Some specimens display a distinctive opening that truncates the anterior area (Fig. 5B), indicating that the pedal gape was open at the time of infilling. This feature is observed in specimens of different sizes suggesting that the absence of

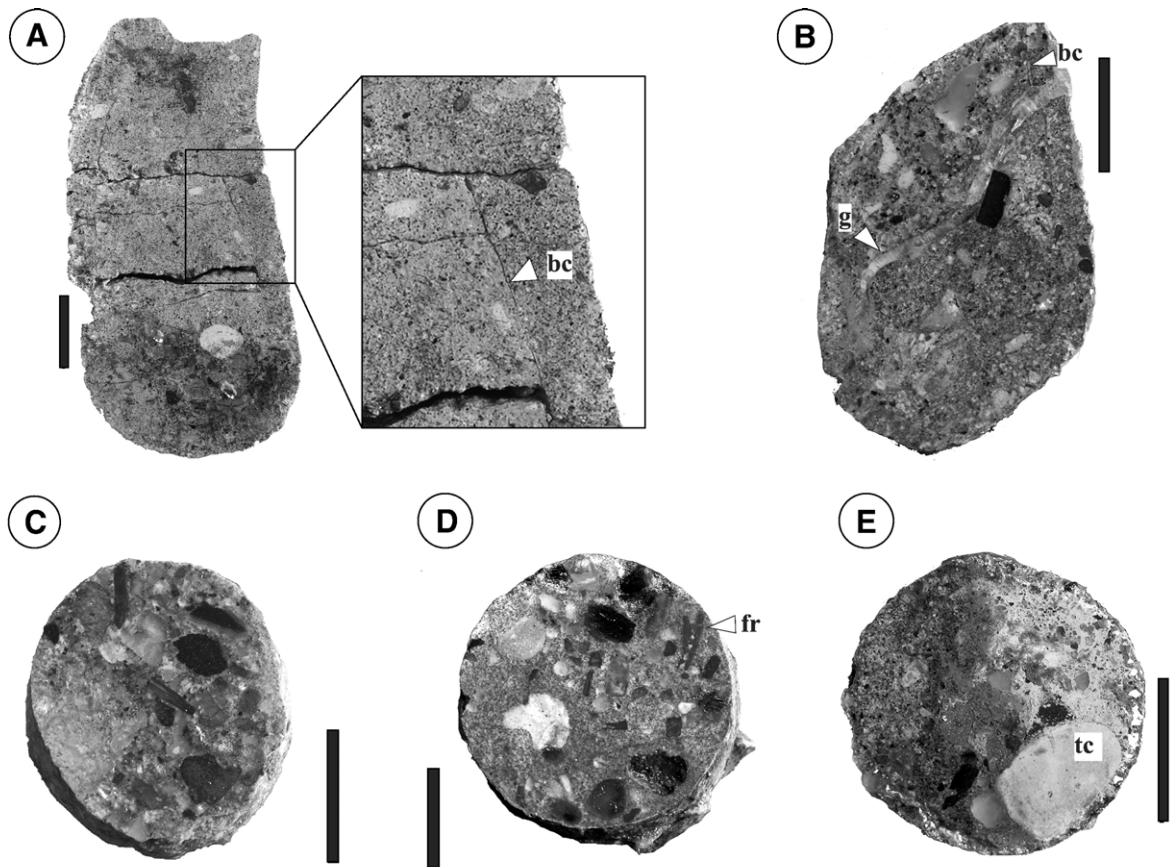


Fig. 6. Polished sections of *Gastrochaenolites ornatus*. A and B correspond to longitudinal sections of the specimens, showing the boundaries of the casts (bc), indicated by white arrows. In B the presence of a gypsum layer (g) is indicated. C–E correspond to cross section views of the polished specimens. In these examples, the boundaries of the casts are not as evident as in longitudinal sections. The fillings of these specimens are mainly composed of tuffaceous clasts (tc), coarser clasts and fossil remains (fr). Scales are 1 cm long.

a callum is not a consequence of the specimens being juveniles, but probably a real feature of these bivalves, arguing, therefore, that the producers of these burrows belong to Pholadinae. However, the possibility that the callum was not preserved cannot be completely discarded. In addition to the presence of a callum, all genera of Jouannetinae have a more globular shape than the material from the Chenque Formation, making them easy to be ruled out as the tracemakers. *Martesia* and *Chaceia*, belonging to Martesiinae, also differ in morphology.

