

Paleobiology of firmground burrowers and cryptobionts at a Miocene omission surface, Alcoi, SE Spain

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Abstract.—A well-preserved omission surface (sedimentary discontinuity) in an outcrop near Alcoi in southeastern Spain displays trace fossils and body fossils that reflect a dynamic benthic community during the Miocene (Langhian–Tortonian). This outcrop, besides being the type locality of *Spongiomorpha iberica* Saporta, 1887, exhibits other abundant trace fossils, such as *Glossifungites saxicava* Łomnicki, 1886 and *Gastrochaenolites ornatus* Kelly and Bromley, 1984. These trace fossils are restricted to a single stratigraphic horizon and constitute a typical firmground ichnoassemblage of the *Glossifungites* ichnofacies. The interiors of some of the *Glossifungites* and *Spongiomorpha* burrows were occupied by encrusting balanomorph barnacles (*Actinobalanus dolosus* Darwin, 1854). This paper is the first report of cryptic barnacles colonizing the interior of open burrows that constitute a typical firmground ichnocoenose in the fossil record. Detailed ichnologic study demonstrates that the ichnospecies *Glossifungites saxicava* stands as a valid ichnotaxon and is not a synonym of the ichnogenus *Rhizocorallium*, as has been suggested by some previous workers.

Introduction

In the geologic record, omission surfaces are discontinuities within sedimentary sequences that represent major changes in paleoenvironmental conditions at the seafloor due to a pause in sedimentation that may or may not reflect a fluctuation in sea level and/or an erosional episode. Paleoecologic studies of omission surfaces are interesting and important because they highlight the ecologic and ethologic responses of members of the benthic community to dynamic seafloor conditions. Especially important in this regard is a detailed analysis of the ichnocoenoses (trace fossil communities) that inhabited the substrate before, during, and after the hiatus that is marked by the omission surface (Goldring and Kaźmierczak, 1974; Bromley, 1975; Pemberton and Frey, 1985; Lewis and Ekdale, 1992; Wilson and Taylor, 2001; Taylor and Wilson, 2003). This paper reports ichnologic and paleobiologic aspects of a well-preserved omission surface in the Miocene of southeastern Spain.

The first report of the unusual trace fossil locality near Alcoi in southeastern Spain was written by Saporta (1887), who studied fossil material that had been sent to his institution, the Muséum National d'Histoire Naturelle in Paris, by Juan Vilanova y Piera, one of the most remarkable nineteenth-century Spanish naturalists. Saporta described two different types of fossils from the Alcoi site, which he interpreted as sponges. One of them, *Taonurus ultimus*, was already known from other localities, while the second, *Spongiomorpha iberica*, was first described as a new genus and species. In the

following years, little attention was paid to this fossil locality, except for Boscà (1917), who provided a detailed description of the site and its location west of Alcoi near a farmhouse known as Can Pardinetes. Later, the actual nature of *Spongiomorpha iberica* was made clear by several authors (Kennedy, 1967; Bromley and Frey, 1974; Häntzschel, 1975), who interpreted it as a trace fossil created by crustaceans. Bromley and Frey (1974) considered *Spongiomorpha iberica* as a nomen dubium because of the inadequate original description and the lack of type specimens. Fortunately, Vilanova y Piera also had sent some material to the Museu Geològic del Seminari Conciliar in Barcelona, where it was examined by Calzada (1981), who designated a new neotype specimen and provided a new description in accordance with the trace fossil nature of the taxon. Calzada (1981) could not find the type locality, but he described a new Miocene site in Murcia, also in SE Spain (see also Gibert and Ekdale, 2010). Thanks to the help of a local amateur group, the Asociación Paleontológica Alcoyana ISURUS, the authors of the current paper were able to find the Boscà (1917) site near Can Pardinetes.

The following trace fossils are abundant and well preserved at the Miocene locality at Can Pardinetes: *Spongiomorpha iberica*, *Glossifungites saxicava* (*Taonurus ultimus* of Saporta, 1887 and *Rhizocorallium jenense* of Gibert, 2011), and *Gastrochaenolites ornatus* Kelly and Bromley, 1984. These trace fossils are restricted to a single stratigraphic horizon and constitute a typical firmground ichnoassemblage of the *Glossifungites* ichnofacies as described by Seilacher (1967; see also Pemberton

and Frey, 1985). The stratigraphic significances of *Glossifungites* surfaces have been widely explored (and exploited) in a plethora of papers (e.g., Pemberton et al., 2004; Buatois and Mángano, 2011), but other aspects concerning the paleobiology of firmground burrowers have not been addressed widely. Firmground trace fossil ichnocoenoses usually are relatively short-lived in comparison with the more complex softground ichnocoenoses. Firmground trace fossils often preserve bioglyphs that offer valuable potential for interpreting tracemaker identity and behavior. In addition, burrowing in firmgrounds can modify the seafloor, creating additional niche space by essentially turning a two-dimensional surface into a three-dimensional gallery, such as is the case here, where open burrows were occupied by *Actinobalanus dolosus* (Darwin, 1854), a balanomorph barnacle (Crustacea: Cirripedia). The objectives of this contribution are (1) to provide a description of the study site and the trace fossils, (2) to offer new ichnotaxonomic perspectives of some of the trace fossils, (3) to analyze the paleobiological significance of the traces and associated body fossils, and (4) to provide a genetic interpretation of the firmground paleocommunity based on ichnologic, paleobiologic, and sedimentologic data.

Repositories and institutional abbreviations.—The material described here is stored in four institutions: the Museo Nacional de Ciencias Naturales (MNCN) in Madrid (Spain), the Museu Geològic del Seminari Conciliar de Barcelona (MGSCB) in Spain, the Ichnological Collection of the Faculty of Geology of the University of Barcelona (UB-IC) in Spain, and the Museo Paleontológico y de las Ciencias ISURUS (MPCI) in Alcoi (Spain). All the specimens were recollected at the type locality of *S. iberica*, 9 km west of Alcoi.

Geological and geographical setting

The study locality is at Can Pardinetes within the Parc Natural del Carrascal de la Font Roja, 9 km west of Alcoi (Alicante province, SE Spain). The Miocene units bearing the trace fossils were deposited in one of the so-called Eastern Prebetic Basins (Sanz de Galdeano and Vera, 1992) in the External Zones of the Betic Cordillera (Fig. 1), which, together with the Moroccan Rif, constitutes the westernmost part of the Alpine Mediterranean Chains. Folding and diapirism controlled these small Neogene basins (Cater, 1987; Sanz de Galdeano and Vera, 1992; Ruig, 1992; Martínez del Olmo, 1999), but their precise geometry is not well known due to the structural complexity of the region.

Cater (1987) recognized three post-Burdigalian depocenters in the NE sector of the Prebetic Zone. One of them corresponds to the Alcoi-Concentaina area and constitutes a NE-SW elongated depression filled by Neogene sediments and bounded by two anticlines, which affect the Mesozoic and Paleogene units that form the Serra de Mariola and Serra de Menejador. The Miocene succession in this sector was described by Cater (1987). Most of it consists of about 1,000 m of pelagic mudstones known as the Masia del Garrofero Formation (Cater, 1987), which correspond with the informally named ‘Tap’ marls that occur extensively in the Eastern Betics. The age of this unit is late Langhian to early Tortonian (Cater, 1987; Ott d’Estevou et al., 1988; Geel et al., 1992).

