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Ichnogeny and bivalve bioerosion: examples from shell and wood substrates

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ABSTRACT

The ichnospecies *Gastrochaneolites dijugus* Kelly and Bromley 1984 and *Teredolites longissimus* Kelly and Bromley 1984, attributed to the boring activity of gastrochaenoid and pholadid bivalves, are described respectively from the Miocene Vilanova Basin and the Pliocene Almería-Níjar Basin. Miocene and Pliocene traces are preserved as positive casts associated to invertebrate shells and wood fragments, respectively; in both cases, the host substrate (shells and wood) has been lost almost entirely by different taphonomic processes (mainly dissolution). For the first time in the fossil record, the complete ichnogenetic sequence of these two ichnospecies is described and figured.

KEYWORDS

Ichnogeny; bioerosion; boring bivalves; Miocene; Pliocene

Introduction

Ichnogeny, the new ichnological concept introduced by Belaústegui et al. (2016), makes reference to the origin and development of a modern or fossil trace (bioerosion or bioturbation) in relation with the respective causative behavior and/or the ontogeny of its tracemaker. In that sense, Belaústegui et al. (2016) described two main scenarios: (1) ichnogeny closely related to ontogeny; and (2) ichnogeny independent of ontogeny.

Several previous studies may be included within the conceptual framework of ichnogeny. Following this first scenario (i.e., ichnogeny closely related to ontogeny), it is known that the burrowing or boring behavior of different kinds of organisms may change during the different stages of their respective ontogenetic cycles. Examples can be found among crustaceans (Verde and Martínez 2004), chelicerates (Martin and Rindsberg 2007), mollusks (Urrutia and Navarro 2001) or insects (Muñiz et al. 2014).

In contrast, the footprints resulting from the first steps of a baby (except for its size) are equal to and formed in the same way as those of an adult woman or man. In that particular case, it is not complicated to identify that second scenario of 'ichnogeny independent of ontogeny' proposed by Belaústegui et al. (2016). In fact, there are also many examples in the literature that describe the gradational series of consecutive stages (i.e., 'ichnogenetic stages') that occur from the inception to the final development of a bioerosion or bioturbation structure (e.g., Bromley and D'Alessandro 1984; Myint 2001; Neto de Carvalho and Pessoa e Costa 2001; Bromley et al. 2007; Falkingham and Gatesy 2014; Wisshak et al. 2018). Since the boring or burrowing (including surface bioturbation) behaviors of the tracemakers commonly remain constant throughout their lives, the ontogeny is not considered as a crucial causative factor of such traces.

With regard to the bioerosion structures produced by two well-known groups of boring bivalves (gastrochaenoids and teredinids), two clear examples of 'ichnogeny closely related to ontogeny' are described. In particular, it may be observed the ichnogenetic sequence of the ichnospecies *Gastrochaenolites dijugus* and *Teredolites longissimus* from the Miocene of the Vilanova Basin (Catalonia, NE Spain) and the Pliocene of the Almería-Níjar Basin (Andalusia, SE Spain), respectively. Given the nature of these bivalves, two different kinds of substrates are also implied in this study, mollusk shells and wood.

Gastrochaenolites from the Miocene Vilanova Basin

Geographical and geological setting

This outcrop, known as Pi Gros and designated as an ichnofossil-Lagerstätte by Belaústegui, Domènech, and