On the other hand, the presence of a weak ventro-umbonal sulcus is a feature almost exclusive of the Martesiinae and Jouannetinae, except only for *Zirfaea* (Pholadinae). *Zirfaea* is considered transitional between the Pholadinae and Martesiinae, and its species are adapted to bore in hardgrounds and excavate in consolidated mud (Cox et al. in Moore, 1969). This genus

shares several features in common with the Miocene material (i.e., the elongate oval outline, the apparent lack of callum, the weak umbonal–ventral sulcus). In addition, at least one species of *Zirfaea* is known to produce *Gastrochaenolites ornatus*. Kelly and Bromley (1984) noted that the holotype of *G. ornatus* contains remains of *Z. crispata*. However, *Zirfaea* has wide gapes at both ends. Although most specimens here have been truncated by erosion (i.e., posterior ends are not preserved), some display a narrow posterior end (Fig. 5A). *Zirfaea* also has a small and more or less triangular mesoplax, which is not present in the Miocene shell molds. Absence of accessory plates, however, are most likely due to a preservational bias. Recently, del Río (2004) described Tertiary molluscan assemblages from Patagonia, recording *Pholadidea patagonica* at the base of the Chenque Formation. However, *Pholadidea* has the

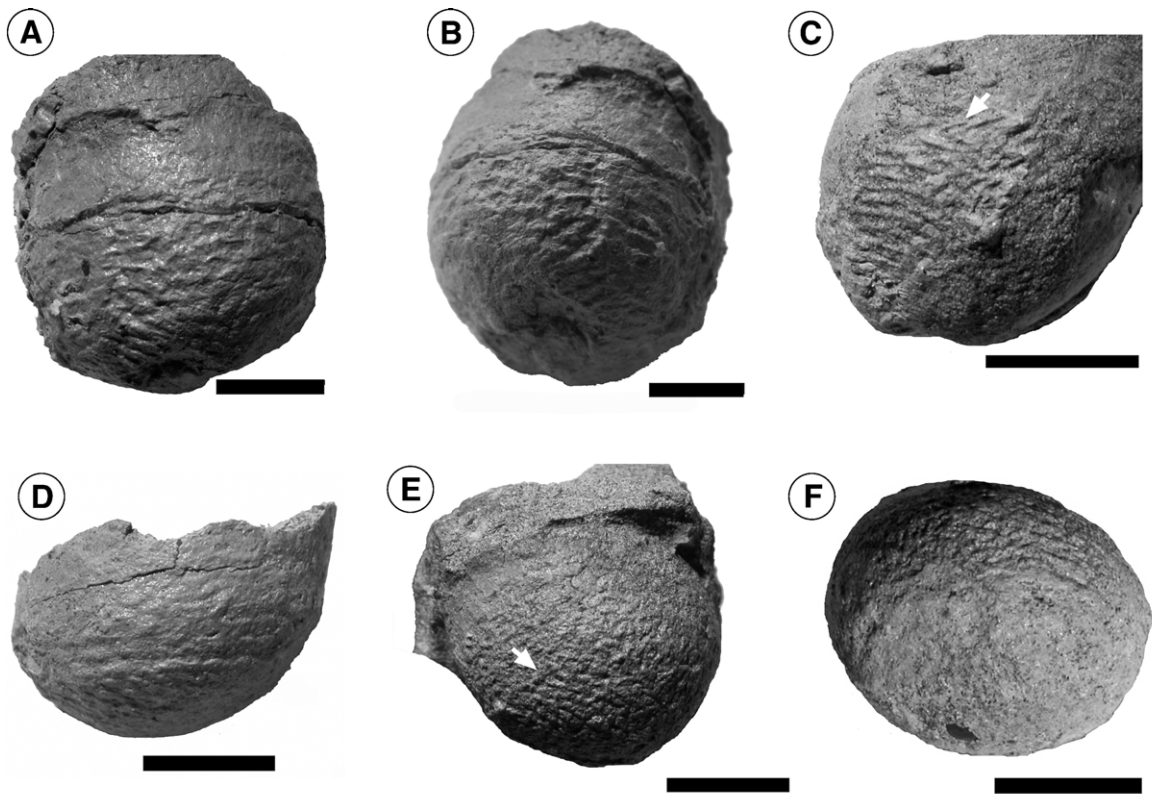


Fig. 7. Lateral view of the ichnofossils. In A, B, D and F, the sculptures are clearly arranged in a circular pattern. A and B show different views of the same specimen. In C and E, the white arrows indicate the place where there is overlapping of the oblique and horizontal scratches. These scratches are similar to the ones shown by Mikuláš et al. (2003, Fig. 3B and F) for Cretaceous examples.

characteristic wide callum (del Río, 2002, Fig. 9C and I), which has not been observed in the studied material.

Preservation of bivalves within their biogenic structures is relatively common in Tertiary deposits. Kennedy (1993) studied some specimens from the Miocene of California and described a new species, *Chaceia fulcherae*, which is relatively large with umbonal–ventral sulcus moderately well defined, and without a callum or dorsal extension of a callum. The majority are preserved within their burrows (Kennedy, 1993, Figs. 2, 4–8). The biogenic structures assigned to *Gastrochaenolites