The studied outcrop is poorly exposed and covered by vegetation. Trace fossils occur in the Tap marls and are found near the base of an approximately 3 m-thick carbonate unit, which is intercalated within the Tap. This carbonate unit is characterized by calcirudites with rounded lithoclasts derived from nearby Paleogene

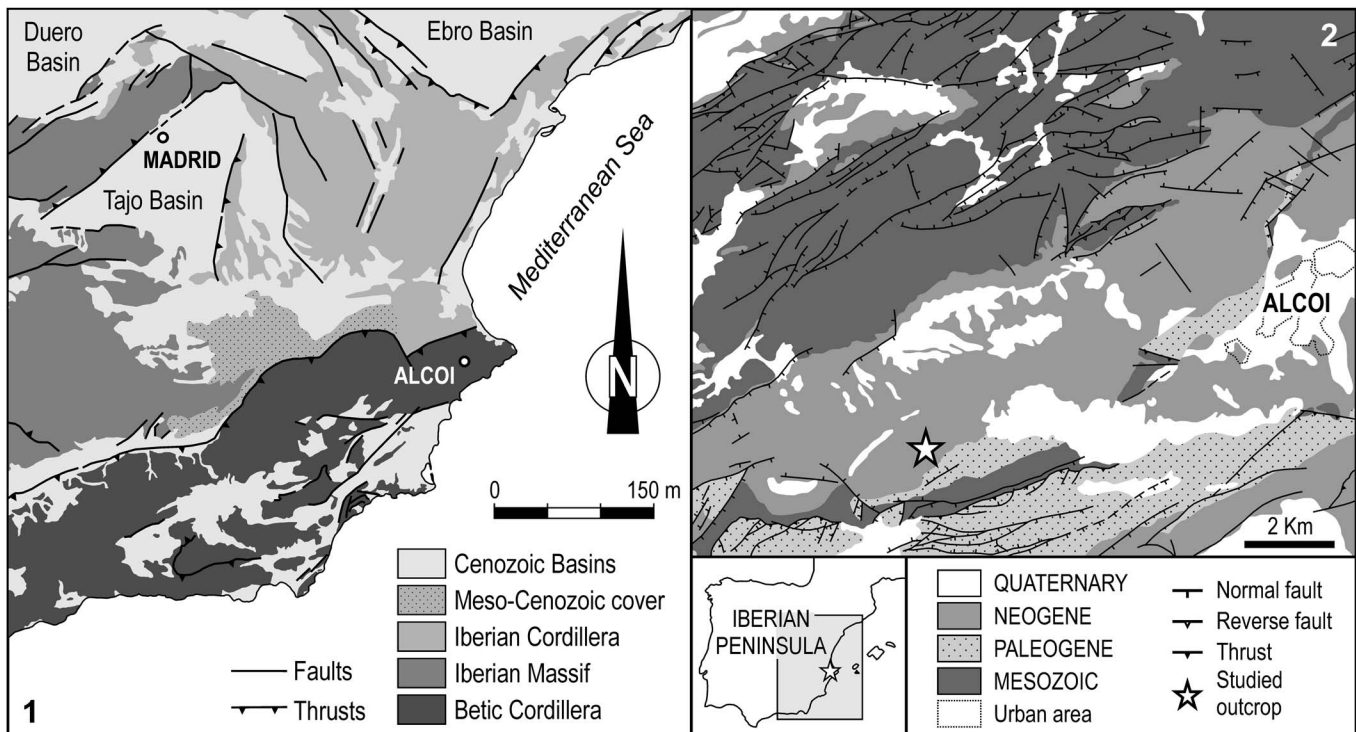


Figure 1. Geographic and geologic setting. (1) Geologic map of eastern Spain, showing the location of Alcoi. (2) Simplified geographical map of the study area (white star) and the location of the studied outcrop (*Spongeliomorpha* type locality) in the Iberian Peninsula.

limestones and horizontally laminated calcarenites in the uppermost section. Trace fossils occur in situ as full reliefs filled by the same fine-grained quarzitic calcarenite that is present in the matrix of the overlying carbonate unit, as well as hyporeliefs at the base of this unit. With respect to body fossils, the Tap marls are rich in foraminifera, including *Martinottiella communis* (d'Orbigny, 1846), *Textularia* sp., *Lenticulina calcar* (Linnaeus, 1767), *Plectofrondicularia* sp., *Globulina* sp., *Bulimina* sp., *Florilus boueanum* (d'Orbigny, 1846), *Ammonia beccarii* (Linnaeus, 1758), *Globigerina bulloides* d'Orbigny, 1826, and *Orbulina* sp. Macrofossils mainly consist of balanomorph barnacles (*Actinobalanus dolosus* [Darwin, 1854]) and pholadid bivalves (presumably *Barnea* sp.) preserved in life position within the burrows.

Systematic paleontology

Glossifungites saxicava (Fig. 2), *Spongliomorpha iberica* (Fig. 3), and *Gastrochaenolites ornatus* (Fig. 4) are the three

ichnotaxa identified in the Miocene of Alcoi (SE Spain). This is not an exhaustive systematic revision; however, remarks are provided in order to clarify some ichnotaxonomic problems.

Ichnogenus *Glossifungites* Łomnicki, 1886

Type species.—*Glossifungites saxicava* Łomnicki, 1886 from the Miocene deposits of the Lviv region, Ukraine, by original designation.

Glossifungites saxicava Łomnicki, 1886

Figure 2.1–2.14

Holotype.—No holotype specimen was designated by Łomnicki.

Emended Diagnosis.—Horizontal to oblique, tongue-shaped burrows with a central area more depressed or narrower than the outside edge. The distal part is usually wider than the aperture, which approaches a figure-eight shape. The outer surface is

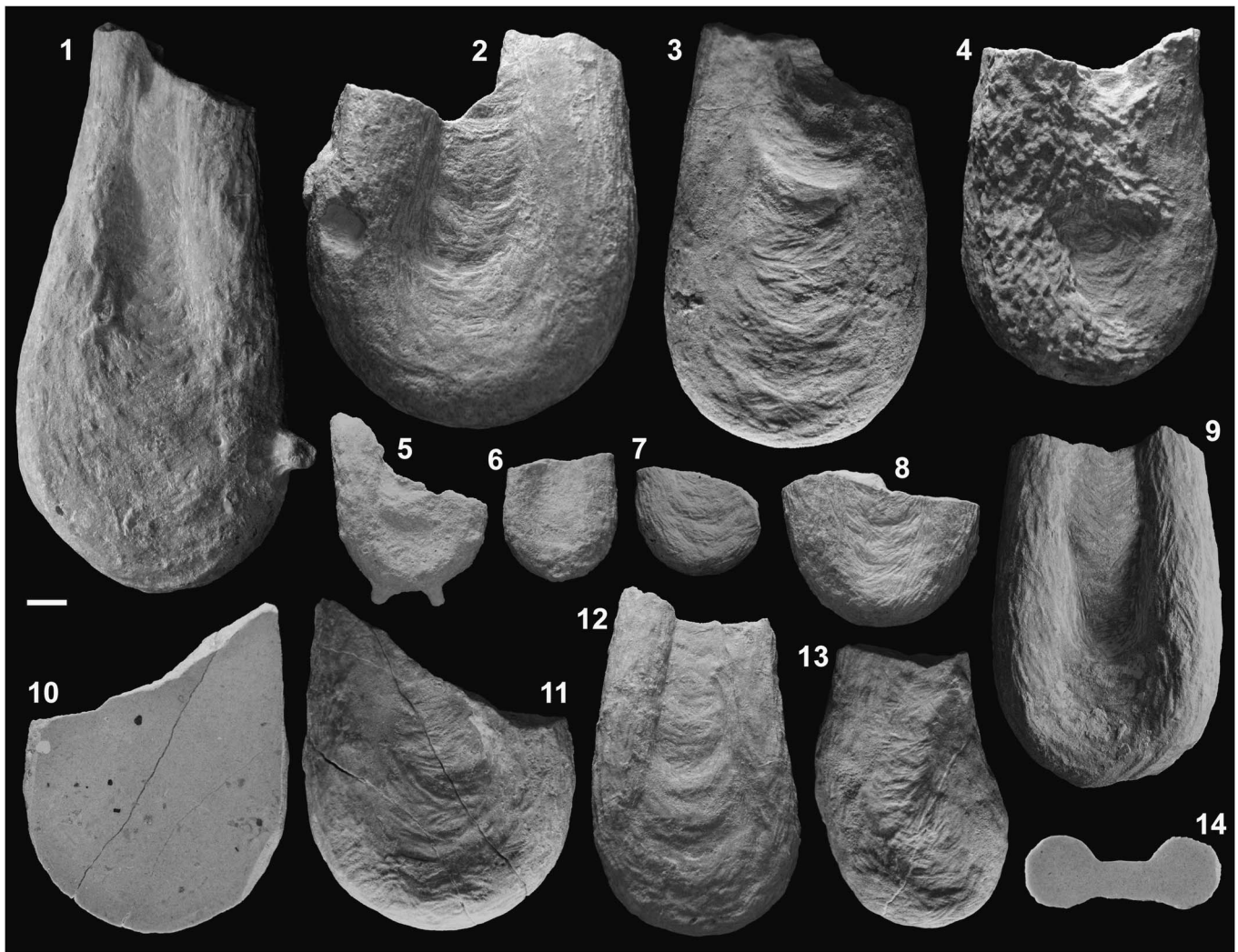


Figure 2. *Glossifungites saxicava* Łomnicki, 1886, Miocene, Alcoi (SE Spain). (1) Very complete specimen (UB-IC 570); a *Spongliomorpha* branch is observable in the lower part. (2, 3, 6–9, 12, 13) Different specimens with different sizes showing bioglyphs, i.e., longitudinal ridges along the outside edge and shorter crisscrossed ridges in the depressed central area (UB-IC 571, 572, 575 to 578, 580, MPC1 CIAI-01332, and UB-IC 581, respectively). (4) Specimen colonized secondarily by the *Spongliomorpha* tracemaker (UB-IC 573). (5) Specimen exhibiting two blind and twin tunnels in the lower part (UB-IC 574). (10, 11) Two sides of the same longitudinally cut specimen; the polished inner side (10) shows no evidence of any kind of spreite or filling structure (UB-IC 579). (14) Transverse polished section, no spreite or filling structure is observed in the central area (UB-IC 582). Scale bar = 1 cm.

covered by bioglyphs: longitudinal ridges disposed along the outside edge and shorter crisscrossed ridges located in the depressed central area. In both cases, bioglyphs are oriented roughly parallel to the overall tongue-shaped morphology. Burrows are passively filled, i.e., lacking any kind of spreiten (adapted from Łomnicki, 1886).