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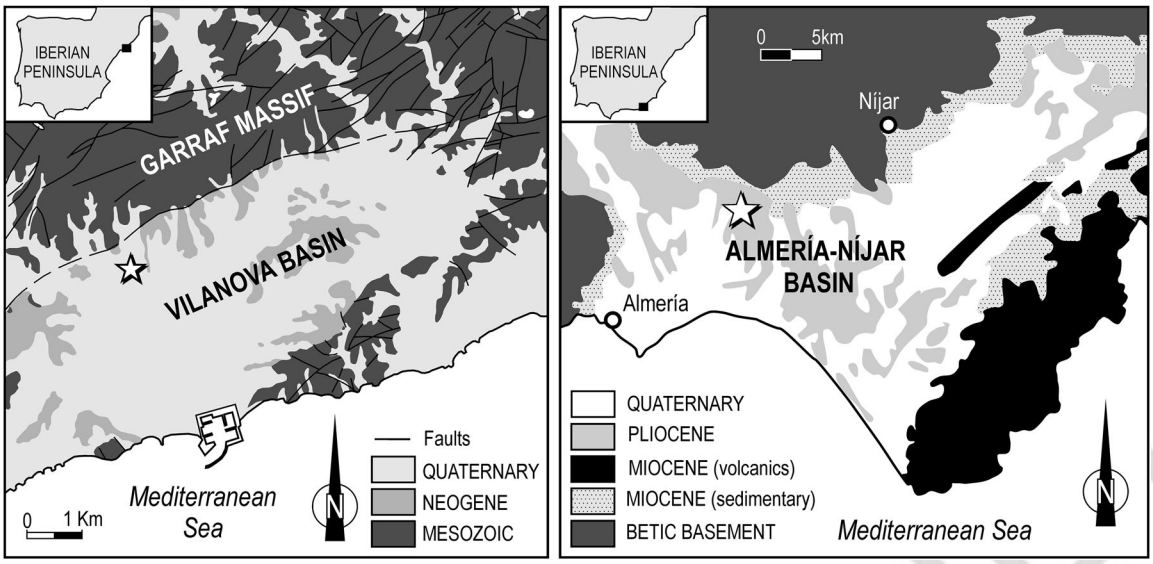

Figure 1. Geographic and geologic setting of the studied area. (A) Simplified geologic map of the Vilanova Basin and its location on the Iberian Peninsula (modified from Belaústegui, Domènech, and Martinell 2018). (B) Simplified geologic map of the Almería-Níjar Basin and its location on the Iberian Peninsula (modified from Muñiz, de Gibert, and Esperante 2010). White stars show the locations of 'Pi Gros' and 'Monte Palmo de Salas' outcrops, respectively.

Martinell (2018), is located near the town of Vilanova i la Geltrú, about 50 km southwest of Barcelona (NE Spain). The sedimentary rocks here are part of the Miocene infill of the Vilanova Basin (Figure 1A), an extensional basin situated over the Mesozoic basement that constitutes the Garraf Massif, which in turn is located within the Catalan Coastal Ranges (Cabrera et al. 2004). The Vilanova Basin is part of the onshore section of the Valencia Trough, an extensional system developed during the latest Oligocene and Miocene between the eastern part of the Iberian Peninsula, and the Balearic promontory to the east (Fontboté et al. 1990; Bartrina et al. 1992; Roca and Guimerà 1992; Roca et al. 1999).

Within the infill of the Vilanova Basin, Ramos-Guerrero et al. (1994) differentiated four main units. The sedimentary rocks studied herein consist of a mollusk coquina that should correspond with the lower part of their Upper Detrital Unit (M3). These sedimentary rocks have been dated as middle Miocene (probably Serravallian) (Agustí and Moyà-Solà 1991; Ramos-Guerrero et al. 1994; Batllori and Moreno 2003). Unfortunately, as Belaústegui, Domènech, and Martinell (2018) already commented, the Pi Gros outcrop no longer exists since it was destroyed during the construction of an industrial park over a decade ago.

Descriptive ichnology

The studied coquina from the Miocene Pi Gros outcrop exhibits a highly diverse molluscan association. Most of the body fossils (mainly gastropods and bivalves; see Belaústegui, Domènech, and Martinell 2018 and references therein) that compose this coquina are external and internal molds (sensu McAlester 1962; see Belaústegui, Domènech, and Martinell 2018 for a more detailed taphonomic explanation).

Associated with the molds of these mollusks is a plethora of bioerosion structures preserved as positive casts. Belaústegui, Domènech, and Martinell (2018) described five main ichnotaxa: *Caulostrepsis contorta* Bromley and D'Alessandro 1983, *C. taeniola* Clarke 1908, *Entobia cateniformis* Bromley and D'Alessandro 1984, *E. geometrica* Bromley and D'Alessandro 1984, and *Gastrochaenolites dijugus* Kelly and Bromley 1984. Among them, this contribution will be focused on such specimens corresponding to *G. dijugus*.

