Paleobiology of the Crustacean Trace Fossil Spongeliomorpha iberica in the Miocene of Southeastern Spain

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The trace fossil *Spongeliomorpha iberica* locally occurs in the Tortonian (Upper Miocene) marine strata of the Fortuna basin in southeastern Spain, and its excellent preservation state allows a reliable reconstruction of its main morphologic features. The burrow systems are branched (but not anastomosing), and they include numerous, short, blind tunnels. The burrow walls are strongly ornamented with bioglyphs displaying a rhomboidal pattern, consisting mostly of individual "Y"-shaped scratches. Smaller, secondary bioglyphs consist of sets of less incised transverse scratches. These features allow us to assign the ichnospecies to a decapod crustacean, most likely an alpheid or thalassinidean shrimp. The burrow apparently served as a refuge for the inhabitant, which fed upon microorganisms growing on the walls of the burrow by means of scraping the interior surfaces with the maxillipeds or other mouth parts. It is also likely that the shrimp used the multiple blind tunnels to store organic material (probably plant detritus) to be used for later consumption. The crustaceans colonized mud firmgrounds, which were formed by erosion during a rapid sea-level fall. Thus, the burrows occur in direct association with erosional regressive surfaces and therefore are good stratigraphic indicators of abrupt paleoenvironmental change.

Key words: Arthropoda, Crustacea, Decapoda, *Spongeliomorpha*, ichnology, trace fossil, bioglyph, Miocene, Spain.

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Introduction

Understanding the paleobiology of trace fossils is a clue and fundamental aspect of ichnology. There are three main questions to be answered in such an analysis: who?, how? and why? In other words, we need to learn about the tracemaker, the fabricational (constructional) aspects and the function (purpose) of the trace fossil. These questions are not always easy to answer and are intimately related. Taxonomic fingerprints (Seilacher 2007) are morphological features that may be considered as the diagnostic signature of a particular tracemaker. Among them, bioglyphs are ornaments seen in burrow walls that are produced by the activity of their inhabitants (Bromley et al. 1984; Bromley 1996; Mikuláš 1998; Ekdale and Gibert 2010). Bioglyphs not only are excellent taxonomic fingerprints, but also they can provide detailed information about behavioral aspects, such as burrow construction, use and maintenance.

Spongeliomorpha iberica Saporta, 1887 is a branched burrow system that may be attributed with confidence to crustaceans. This trace fossil is characterized by the presence of bioglyphs consisting of a complex pattern of deeply incised scratches that are seen in burrow casts as external

ridges. Calzada (1981) re-examined specimens from the type locality in Alcoi (Alicante Province, southeastern Spain), and he described a new occurrence in Muela de Maraón (Murcia Province), located approximately 100 km to the southwest of the type locality in sediments of similar Upper Miocene age.

This paper describes the trace fossils from Muela de Maraón, paying particular attention to bioglyphs as well as other morphological features in order to analyze their paleobiological significance and determine the identity of the tracemaker of the burrows, the way they were constructed, and their function.

Institutional abbreviations.—MGSCB, Museu de Geologia, Seminari Concilliar de Barcelona; IC-UB, University of Barcelona (Ichnological Collection); UUIC, University of Utah (Ichnological Collection).