Description.—It is possible to observe a gradation of burrow sizes, with lengths ranging from 45 to 162 mm and a maximum width varying between 28 and 89 mm, narrowing toward the aperture (from 51 to 23 mm wide). Aperture height ranges from 8–25 mm at the outside edge to 3–11 mm in the central area. With respect to the bioglyphs, scratches are 1 mm wide and vary from 4 to 31 mm long. No spreiten structures are observable in the infill of these burrows, which is totally homogeneous (Fig. 2.10, 2.14). Occasional ramifications may occur; exceptionally, a small specimen (35 mm maximum width; Fig. 2.5) shows two short, twin, and blind tunnels in its most distal part.

Materials.—UB-IC 570 to 637 and MPC1 (CIAI-00114, 00891, 01028, and 01332 to 01336). There are also specimens deposited by Prof. J. Vilanova y Pera in the MNCN (MNCNI-18238, 18240, 18241, 18612, and 38909).

Remarks.—The original diagnosis of Łomnicki (1886), as translated into English by Uchman et al. (2000, p. 185, 187–188), described *Glossifungites saxicava* from the type section in the Ukraine as “...tongue-like or hoof-like borings, which reach down into the rock, and which are filled with coarse sand that is composed of smoothly abraded grains. Better preserved specimens show one of the surfaces (the lower, if horizontal) to be smoother, with cylindrically thickened margins, which are longitudinally striated, parallel to the margin. The second surface (upper is flat, with slightly thickened margins, and with much coarser sandstone grains” There is no mention that the sediment filling the trace fossil corresponds to material that was reworked by the burrowing animal, as in a spreite. Łomnicki ascribed the origin of these fossils to ‘lithophagous sponges,’ presumably somewhat akin to modern rock-boring clionaid sponges.

The Alcoi specimens of *Glossifungites* appear to be essentially identical to those described by Łomnicki from the Ukraine, and the original drawing of the trace fossil by Łomnicki (1886, pl. 3, fig. 64a, b; reproduced in Uchman et al., 2000, fig. 4) looks exactly like *Glossifungites* specimens from Alcoi. The reported dimensions of the traces from the two sites also are similar. Thus, it is quite reasonable to conclude that the Alcoi specimens fit with the ichnogenetic and ichnospecific diagnoses of *Glossifungites saxicava* Łomnicki, 1886.

Some subsequent workers have regarded *Glossifungites saxicava* to be a junior synonym of *Rhizocorallium jenense* Zenker, 1836 (see discussions in Uchman et al., 2000; Knaust, 2013). *Rhizocorallium* generally is described as a U-shaped spreiten burrow, typically subhorizontal to horizontal, and usually entirely protrusive. In *Rhizocorallium*, the sediment occupying the interlimb area between the two tubes of the ‘U’ is clearly sediment that was reworked by the burrower as a spreite consisting of the ghosts of successive tunnels that have been shifted distally as the burrower extended the U tube. This sort of

spreiten structure is absent from *Glossifungites saxicava*, so it is inappropriate to synonymize this ichnospecies with *R. jenense*.

In the Miocene of Alcoi, specimens of *G. saxicava* are preserved often as full reliefs and hyporeliefs. In the latter case, only the aperture area is preserved (Fig. 5). Burrow casts are filled by fine-grained carbonates from the overlying unit. In addition, calcareous basal plates of *Actinobalanus dolosus* (Cirripedia) encrusting the burrow walls are observable in the outer part (Fig. 6.1–6.2). Thin sections show that these barnacles are located in life position within the burrows and frequently occur only on the upper side (i.e., the roof) of them (Fig. 7). Fifty-five specimens have been analyzed, documenting that 22% exhibit basal plates of *A. dolosus*, which represent clusters of up to 41 individuals.

Ichnogenus *Spongeliomorpha* Saporta, 1887

Type species.—*Spongeliomorpha iberica* Saporta, 1887 from the Miocene locality of Can Pardinetes, 9 km west of Alcoi, southeastern Spain, by original designation.

Spongeliomorpha iberica Saporta, 1887 Figure 3.1–3.6

Neotype.—MGSCB specimen number 33010, selected by Calzada (1981, p. 192), Barcelona, Spain. Figured by the cited author (pl. 2, fig. 2).

Emended Diagnosis.—Cylindrical to elliptical, simple to complex, and mainly horizontal burrow systems, showing Y- and/or T-shaped branching, characterized by an ornamented and unlined wall (i.e., with bioglyphs). Bioglyphs consist of sharp Y-shaped ridges, longitudinally disposed with respect to the main axis of the burrow, and sets of shorter, parallel, rectilinear ridges oriented perpendicularly to the axis of the burrow. Short, blind tunnels with a very characteristic tapering termination are very common (after Calzada, 1981; Gibert and Ekdale, 2010; Gibert, 2011).

Description.—Cross sections of the burrows are subcircular to ovate (14 to 33 mm diameter). Tunnels are commonly rectilinear (Fig. 3.1, 3.5), and Y-shaped branching points are common (Fig. 3.3, 3.4). Blind tunnels with sharply tapering terminations are very abundant (Fig. 3.2). Bioglyphs consist of a rhomboidal pattern composed of Y-shaped scratches (1 mm thick, 2–4 mm wide, and 6–11 mm long). The sets of shorter, parallel, rectilinear ridges described by Gibert and Ekdale (2010) in the *S. iberica* specimens from the Miocene of the Fortune Basin (Murcia, SE Spain) have not been observed in the specimens from Alcoi, probably because these latter bioglyphs have a slightly worse preservation potential.

Materials.—UB-IC 638 to 670, and MPC1 (CIAI-00115, 00116, 01029, 01030, and 01337 to 01341). There are also specimens (syntypes) deposited by Prof. Vilanova y Pera in the MNCN (MNCNI-06706 and 18239).

Remarks.—Ichnogenera *Thalassinoides* Ehrenberg, 1944 and *Ophiomorpha* Lundgren, 1891 have been proposed as junior