Complete specimens belonging to *G. dijugus* from the Miocene Pi Gros outcrop exhibit a clavate or flask-shaped chamber (0.8 to 22 mm long) with a circular to oval cross-section (0.8 to 12.8 mm wide), connected with a narrow neck region (up to 18.8 mm long and 5 mm wide) that has two fused cylindrical elements and exhibits an eight-shaped aperture (Figure 2; see Belaústegui, Domènech, and Martinell 2018 for more details). In addition, some of the casts contain the shells of the presumed bivalve tracemaker (possibly *Gastrochaena*) preserved in their sedimentary fill.

Ichnogeny

A gradation of ichnogenetic stages (sensu Belaústegui et al. 2016) is observable in several specimens

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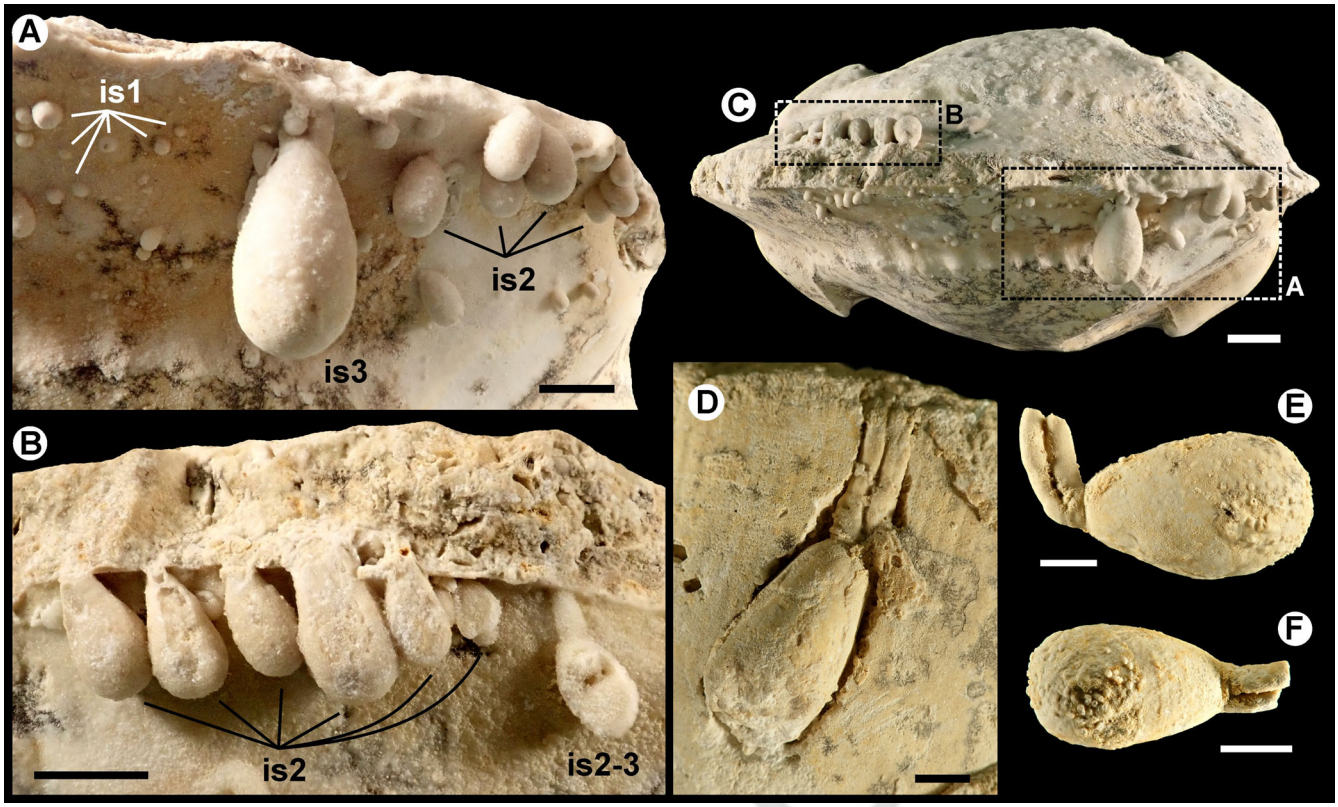

Figure 2. Ichnogeny of *Gastrochaenolites dijugus*. (A) Details of borings shown in C; example of the three ichnogenetic stages (is1, the first one, to is3, the last one) in the same specimen. (B) Details of borings shown in C; it is possible to observe the second ichnogenetic stage (is2) and its transition to the third and last ichnogenetic stage (is2-3). (C) General view of the internal mold of a complete and articulated bivalve (*Pelecyora* sp.) on which are located A and B. (D–F) Three details of the third and last ichnogenetic stage. Scale bar is 5 mm in A, B, D–F and 10 mm in C.