ornatus* exhibit internally an ornate pattern similar to the specimens analyzed here. Another example was recorded by Gaździcki et al. (1982) from the Oligocene of King George Island, Antarctica. They observed several discontinuity surfaces intensely reworked by excavations still containing the shells of their bivalve producers (Gaździcki et al., 1982, Fig. 4). The bivalves were attributed to the marteisine *Penitella*, and illustrations of the internal molds clearly reflect the presence of the callum. They are reminiscent in general shape and size to the Miocene *Gastrochaenolites* clusters.

3.3. Taphonomy of the bivalve body fossils

Pholadidae have aragonitic valves, but in these Miocene burrows the valves were dissolved and only casts and external molds were preserved. This type of preservation is typical among aragonitic bivalves, because aragonite is unstable and commonly dissolves during early diagenesis within the taphonomically active zone. In addition, bivalves that excavate in unlithified substrates have thinner valves than those that perforate in hardgrounds (Evans, 1967; Savazzi, 1999). Although *Gastrochaenolites* was excavated as holes in the fine-grained, tuffaceous sandstone of the Sarmiento Formation, the analyzed structures are preserved as three-dimensional casts composed of sediments of the overlying Chenque Formation. Accordingly, original scratches or grooves produced on the burrow wall are preserved as positive ridges on the cast (Figs. 4 and 7).

A thin burrow lining is observed in many specimens; this lining may have resulted from erosion of fine-grained particles of the host sediment by the spines during the excavation process. Turner (1954) proposed that particles

eroded from the substrate could be wedged in the mucus-filled depressions between spines and could aid abrasion (see also Savazzi, 1999). The felsic tuffaceous sediments of the Sarmiento Formation could well have served as the abrasive. This sediment may also have provided optimal conditions for the formation of an external mold prior to the dissolution of the valves. Once the shells were dissolved, passive filling of the shell molds resulted in the molding of the shell ornament directly on the exterior of the shell casts. Later stages of brittle deformation of the casts resulted in cracks filled in with gypsum (Fig. 6B).