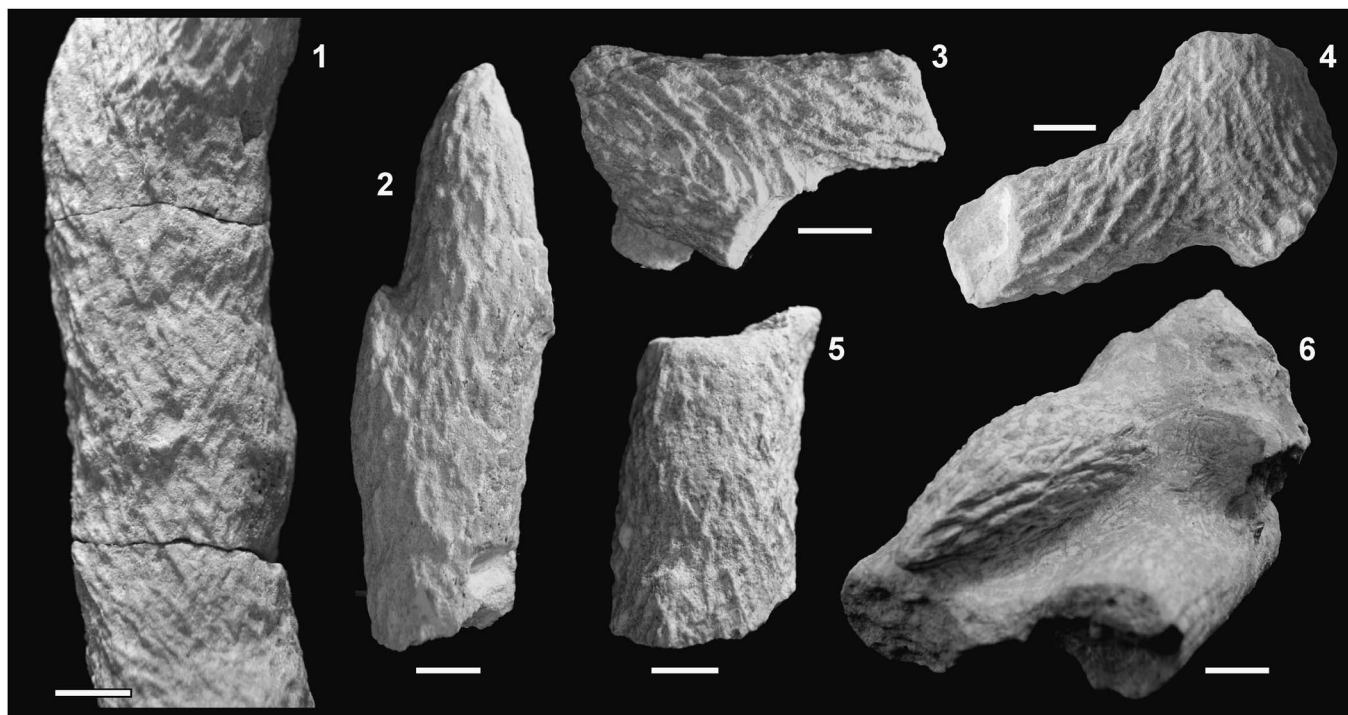


Figure 3. *Spongiomorpha iberica* Saporta, 1887, Miocene, Alcoi (SE Spain). (1, 5) Three specimens showing the diagnostic Y-shaped bioglyphs (UB-IC 638 and 641, respectively). (2) Blind tunnel with a tapering termination (UB-IC 639). (3, 4) Y-shaped branching points (MPCI CIAI-01337 and UB-IC 640, respectively). (6) *Spongiomorpha* blind tunnel associated with a *Glossifungites* burrow (UB-IC 642). Scale bars = 1 cm.

synonyms of *Spongiomorpha* Saporta, 1887 (Fürsich, 1973, 1974a; Schlirf, 2000) since all three ichnogenera are considered as branching burrow systems that are differentiated only by wall features, which are in turn related to different consistencies of the substrate during burrowing. Following Gibert and Ekdale (2010), we consider these three ichnotaxa as separate and valid ichnogenera. While *Ophiomorpha* burrows exhibit a characteristic pelleted lining, a specialized burrowing behavior observed in some modern callianassid shrimps (e.g., Weimer and Hoyt, 1964; Gibert et al., 2006), *Spongiomorpha* and *Thalassinoides* never possess pellets in their walls. In turn, these two ichnogenera, respectively, are differentiated by exhibiting walls that may or may not be covered by bioglyphs. Besides bioglyphs, Gibert and Ekdale (2010) also proposed two additional ichnotaxobases to differentiate between these two ichnogenera: (1) the abundance of blind tunnels with very sharply tapering terminations observed in *Spongiomorpha*, and (2) the absence of an anastomosing-tunnel geometry as seen in *Thalassinoides*.

In summary and continuing the studies of Calzada (1981), Gibert (2011), and Belaústegui et al. (2014), we emphasize the importance of *S. iberica* as a valid ichnogenus and ichnospecies and highlight the Miocene of Alcoi (SE Spain) as its type locality.

In the Miocene of Alcoi, *S. iberica* is preserved as full reliefs and hyporeliefs (Fig. 5). As with *G. saxicava*, the burrow infill has the same composition as that of the overlying carbonate unit, and barnacles (*A. dolosus*) encrusting the walls inside some burrows (Fig. 6.4–6.6) are observable. In this case, barnacles appear in 33% of the 33 analyzed specimens, and they are found in clusters of up to 12 individuals.

Ichnogenus *Gastrochaenolites* Leymerie, 1842

Type species.—*Gastrochaenolites lapidicus* Kelly and Bromley, 1984 from the Basal Spilsby Nodule Bed, Spilsby Sandstone, middle Volgian, Nettleton, Lincolnshire, England, by original designation.

Gastrochaenolites ornatus Kelly and Bromley, 1984
Figure 4.1–4.7

Holotype.—NHMUK 32602, S. Woodward Collection, Natural History Museum of UK, London, UK. Figured by Kelly and Bromley (1984, fig. 7).

Diagnosis.—See Kelly and Bromley (1984).

Description.—Studied traces have the typical flask-shaped, or clavate, morphology of the ichnogenus *Gastrochaenolites*. They are circular to oval in cross section (23 to 29 mm maximum diameter); their morphology is commonly rectilinear although some specimens may be slightly curved (80 to 91 mm long); and they possess circular to oval apertures (16 to 23 mm diameter). The deepest parts (bases) of the boring exhibit circular or spiral bioglyphs, commonly continuous and concentrically serrated or arranged in zig-zag ridges (1 to 2 mm thick). Some specimens exhibit a small nipple-like protuberance in the apex of the base (up to 4 mm long; Fig. 4.5).

Materials.—UB-IC 671 to 694, and MPCI (CIAI-00890, and 01342 to 01346). There are also specimens deposited by

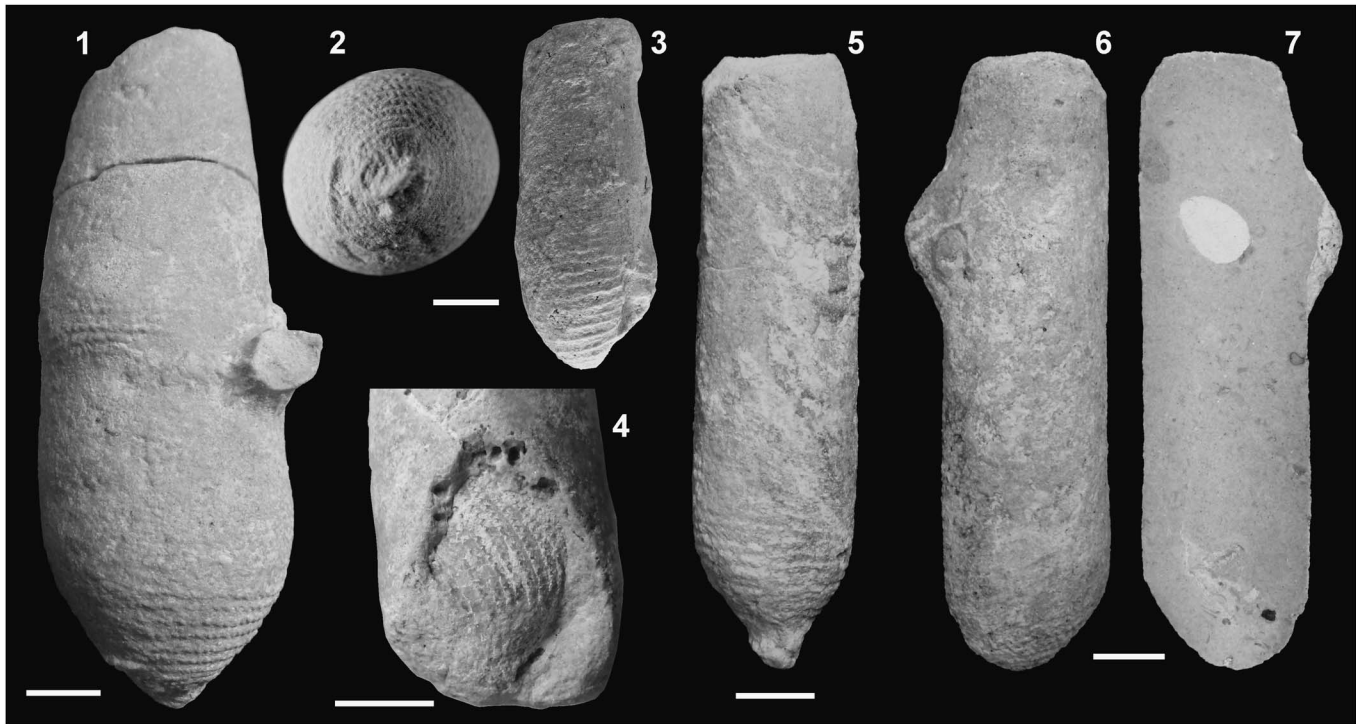


Figure 4. *Gastrochaenolites ornatus* Kelly and Bromley, 1984, Miocene, Alcoi (SE Spain). (1) Specimen showing two areas with bioglyphs and a *Spongeliomorpha* branch (UB-IC 671). (2) Basal view of (1). (3) Specimen exhibiting a clearly spiral ornamentation (MPCI CIAI-01342). (4) Fragmented specimen partially showing the shell of the bivalve tracemaker (UB-IC 672). (5) Specimen with a blind nipple-like protuberance in the apex of the base (UB-IC 673). (6, 7) Two sides of the same longitudinally cut specimen; the polished inner side (7) shows a white and rounded marl clast (UB-IC 674). Scale bars = 1 cm.