(Figure 2A–C). Following Belaústegui et al. (2016), *G. dijugus* constitute a clear example of ichnogeny closely related to the ontogeny of the producer. Three ichnogenetic stages have been identified:

A) a first stage that consists of hemispheric (and occasionally slightly ellipsoidal) borings ranging from 0.9 to 1.8 mm in diameter (Figure 2A,C);

B) during the second stage a teardrop-shaped morphology, typical of the *Gastrochaenolites* ichnogenus, is developed (maximum diameter ranging from 1.9 to 4.2 mm; Figure 2A–C);

C) the third and last stage is characterized by the development of two fused cylindrical elements (showing a straight or curved trajectory) in the apertural area, typical of the ichnospecies *G. dijugus* (Figure 2A,C–F).

Teredolites from the Pliocene Almería-Níjar Basin

Geographical and geological setting

Examples of fossil wood containing borings were found at Monte Palmo de Salas in the northern margin of the Almería-Níjar Basin (Figure 1B), a small Neogene basin in southeastern Spain. The infill of this basin is mainly composed of Miocene and Pliocene sedimentary rocks, unconformably overlain by Quaternary sediments (Goy and Zazo 1982; Montenat, Ott d'Estevou, and La Chapelle 1990; Serrano 1990; Aguirre and Jiménez 1997, 1998; Aguirre 1998; Aguirre and Sánchez-Almazo 1998). The Pliocene sedimentary interval was divided into two different lithostratigraphic units: a lower Pliocene to lowermost upper Pliocene Unit I; and an upper Pliocene Unit II (Aguirre 1998; Yesares-García and Aguirre 2004).

The *Teredolites* specimens studied herein are part of the Unit I. This unit consists, from base to top, of blue-grey mudstones that pass gradually into yellow-green siltstones, fine-grained sandstones, medium-grained micaceous sandstones and conglomerates. They constitute a regressive deltaic sequence from offshore to delta front facies (Aguirre 1998; Pérez-Muñoz et al. 2001). The terrigenous facies are interbedded with bioclastic beds, which were interpreted as distal and proximal tempestites by Aguirre (1998); locally, these beds may be rich in cetacean remains (e.g., Muñiz, de Gibert, and Esperante 2010). The top