4. Constructional morphology

Bivalves adapted to mechanically excavate in firm (but unlithified) substrates or to bore into lithified substrates, have developed modifications in both their internal morphology as well as in their valves. For instance, Purchon (1955) mentioned some anatomical characteristics of *Zirfaea*, such as the loss of the ligament, the presence of a wide pedal gape, the growth rings with spines only on the anterior outer surface of the valves, and the development of a platform built on the outer surface of the shell for the anterior adductor muscle's attachment. Studies on the movement of modern pholadid borers postulate the existence of cycles of successive contractions of the anterior and posterior adductor muscles, which cause the movement of the valves in different directions, with consequent abrasion of the walls during boring (Nair and Ansell, 1968; Trueman, 1975; Röder, 1977). Comparable movements and morphological adaptations have also been recognized in those pholadids adapted to excavate in firm substrates (Röder, 1977; Savazzi, 1999). Specifically, Seilacher (1985) noted that the valves of the rock-borers have two axes around which they can pivot, in such a way that their marginal spines produce a series of scratch ornament arranged in successions as if they were a row of chisels. This pattern is similar to that observed in the walls of the Miocene specimens of *Gastrochaenolites*. Interesting enough, the Chenque material was produced in a firm substrate and not strictly in a lithified substrate as envisaged by Seilacher's model (see Seilacher, 1985, Fig. 2g–i).

Yonge (1964) distinguished a rotational movement of the bivalves inside their excavations, alternating first in one direction and then in the other. In addition to these clockwise and anticlockwise movements (between 25° to 30°), there is a complete rotational movement (360°), by changing the position of the foot (Trueman, 1975). This complete rotation results in the circular shape of the perforation/excavation typically observed in cross-sectional and basal views of *Gastrochaenolites*.

The scratch patterns preserved in the Miocene *Gastrochaenolites* allow reconstruction of the rotational movements like those observed in extant species. Fig. 8 summarizes the typical movements of pholadid bivalves during boring/excavation. Fig. 8A and B indicate the retraction of the bivalve due to contraction of the pedal retractor muscle. Fig. 8C represents the contraction of the posterior adductor muscles. This contraction would cause opening of the valves, with the subsequent friction of the marginal spines against the sediment, producing the formation of oblique scratches. These scratches are arranged in a circular pattern at the basal part of the ichnofossils (Fig. 7A, C and E). Fig. 8D represents the movement made by the bivalves when performing a complete rotation inside their excavation. This rotational movement may have generated the horizontal scratch patterns identified in the Miocene *Gastrochaenolites*. The horizontal bioglyphs are mostly preserved in the lower portions of the main chambers, but immediately above the oblique scratches (Fig. 7A–E).

5. Implications for Ichnotaxonomy

Clavate biogenic structures reported herein fit within the ichnospecies *Gastrochaenolites ornatus*. However, *Gastrochaenolites* was defined primarily to designate clavate borings developed in hard (lithified) substrates, including mollusk shells, coral, and limestone (Kelly and Bromley, 1984), and thus employment of this ichnogenus for structures developed in firmground substrates is controversial. Mikuláš et al. (2003) noted that this use of *Gastrochaenolites* contradicts the general consensus of using the substrate as an ichnotaxobase (Pickerill, 1994, p. 5; Bertling et al., 2006, p. 275). Ekdale and Bromley (2001) also raised this point with respect to *G. oelandicus*. Some of their specimens seem to be borings (i.e., developed in hardgrounds) and some may be burrows (i.e., developed in firmgrounds). These authors discussed whether substrate constitutes a valid criterion to be used as an ichnotaxobase. Giving burrows and borings different names seems reasonable when the ichnofossils reflect different behavioral adaptations (i.e., *Skolithos* versus *Trypanites*). However, it would be confusing to give different ichnotaxonomic names to morphologically identical structures built in different substrates, when the same ethology and mode of construction is involved (Ekdale and Bromley, 2001). In fact, modern pholadids, which excavate in firm substrates, use comparable movements to those employed during perforation in hard substrates (Savazzi, 1999). Furthermore, the Miocene ichnofossils analyzed are identical to *G. ornatus* produced in hardgrounds, and therefore are assigned to