Prof. Vilanova y Piera in the MNCN (MNCNI-13543, 18242 and 18243).

Remarks.—Ichnogenus *Gastrochaenolites* is defined primarily as clavate (club-shaped) borings made in hard substrates, which are commonly attributed to the boring activity of bivalves (Bromley, 2004). However, it is known that some boring bivalves also are able to colonize both soft (unlithified) and hard (cemented) substrates (Savazzi, 1999; Belaústegui et al., 2013). In the Miocene of Alcoi, pholadid bivalves were the producers of these structures. Among the Pholadidae, there are species that may be both rock borers and firm (compacted but unlithified) mud burrowers, and they use the same mechanical technique to bore as to burrow into the substrate, producing almost the same traces in both cases (Savazzi, 1999). Although substrate character may be considered as a high-ranking ichnotaxobase, Carmona et al. (2007) point out that in these cases (i.e., organisms able to produce identical structures by both boring and burrowing), the erection of new ichnotaxa based solely on substrate character could be misleading, so they regarded the ichnogenus *Gastrochaenolites* as available for bivalve burrows in firm but unlithified substrates as well as for borings in lithified substrates. Their approach is followed in this paper.

Specimens showing the nipple-like protuberance in the deepest part of the boring are similar to the amphora-shaped ichnospecies *Amphorichnus papillatus* Männil, 1966. Regardless of its unclear taxonomic validity (Frey and Howard, 1981), *A. papillatus* has been clearly identified as a burrow, not a boring. In any case, due to the great morphological affinities

with the ichnogenus *Gastrochaenolites* and the lack of bioglyphs in *Amphorichnus*, we prefer the ichnospecies *G. ornatus* as the name of these bioturbation structures. These terminological considerations do not affect the paleoecologic and paleoethologic interpretations that follow.

G. ornatus is the most abundant of the three ichnospecies identified in the Miocene of Alcoi. This ichnotaxon occurs mainly as full reliefs; hyporeliefs also may be present, but commonly only the base (distal part) is preserved (Fig. 5). In one case, the shell of the bivalve tracemaker is partially exposed in the base of the boring (Fig. 4.4).

Discussion

Spreite and nonspreite burrows.—An ethologically and ichnotaxonomically important feature of some trace fossils is a spreite, which is widely regarded by ichnologists as a site of reworked sediment consisting of closely spaced tunnel walls that were packed together as the burrow tunnel was repeatedly shifted laterally (broadside) through the sediment (Seilacher, 1964, 2007; Frey, 1973; Häntzschel, 1975; Ekdale et al., 1984; Bromley, 1996; Buatois and Mángano, 2011; Rindsberg, 2012; Uchman and Wetzel, 2012). The behavioral significance of a spreite is that it represents the continuous activity of a burrower that processes sediment by successively moving its burrow short distances sideways, creating a series of previously occupied, sediment-filled, ghost tunnels compacted side by side in either a protrusive or retrusive direction (i.e., away from or toward the apertures, respectively). The spreite thus represents sediment

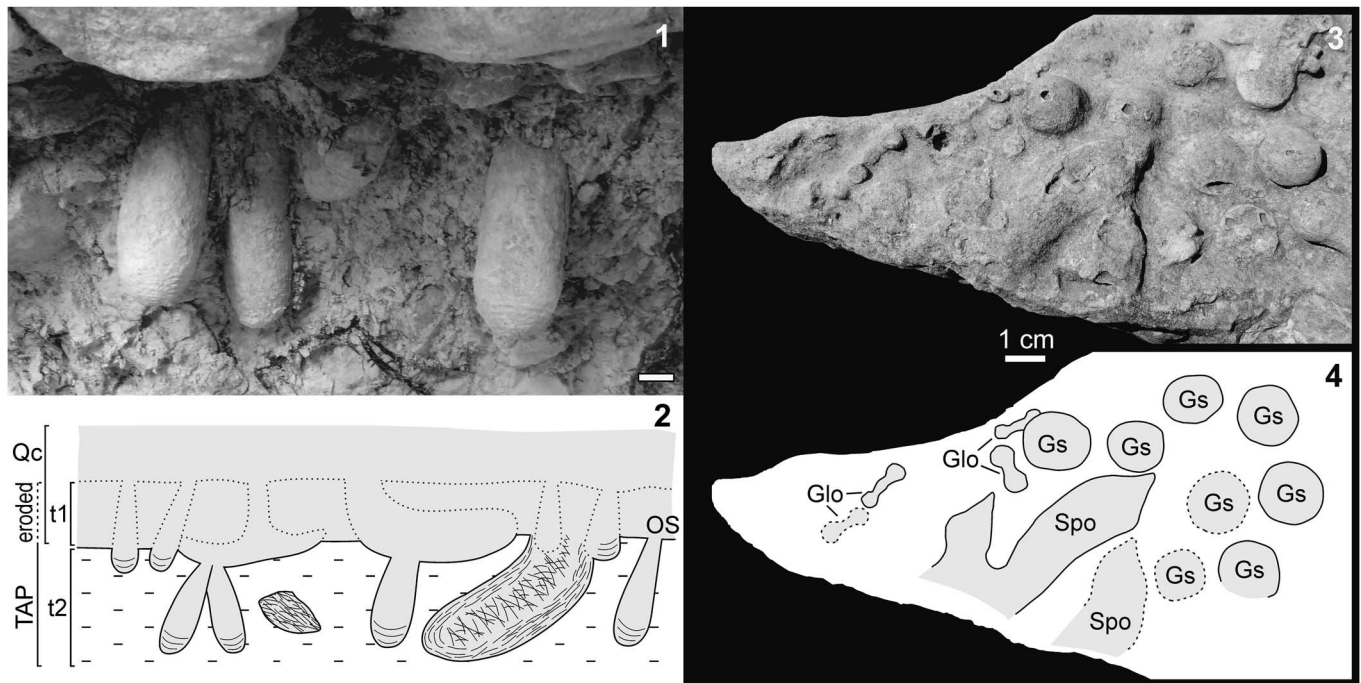


Figure 5. Alcoi outcrop. (1) Field view of the studied unit from Alcoi, trace fossils are in situ, included in the white marls (Tap), and immediately below the quartzitic calcarenite. (2) Diagram of the interpreted depositional sequence for the studied trace fossil unit. (3) Hyporeliefs on the base of the upper carbonate unit. (4) Schematic representation of (3). t1 = time 1; t2 = time 2; Qc = quartzitic calcarenite; OS = omission surface; TAP = Tap white marls; Gs = *Gastrochaenolites*; Glo = *Glossifungites*; Spo = *Spongiomorpha*. Scale bars = 1 cm.

that was actively reworked by the animal and is not just a passive fill of an open burrow. *Rhizocorallium*, a well-known ichnogenus in the geologic record, is a predominantly horizontal U-shaped burrow with a distinct spreite located between the two parallel limbs of the U-shaped tunnel (Häntzschel, 1975; Schlirf, 2011; Knaust, 2013). Although the U-shaped burrows at Alcoi were assigned to *Rhizocorallium* Zenker, 1836 by Gibert (2011), it is clear that they do not contain a spreite. Instead, the Alcoi burrows are tongue-shaped slots that were passively filled by sediment that exhibits no evidence of biogenic reworking. The originally open nature of these tongue-shaped burrows is clearly evidenced by three crucial observations: (1) the clear-cut bioglyphs on the interior burrow margins, (2) the passively compacted sediment in the central part of the ‘tongue,’ and (3) the occurrence of barnacles attached to the interior of margins of the burrow. Łomnicki (1886) appropriately assigned these burrows to *Glossifungites saxicava*, which is not a spreiten burrow. The ichnogenus *Glossifungites* therefore is not the same as *Rhizocorallium*. Despite some published opinions to the contrary (Fürsich, 1974b; Knaust, 2013), *Glossifungites* is not a synonym of *Rhizocorallium*; it stands apart as a valid ichnogenus, to which the tongue-shaped burrows at Alcoi are appropriately assigned.