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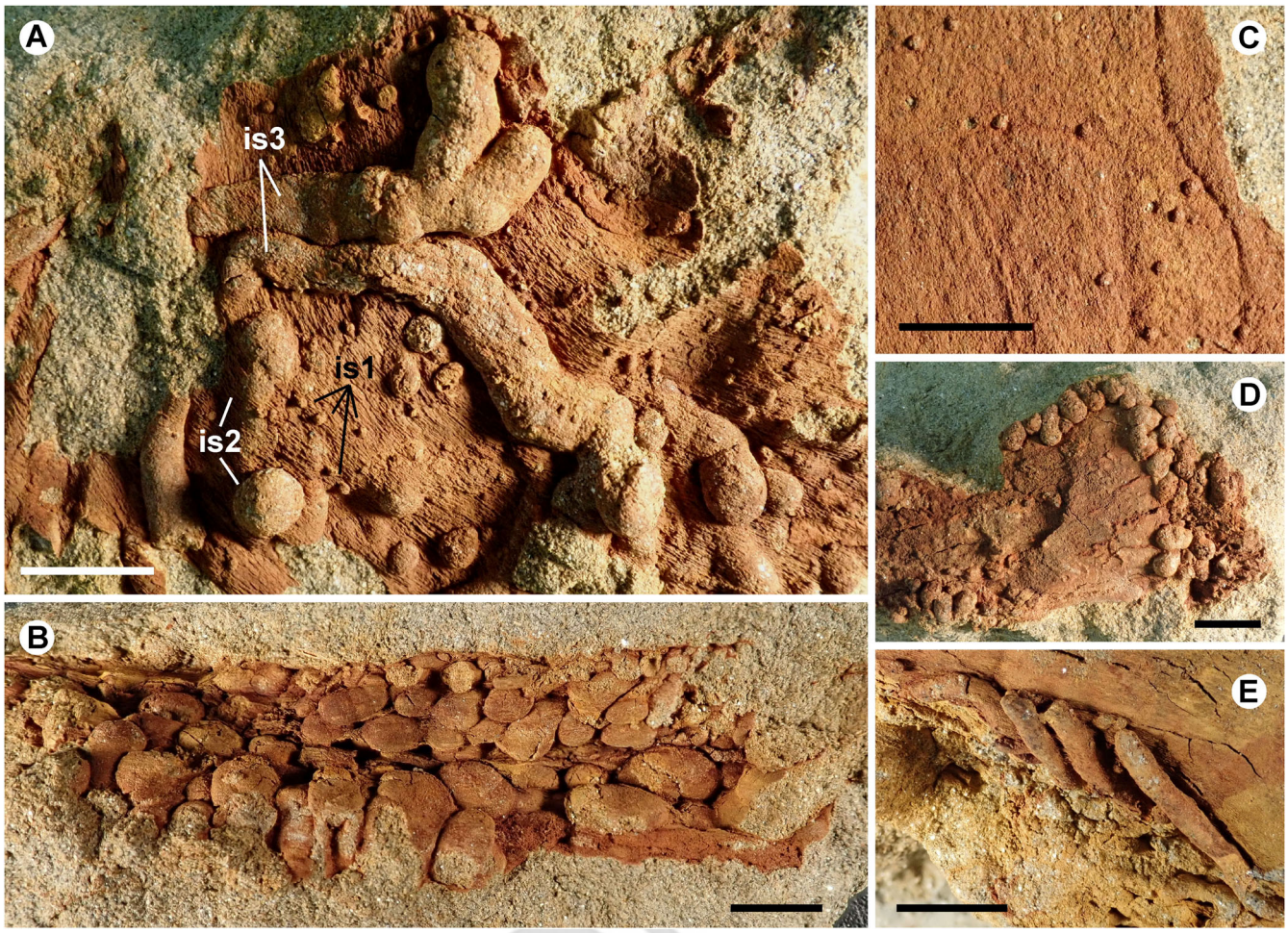

Figure 3. Ichnogeny of *Teredolites longissimus*. (A) Wood fragment showing the three ichnogenetic stages (first, is1; second, is2; and third, is3). (B) Intensely bioeroded wood fragments with specimens at its second ichnogenetic stage. (C) Hemispheric borings corresponding to the first ichnogenetic stage. (D) Dominance of specimens during the second ichnogenetic stage (clavate morphology). (E) Four specimens during the third and last ichnogenetic stage. Scale bars are 5 mm.

of Unit I is characterized by a rodolith bed formed in a shallow platform setting indicating the end of terrigenous input (Pérez-Muñoz et al. 2001).

Descriptive ichnology

Wood fragments are relatively common in the yellow-green siltstones of the base of Unit I. Several of these wood fragments exhibit abundant bioerosion structures belonging to the ichnospecies *Teredolites longissimus* Kelly and Bromley 1984 (see Donovan 2018 for a new proposal of ichnotaxonomic adscription). As occur at the Miocene Pi Gros outcrop (see above), the borings are preserved as positive casts filled with the same sediment composition that those of the enclosing matrix. Most part of the vegetal tissue (i.e., the wood) has disappeared and only its most external part is preserved; this reason prevents its taxonomic adscription.

Best preserved specimens of *T. longissimus* exhibit a clavate and cylindrical morphology with uniform circular to subcircular cross-sections along their entire length (from 2 to 7 mm in diameter) and rounded-to-subrounded ends (Figure 3A,E). These borings are commonly longer than wide, and exhibit straight to sinuous trajectories. The longer specimens are predominantly parallel to the grain of the wood. Occasionally, the abundance of borings may give the false impression of branching. Shell remains of the producers (cf. Teredinidae), together with those of the calcareous linings segregated by them, are rare and fragmentary.

Ichnogeny

As occur in the previous studied case, a gradation of ichnogenetic stages has also been interpreted from the bioerosion structures observable in the Pliocene wood remains of the Almería-Níjar Basin. These constitute

another clear example of ichnogeny closely related to the ontogeny of the producer (see Belaústegui et al. 2016).