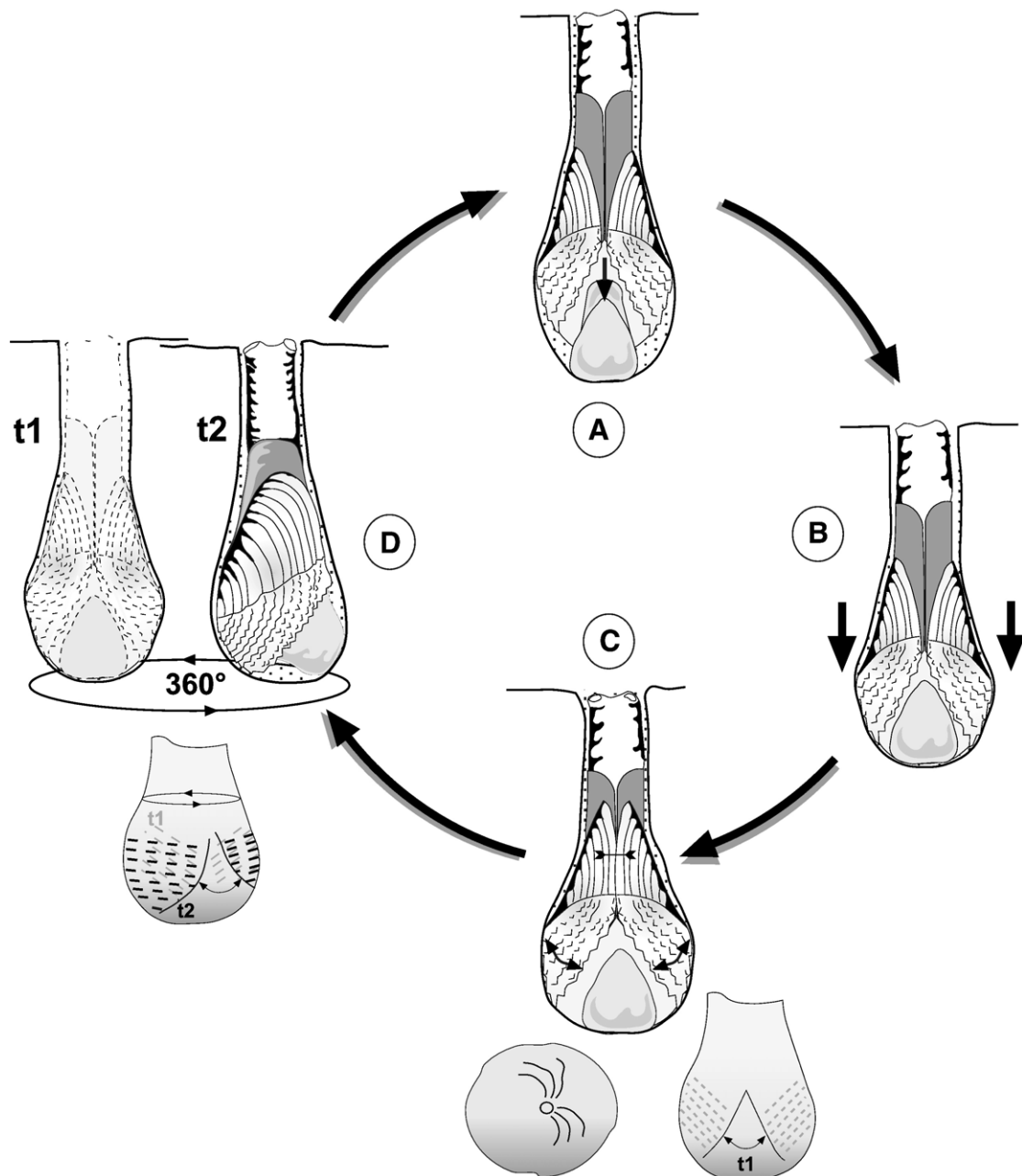


Fig. 8. Schematic representation of the typical movements of the bivalves during excavation (based on Trueman, 1975 and modified to represent the information obtained from the Miocene ichnofossils). In A, the pedal retractor muscles cause retraction of the valves and downward movement of the bivalve (B). In C, the contraction of the posterior adductor muscles is represented. These muscles are attached at the posterior end of the valves, and their contraction produces the abrasion of the excavation walls with the spines located on the anterior margins of the valves. This movement produces the oblique scratches seen on the surface of the ichnofossils. The schematic drawings below C represent the basal and lateral views of the excavations during this first cycle (t1) of movements. D — A second cycle of movements (t2) starts when the bivalve rotates inside its excavation. The schematic drawing below D shows the idealized pattern of scratches that is produced through successive rotational movements of the bivalves during t1 (in grey) and t2 (in black).

this ichnospecies based on morphofunctional analysis. In conclusion, using the substrate as an ichnotaxobase in this particular case would be artificial and misleading.