Tracemakers.—*Spongiomorpha* burrow systems, characterized by the presence of bioglyphs, commonly are attributed to the burrowing activity of decapod crustaceans (e.g., Fürsich, 1973; Seilacher, 2007). Burrowing activity of modern crustaceans is well known, especially by decapods such as thalassinidean and alpheid shrimps, astacideans (lobsters and crayfish) and brachyuran crabs, or by other kinds of crustaceans such as

stomatopods (mantis shrimps) (Atkinson and Taylor, 1988; Atkinson et al., 1997). Gibert and Ekdale (2010), based on a detailed study of the Miocene *S. iberica* from Muela de Maraón (Murcia, SE Spain), proposed thalassinidean and alpheid shrimps as the possible tracemakers of *S. iberica* since these kinds of crustaceans generate today geometrically complex burrow systems with turnarounds and chambers very similar to those of this ichnotaxon.

Seilacher (2007), Ekdale and Gibert (2010), and Gibert and Ekdale (2010) interpreted three burrowing behaviors from the three different bioglyphs present in *Spongiomorpha*: (1) Y-shaped ridges were interpreted as the plucking action of the chelipeds and mainly related to digging ahead, (2) long longitudinal ridges were attributed to pereopods widening the tunnel, and (3) shorter, transverse ridges were related to the ventilation tasks carried out by uropods or to the gnawing of maxillipeds or other mouth parts to graze on bacterial film located in the tunnel wall. In the *S. iberica* of Alcoi, only those interpreted as produced by chelipeds and very rarely by pereopods have been identified.

Glossifungites was first interpreted by Łomnicki (1886) as borings produced by lithophagous sponges and subsequently filled by coarse sands. However, despite the fact that *G. saxicava* sometimes has been referred to as *R. jenense*, this ichnotaxon commonly has been attributed to the burrowing activity of crustaceans (see Knaust, 2013 and references therein). In addition, Knaust (2013) proposed chewing annelids as possible producers. However, as with *Spongiomorpha*, the presence of different bioglyphs would support the proposal according to which an animal (very likely a crustacean) with rigid appendages capable of scratching the firm mud in different

ways was the tracemaker. By contrast, it would be expected that the bioglyphs produced by annelid jaws (see Knaust, 2013) would be more repetitive (with a unique morphology) and smaller than those observed in the *G. saxicava* of Alcoi. The modern amphipod *Corophium* excavates U-shaped burrows and frequently has been suggested as a possible analogue of the *Rhizocorallium* tracemaker (Gibert, 2011). However, the tongue-shaped morphology of *Glossifungites* has not been observed in modern amphipod burrows or in other kinds of crustacean burrows. Nevertheless, this tongue-shaped architecture also might correspond to the slightly different burrowing behavior of amphipods adapted to colonizing firm substrates.

In the Miocene outcrop at Can Pardinetes, it is possible to observe a continuous gradation of sizes in *Glossifungites* specimens (Fig. 2), all of them sharing identical morphological features. This would suggest the presence of different ontogenetic stages and hence the coexistence of juvenile and adult individuals of the same species in the same sedimentary horizon.

As stated, *Gastrochaenolites* generally is defined as clavate (club-shaped) borings produced by bivalves in hard substrates (e.g., Bromley, 2004). However, it is known that traces with identical morphology can be produced in softer materials and preserved in the lithified record (Savazzi, 1999; Belaústegui et al., 2013). An identical morphology enables the use of the same ichnotaxonomic nomenclature, despite the different original substrate. In the Miocene outcrop of Can Pardinetes, the origin of these structures is attributed to the activity of a bivalve, very likely belonging to the pholadid genus *Barnea*. In one *Gastrochaenolites* specimen, the shell of the tracemaker is partially exposed in the base of the boring (Fig. 4.4). A finely cancellate sculpture is visible, but there are no more traits to permit a more accurate identification. Some bivalve internal molds also have been collected, corresponding to sediment infills of closed shells. Presumably they also represent shells of the borers, but the absence of identifying features of a pholadid has impeded a more accurate identification.

Cryptobionts.—Morton and Challis (1969) utilized the term ‘cryptobiont’ to designate communities enclosed within living or dead coral and revealed only by cracking the substratum, thus distinguishing between pioneering species that bore or excavate galleries and secondary species that nestle or take refuge in those galleries abandoned by the pioneers. In the same sense as these authors, Shirayama and Horikoshi (1982) used the term ‘cryptobionts’ to divide these secondary species in two groups: mobile species that utilize natural interstices and or biogenic crevices or holes in the coral skeleton, and immobile species that are embedded passively in the coral skeleton by coral growth.

In studying marine boring microorganisms, Golubic et al. (1975) differentiated among ‘epiliths’ (living on the surface of the substrate), ‘chasmoliths’ (adhering to the surfaces of fissures and cavities within the substrate), and ‘endoliths’ (penetrating into the substrate). Subsequently, Golubic et al. (1981) redescribed ‘endoliths’ as colonizers of the interior of rocks, and he divided them into ‘chasmoendoliths’ (colonizers of clefts in the rock), ‘cryptoendoliths’ (hidden colonizers of structural cavities within porous rocks, including spaces produced and vacated by euendoliths), and ‘euendoliths’ (rock-boring organisms).

Finally, Kobluk (1988b) proposed a uniform terminology to designate cryptic marine organisms inhabiting reefs and other settings. Among other terms, Kobluk (1988b) defined ‘cryptobiont’ as “an individual organism or species within the cryptos, or living in a crypt”; ‘crypt’ as “general term to refer to the habitats within all kinds of cavities or completely or partially enclosed void spaces”; ‘cryptos’ as “organisms as a group with a hidden mode of life living protected from full or direct exposure to major physical environmental factors”; and ‘cryptic’ as “adjective referring to organisms belonging to the cryptos” (p. 381, table 1). Kobluk’s terminology is followed in this manuscript.

Cryptobionts are common in the fossil record. In the review of pre-Cenozoic cryptobionts associated with reefs and mounds that was offered by Kobluk (1988a), the oldest occurrences date back to the Cambrian and Ordovician (see also Hong et al., 2014). To a lesser extent, even the activity of infaunal soft- and mainly hard-substrate cryptobionts is known in marine paleoenvironments (see Uchman et al., 2003 and references therein). Today, the most common organisms with cryptic habits are algae, foraminifera, sponges, corals, polychaetes, mollusks, bryozoans, and brachiopods (Kobluk and Lysenko, 1993; Lukeneder and Harzhauser, 2003; Taylor and Wilson, 2003; Zuschin and Mayrhofer, 2009; Schlagintweit and Bover-Amal, 2012).

In the Miocene outcrop of Can Pardinetes, it is possible to observe calcareous basal plates of balanomorph barnacles (Crustacea: Cirripedia: Thoracica) in the outer surface of several *Glossifungites* and *Spongiomorpha* specimens (Fig. 6), but never on *Gastrochaenolites* traces. Thin sections clearly show that the basal plates of these barnacles are attached directly to the walls of the burrows since they are associated with the wall plates, which are preserved in their original life position inside the burrow infills (Fig. 7). Occasionally, opercular plates also have been observed inside the barnacle shells (Fig. 7.1). There is no doubt that these barnacles colonized the interiors of the burrows by attaching to the burrow walls, and therefore they can be regarded as cryptobionts. The total number of clustered barnacles in *Glossifungites* specimens is variable (from 3 to 41), and the diameter of basal plates varies from 3.7 to 10.3 mm. In *Spongiomorpha*, basal plates range from 2.4 to 8.2 mm, with clusters of up to 14 barnacles. Maximum observed height is 2 mm. *A. dolosus* is a thoracican cirripede species that is present in the European Neogene, including the middle Miocene of France (Davadie, 1963) and Pliocene of the United Kingdom (Darwin, 1854; Menesini, 1964; Newman et al., 1969). This paper reports its first record of occurrence in cryptic environments.