Three main ichnogenetic stages have been identified:

A. the first stage consists of simple and hemispheric borings less than 1 mm in diameter (Figure 3A,C);
B. a longitudinal elongation is produced during the second stage, reaching a cylindrical and low sinuous morphology with a rounded blind end (quite similar to the ichnospecies *Teredolites clavatus*; Figure 3A,B,D);
C. during the third and final stage, the development of the complete and diagnostic architecture of the ichnospecies *T. longissimus* is established (Figure 3A,E).

Uncommonly, several borings belonging to the second ichnogenetic stage occur associated with a larger one of the third ichnogenetic stage. In the description of the ichnospecies *T. longissimus*, Kelly and Bromley (1984) noted (referring to tracemakers) that "juvenile forms pass through a phase having the morphology of *T. clavatus*", which is in fact perfectly concordant with the ichnogeny concept.

According to the ideal use of the ichnogeny concept, Belaústegui et al. (2016) proposed that the erection of new ichnotaxa should be avoided where an ichnogenetic sequence is identified; that is, the different morphologies and/or morphotypes observed during this sequence must be considered as the consecutive ichnogenetic stages of a particular ichnotaxon (that corresponding to the final and complete ichnogenetic stage). Nonetheless, although the second ichnogenetic stage proposed herein for the ichnospecies *T. longissimus* is morphologically comparable to the ichnospecies *T. clavatus*, this second ichnospecies is considered here as a valid and independent ichnotaxon. In fact, *Teredolites clavatus* is common in the fossil record, and commonly this ichnospecies does not present any type of connection and/or association with *T. longissimus* (e.g., Bromley, Pemberton, and Rahmani 1984; Ferrer and de Gibert 2005; Villegas-Martín et al. 2012).

Biologic aspects related to the tracemakers

Little information exists on the ontogeny and growth of Pholadaceans (pholadids, teredinids and xylophagaidids) and Gastrochaenoids in relation to their borings. Growth studies are mostly linked to their importance as edible species (the date mussel *Lithophaga lithophaga*) or as plagues that infest timber structures in marine environments (xylophagous species). The research that has been developed regarding the growth of this kind of boring bivalves (Bagur et al. 2013; Kefi, Boubaker, and Menif 2014; Peharda et al. 2015) is commonly focused on the flesh and/or in the shells.

In relation to Gastrochaenoids, Carter (1978) described some aspects about the boring behavior of tube-dwelling species in relation to their ontogeny, but without sufficient detail to obtain relevant ichnogenetic information. However, in relation to modern teredinids, Nair and Saraswathy (1971) carried out a detailed description of the boring behavior of these bivalves from their larval stages until the adult ones. In fact, these authors presented an exhaustive diagram that shows the complete ichnogenetic sequence of modern bioerosion structures that in the fossil record are assignable to the ichnospecies *Teredolites longissimus*. This diagram fits perfectly with the juvenile phase (comparable to *T. clavatus*) proposed by Kelly and Bromley (1984) and with the three ichnogenetic stages presented in this contribution.

In addition, and studying the growth rate of the teredinid *Lyrodus pedicellatus*, Knight (2018) observed that this species has a short-term free-swimming larval stage (2-24 h), after which (in 2 to 3 days), young specimens suffer metamorphosis and produce spherical borings that gradually changes to tunnels; that is, the same ichnogenetic sequence described by Nair and Saraswathy (1971) and observed in the Pliocene of the Almería-Níjar Basin. Knight (2018) also described that the average rate of tunnel growth of *L. pedicellatus* was 7.14 mm/month^{-1} during the first five months after settlement, with a slowdown in the second month; that can be explained for the necessity of a quick occupation to ensure the survival.

Conclusions

The complete ichnogenetic sequences of the ichnospecies *Gastrochaenolites dijugus* and *Teredolites longissimus* are described from Miocene and Pliocene material of the Vilanova and Almería-Níjar Basins, respectively. Both cases constitute a clear example of 'ichnogeny closely related to ontogeny'; three main ichnogenetic stages have been identified in each case, corresponding to the development of the boring behavior of these kinds of bivalves from larval to adult stages. Neoichnological studies are essential as a key tool to identify ichnogeny.

Acknowledgements

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Disclosure statement

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

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