Substrate may qualify as a high-ranking ichnotaxobase when comparing trace fossils developed in soft-ground, hardgrounds and woodgrounds, particularly

when morphology reflects distinct ways of organism–substrate interactions. However, when the same organism is able to both burrow and bore – as in the case of pholadids (Savazzi, 1999) – and when the excavation technique is identical to the mechanical perforation technique, as demonstrated by the specimens analyzed herein, the validity of the substrate as an ichnotaxobase vanishes.

Just as there would be differences between structures developed in firmgrounds of differing stiffness, similarly hardgrounds encompass a range of true hardness depending on composition (e.g. a cemented carbonate sand versus a pillow basalt). This is particularly important for substrates harder than the valves themselves, because some pholadids use the eroded particles as the abrasive to perforate substrates harder than their own shells (Turner, 1954). Consequently, borings emplaced in the hardest of hardgrounds may exhibit some morphologic differences with respect to those developed in less hard substrates. In conclusion, although traditionally considered a boring, the ichnogenus *Gastrochaenolites* may also record burrowing in firm, compacted, but unlithified substrates.

Bromley and Asgaard (1993) defined the ichnogenus *Phrixichnus* to designate large clavate borings that resemble *Gastrochaenolites* in general morphology and size. However, *Phrixichnus* is clearly distinguished from *Gastrochaenolites* by its ornament of arcuate, concentric grooves, its rectangular/oval cross-sectional shape, the distinction of the wall into ornamented and smooth areas,

and its abrupt changes in direction (Bromley and Asgaard, 1993).

6. Spatial heterogeneity and temporal dynamics of firmgrounds

Together with *Gastrochaenolites ornatus*, decapod boxworks (*Thalassinoides* isp.) are typical components of the firmground association analyzed (Carmona et al., 2006). This association represents the substrate-controlled *Glossifungites* ichnofacies, which is characteristic of stiff, dewatered, unlithified substrates (MacEachern et al., 1992; Pemberton et al., 2001). The *Glossifungites* ichnofacies has been the focus of many studies after the realization of its utility to delineate surfaces with sequence stratigraphic implications (e.g., MacEachern et al., 1992; Pemberton et al., 1992, 2004; Gibert and Robles, 2006). In siliciclastic deposits the *Glossifungites* ichnofacies is commonly associated with erosional exhumation of previously buried sediments, typically linked to changes in relative sea level changes. Colonization of firmground substrates occurs during a depositional hiatus that takes place between the erosional event and sedimentation of the overlying unit. In this Miocene case, the burrowed contact represents a co-planar surface of low-stand erosion and transgressive erosion that produced exhumation of deposits belonging to the Sarmiento Formation. Both bivalves and decapods colonized the