Although the presence of cryptobionts inhabiting the inside of hardground burrow systems (mainly *Thalassinoides*-like) is well documented (e.g., Fürsich and Palmer, 1975; Voigt, 1987, 1988; Wilson and Taylor, 2001), only once before now has the presence of cryptobionts attached to the inner walls of noncemented burrows been described in the fossil record, in particular foraminifera (but not barnacles) within *Thalassinoides* burrows in the Upper Cretaceous of the Netherlands (Hofker, 1965). Furthermore, the occurrence of cirripeds in other fossil cryptic environments (e.g., caverns, grooves, crevices, or hidden spaces between cobbles or boulders) is not widely documented. Aguirre et al. (2014) described the presence of balanoid (*Balanus trigonus* Darwin, 1854) and pyrgomatid (*Pyrgoma* sp.) barnacles inhabiting grooves and

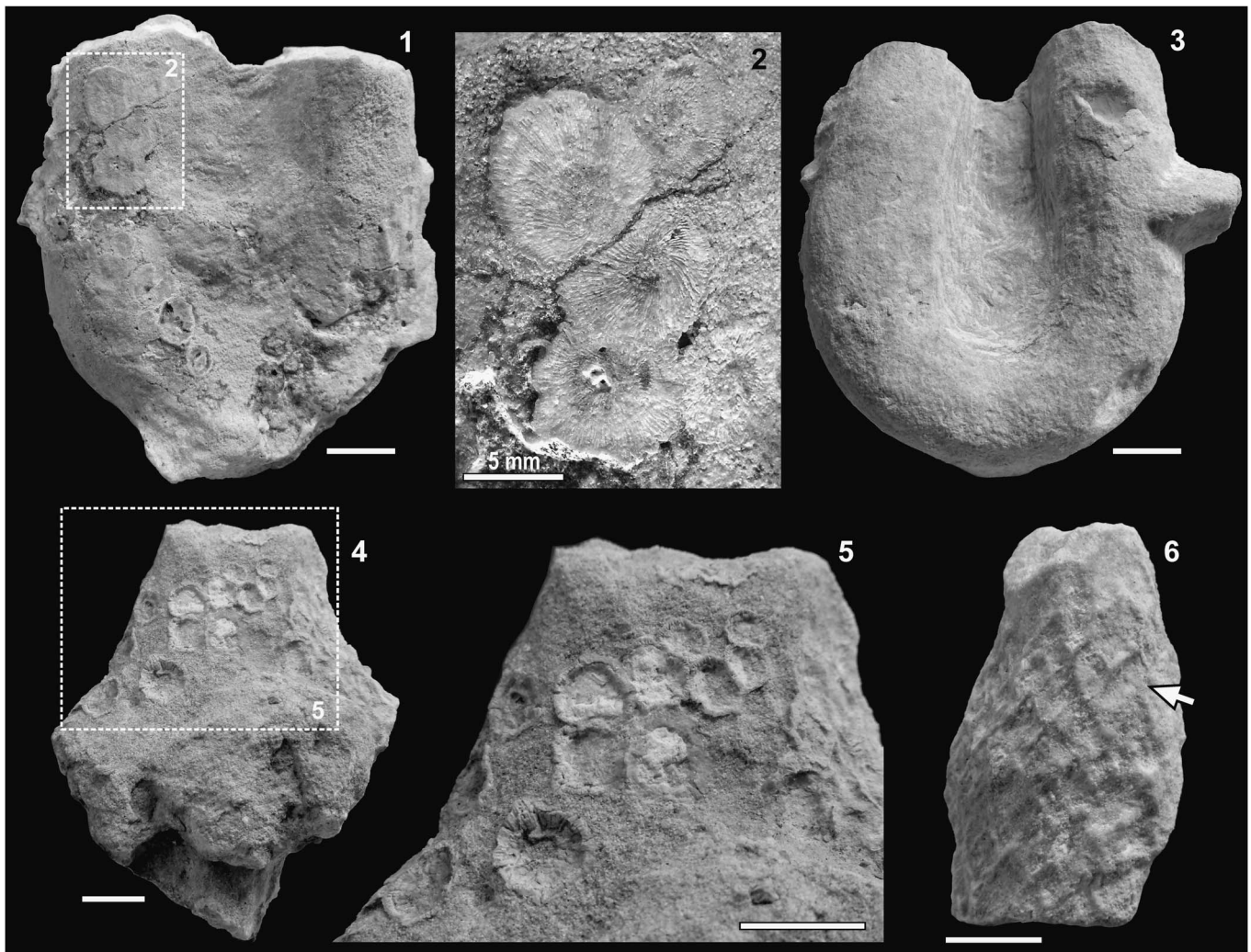


Figure 6. Cryptic barnacles. (1) *Glossifunites* specimen exhibiting several clusters of calcareous basal plates with characteristic radial canals of *Actinobalanus dolosus* (UB-IC 582). (2) Detail of *A. dolosus* basal plates in (1). (3) The lower side of (1), without barnacle basal plates. (4) *Spongiomorpha* specimen exhibiting a cluster of 15 basal plates of *A. dolosus* (UB-IC 583). (5) Detail of *A. dolosus* basal plates in (4). (6) White arrow indicates an *A. dolosus* basal plate in a *Spongiomorpha* specimen (UB-IC 584). (1, 3–6) Scale bars = 1 cm.

crevices of a Pliocene *Dendropoma* reef from the Baix Ebre Basin (NE Spain). Rosso et al. (2015) recorded the occurrence of the barnacles *Balanus perforatus* Bruguière, 1789 and *Verruca spengleri* Darwin, 1854 in a Pleistocene submarine cave in Sicily (Italy). Scarce examples of bioerosion structures attributed to the boring activity of acrothoracican barnacles (ichnogenus *Rogerella*) also have been recorded in fossil cryptic settings (Palmer and Fürsich, 1974). Today, such genera as *Amphibalanus*, *Chthamalus*, and *Euraphia* (Balanomorpha) are common inhabitants in grooves and crevices in different locales around the Mediterranean area (Linkin and Safriel, 1971; Crisp et al., 1981; Guy-Haim et al., 2015). The species *Balanus glandula* Darwin, 1854 has been observed colonizing firm-grounds at Willapa Bay, Washington (Gingras et al., 2001).

When studying the effect of light on the growth rate of two Balaninae barnacles, Barnes (1952 and references therein) concluded that wave action and water flow is much more important on the barnacle growth than the effect of light, which is almost insignificant. This fact could indicate that the barnacles colonized the interior of the burrows while these were still

occupied by their producers, likely alpheid or thalassinidean shrimps (at least in the case of *Spongiomorpha* burrow systems), since it is known that these kinds of decapod crustaceans, by pleopod beating, pump oxygen-rich surface water through their burrows promoting good irrigation and ventilation (Dworschak, 1981; Forster and Graf, 1995; Astall et al., 1997; Stamhuis and Videler, 1998a, b, c; Atkinson and Taylor, 2005). In addition to this, some thalassinidean shrimps collect and accumulate organic debris material as a food source in the walls or in chambers of their burrows, and these actions may increase the amount of organic content and bacteria in deeper layers of the sediment (Branch and Pringle, 1987; Dworschak, 2001; Dworschak et al., 2006). Therefore, since the microhabitat generated within these burrows provides: (1) ventilated and oxygenated waters, (2) high bacterial and organic content, and (3) protection against predators, its colonization by cryptic barnacles seems reasonable. In fact, within the burrows of thalassinidean shrimps, the cohabitation (mainly commensalism) of the producers with different organisms such as other decapods (e.g., alpheid shrimps), amphipods,

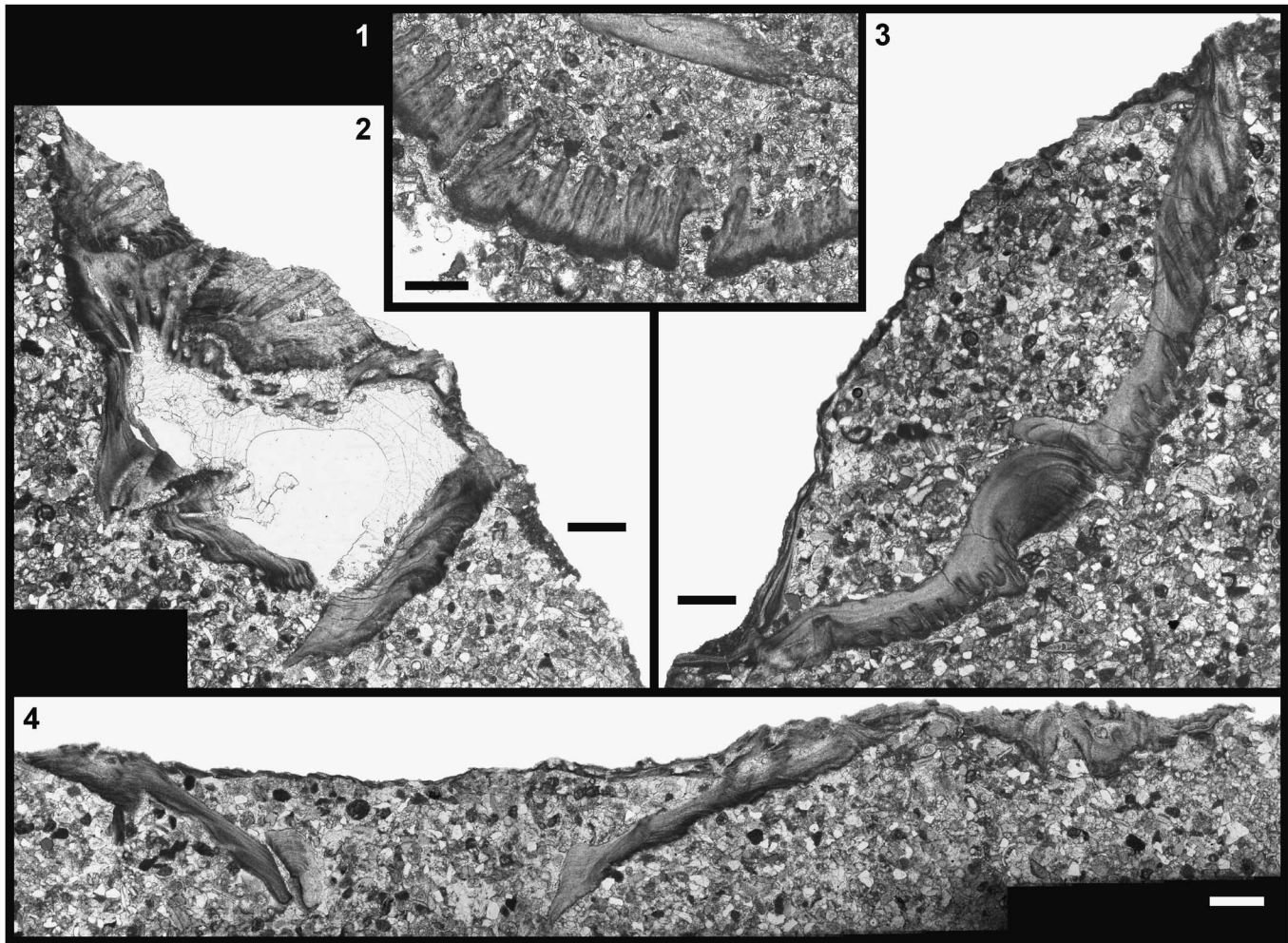


Figure 7. Test structures of *Actinobalanus dolosus* in thin section. (1) Section of the calcareous basal plate of the test showing each axial channel of epithelial blades without lateral extensions. In the upper part of the picture a fragment of an opercular plate can be seen. (2–4) Different sections of the lateral compartmental plates. Scale bars = 500 μ m.

bivalves, polychaetes, or even gobiid fish have been described both in the fossil record and today (Dworschak et al., 2000; Anker et al., 2001; Kneer et al., 2008; Liu et al., 2008; Nara et al., 2008).

Depositional sequence.—The Can Pardinetes outcrop exemplifies several successive colonization stages of an exposed sea floor during the middle to upper Miocene (Langhian-Tortonian), which are represented by a succession within the same ichnocoenose (Fig. 5). The sequence stratigraphic implications suggest a regressive trend with submarine exposure during a sea level lowstand.

First, marly lime sediment was deposited under shallow subtidal marine conditions, and the seafloor was occupied by a benthic fauna, which presumably contributed a preomission suite of trace fossils, which could not be observed in the field during this study due to poor preservation. Then the water shallowed, and sedimentation apparently ceased (with or without erosional events). The seafloor became compacted and firm, creating a firmground omission surface that was occupied by burrowers capable of penetrating the stiff (but uncemented) sediment.

The omission suite of trace fossils includes tongue-shaped burrows (*Glossifungites saxicava*), branching burrow systems (*Spongiomorpha iberica*), and club-shaped dwellings (*Gastrochaenolites ornatus*) that were produced contemporaneously by probably two taxa of crustaceans and one of pholadid bivalves. The three types of trace fossils clearly are connected in some specimens, testifying to their contemporaneity and the high bioturbation intensity at that time. In some cases it is possible to observe *Glossifungites* specimens that were colonized by the tracemaker of *Spongiomorpha*, which partially adapted its burrow to the previous one (Fig. 2.4) or just cut across it (Figs. 2.1, 3.6). The latter case also occurred between *Gastrochaenolites* and *Spongiomorpha* in some specimens (Fig. 4.1). This ichnocoenose was repeated at least two times due to successive erosive events (Fig. 5.2).

These trace fossils constitute a typical firmground ichnoassemblage of the *Glossifungites* ichnofacies as described by Seilacher (1967; Pemberton and Frey, 1985). *Glossifungites* ichnofacies dominated by the ichnospecies *G. ornatus*, as occur in the Miocene of Alcoi, also have been described in the Miocene of Patagonia, Argentina (Carmona et al., 2007). In firmgrounds at Willapa Bay (Washington, USA), Gingras et al.

(2001) described modern *Glossifungites* ichnofacies trace assemblages that are dominated by the burrows of bivalves (genus *Petricola*) and decapod crustaceans (genus *Upogebia*), which generate *Gastrochaenolites*- and *Thalashinoides*-like structures, which share a lot of similarities with the Miocene case studied here.

Cryptic barnacles could have colonized the inner walls of *Spongiomorpha* and *Glossifungites* burrows while these were still occupied by their producers, thus benefiting from the benign and protected microhabitats generated by some kinds of crustaceans within their burrows (see section 'Cryptobionts'). Conversely, these burrows could have been colonized after being abandoned and before being filled by sediment. In either case, barnacles are mostly attached to the roofs of the more horizontally disposed burrows. This preference for the roof of the burrow over the bottom could be explained by: (1) the presence of loose sediment deposited passively in the bottom, which could prevent their attachment and their breathing; (2) avoiding trampling by the host; or (3) a greater degree of compaction of the roof than the bottom. In fact, the preservation of bioglyphs also is generally better on the roof than on the bottom.

Some specimens, mainly those belonging to *Glossifungites* and *Spongiomorpha*, exhibit irregular cavities (Figs. 2.2, 3.2). Thin section evidence rules them out as bioerosion structures, since any clasts in their outer perimeter show no evidence of having been cut or dissolved. Irregular rounded marl clasts have been observed within many specimens (e.g., Fig. 4.7). Since they have the same lithology as those of the surrounding white marls (Tap), they can be considered as mud clasts. The origin of these mud clasts is due to erosional and transport processes and may be related to shrinkage and cracking of mud layers as well as to erosion and reworking by high-energy events (Knight, 2005; Ghandour et al., 2013 and references therein). The marly firm substrate that constituted the seafloor in Alcoi was exposed by at least one erosional event, as evidenced by the record of two omission suites of firmground burrows. During the erosive process, the marly firm substrate may have become fragmented and some of these fragments were redeposited as marl clasts. Some marl clasts fell into the open trace fossils, were deposited by gravity on their bottoms, and finally were buried by the passive infilling of these trace fossils by a fine-grained quartzitic calcareous sand. After diagenesis, burrow casts were totally hardened and cemented as calcarenite. Once this bioturbated unit was exposed to weathering, the differential erosion of looser marly sediments, including the marl clasts located in the outer part of the trace fossils, promoted the formation of these irregular cavities in the burrow casts.

Conclusions

The type locality of *Spongiomorpha iberica*, located in the Miocene of Can Pardinetes (Alcoi, SE Spain), was revisited and studied in detail. Besides *S. iberica*, the ichnospecies *Glossifungites saxicava* and *Gastrochaenolites ornatus* were identified.

Detailed ichnologic study demonstrates that the ichnospecies *G. saxicava* Łomnicki, 1886 is a valid ichnotaxon, and some of the trace fossils found in the Miocene site at Can

Pardinetes are attributed to this ichnospecies. The tongue-shaped, nonspreite burrows belonging to the ichnogenus *Glossifungites* are fundamentally different from the U-shaped, spreite burrows of the ichnogenus *Rhizocorallium*, so it is clear that the two ichnogenera are not synonymous.

This paper contributes the first report of cryptic barnacles (thoracican cirripedes) colonizing the interior of open burrows that constitute a typical firmground ichnocoenose in the fossil record.

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