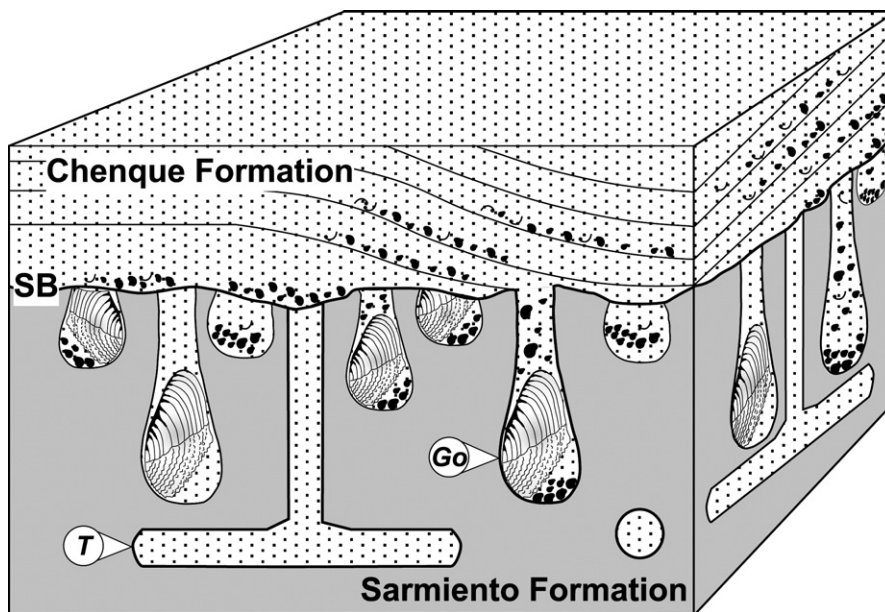


Fig. 9. Schematic representation of the studied erosive surface, showing a complex history of colonization and erosion. The bivalves have wide size ranges, and the burrows show differential truncation of the apertural necks and variable nature of their fills. Go = *Gastrochaenolites ornatus*, T = *Thalassinoides* isp.

firmground surface exposed during transgressive ravinement, penetrating the tuffaceous, compacted deposits of the Sarmiento Formation.

Variations in abundance and distribution of these ichnotaxa were observed along the transgressive surface, with some localities (i.e., west of Bahia Solano, Infiernillo) showing a clear dominance of bivalve burrows and others (i.e., Astra) dominated by crustacean burrows. Colonization in modern firmground surfaces is commonly controlled by three main parameters: texture, substrate firmness and bathymetry (Pemberton and Frey, 1985; Gingras et al., 2001). In the Patagonian examples, bivalve burrows seem to have colonized firmer substrates than crustaceans. While sharp bioglyphs characterize the walls of *Gastrochaenolites ornatus*, no apparent sculptural ornamentation has been observed in crustacean burrows. Grain-size and textural characteristics are essentially the same in all the localities analyzed. Although modern analogues suggest that bivalves tend to occupy shallower-water areas than crustaceans, there is a significant environmental range overlap (Gingras et al., 2001). Furthermore, no proximal–distal trend in trace fossil distribution is apparent along the surface analyzed. Therefore, substrate firmness was the most likely controlling factor, while neither texture nor bathymetry can explain the observed variability in proportion of bivalve and crustacean burrows (Carmona et al., 2006).

Analysis of the ichnologic content, truncation of trace fossils, and the relationship between biogenic structures suggests a complex history for this erosive surface (Fig. 9). In particular, differential erosion of the apertural necks, the variable nature of burrow-fills and wide size-range of the bivalve ichnofossils suggest successive events of ravinement erosion and benthic colonization during the transgression, revealing the presence of a palimpsest surface (Carmona et al., 2006).

7. Conclusions

- (1) The boundary surface between the middle Eocene – lower Miocene continental Sarmiento Formation and the lower Miocene shallow-marine Chenque Formation of Patagonia contains abundant trace fossils (*Gastrochaenolites ornatus*) produced by suspension-feeding bivalves that excavated into the firm, dewatered, fine-grained, tuffaceous substrate of the underlying Sarmiento Formation.
- (2) Bivalves are preserved as casts and external molds in life position within their biogenic structures. Morphologic features preserved indicate that the producers are Pholadids, most likely belonging to Pholadinae.
- (3) Finely preserved bioglyphs allow reconstruction of the mechanical boring/excavation technique consisting of rotational movements. The two identified sets of scratch ornament are interpreted based on comparisons with extant bivalves; the oblique scratch traces were probably produced during contraction of the posterior adductor muscles, while the horizontal type of scratch traces are related to 360° rotational movements.
- (4) In the case that the same organism is able to excavate and bore and the excavation technique is identical to the mechanical perforation technique, the same ichnotaxonomic designation is advised. Accordingly, the ichnogenus *Gastrochaenolites*, commonly assigned to bioerosion structures, is herein regarded as available also for bivalve burrows in firm, compacted, but unlithified substrates.
- (5) The studied firmground represents a co-planar surface of lowstand erosion and transgressive erosion that produced exhumation of deposits belonging to the continental Sarmiento Formation. Variations in the abundance of bivalve and crustacean burrows probably reflect lateral changes in the degree of substrate consistency. The studied firmground is interpreted as a palimpsest surface that reveals successive events of ravinement erosion and benthic colonization during the transgression.

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