Geologic and stratigraphic setting

The Muela de Maraón is a group of small mountains located east of the town of Yéchar in Murcia Province in southeast-
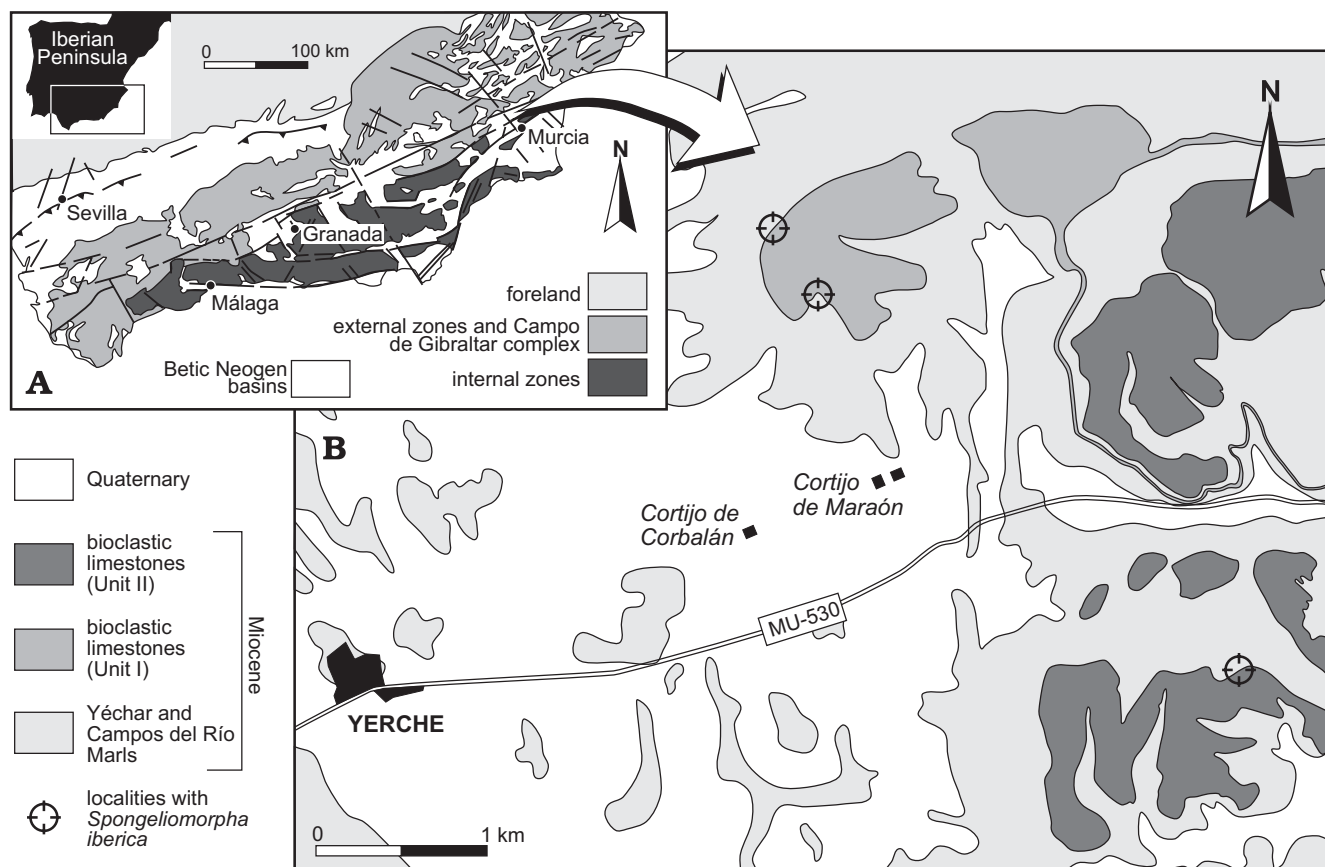
Fig. 1. Geological setting of the study area. **A**. Geological map of the Betic Cordillera, modified from Sanz de Galdeano and Vera (1992). **B**. Geological map of the Muela de Maraón sector, modified from Jerez Mir et al. (1974) and Loiseau et al. (1990).

ern Spain (Fig. 1). The Neogene units in the area are part of the sedimentary infill of the Fortuna Basin, which is a southwest-northeast intramontane trough formed over a left lateral strike-slip zone in the Eastern Betics (Garcés et al. 2001; and references therein). The basin is located between the Internal and the External Zones of the Betic Orogenic Belt, which, together with the Moroccan Rif, constitutes the westernmost part of the Alpine Mediterranean Chain.

The sedimentary infill of the Fortuna Basin consists of Upper Miocene to Pliocene sediments (Lukowsky and Poisson 1990). Loiseau et al. (1990) described the Neogene sedimentary succession in the Archena-Mula sector in the western part of the basin, where the localities of this study are situated. They described five major Miocene units, from base to top: (i) basal detrital limestones, (ii) Yéchar marls, (iii) intermediate limestones, (iv) Campos del Río marls, and (v) a carbonate-sandy unit with gypsum. The marls are dated as Late Tortonian based upon planktic foraminifera, while the fifth unit is considered by Loiseau et al. (1990) as Messinian, although it may be Tortonian if compared with data from the eastern sector (Garcés et al. 2001). Both the Yéchar and the Campos del Río marls are pelagic. The intermediate limestone units are shallow marine bioclastic limestones, 5–10 m thick, interbedded with the marls. In the Sierra de la Muela, there are four such limestone units, and *Spongeliomorpha iberica* occurs in the base of two of them. Loiseau et al.

(1990) report that to the southeast these limestones give rise to collapse structures and calcareous turbidites.

The limestones are bioclastic and include a variety of shallow marine fossils, such as ostreids, pectinids (*Chlamys*, *Pecten*, and *Aequipecten*), ramose bryozoans, colonial corals, regular echinoids, irregular echinoids (clypeasteroids), and rhodoliths. Some shells, particularly large oysters, contain sponge borings (*Entobia*). Other trace fossils present are *Thalassinoides suevicus* and *Ophiomorpha nodosa*.

Samples of the marls underlying the two lower carbonate units have yielded abundant ostracods, foraminifera, and some shark teeth. Foraminifera are dominantly benthic (75%) and include several species of *Cibicides*, *Lenticulina*, and *Globigerina* as the most abundant. The assemblage is characteristic of a shelf setting (Hugo Corbí, written communication 2009). The contact between the marls and the overlying carbonates is very abrupt. *Spongeliomorpha* occur at that boundary in the first and second limestone units.

Descriptive ichnology

Material.—The studied material includes specimens housed in the fossil collection MGSCB (31183, 37969), IC-UB (194, 520–539), UUIC (2086–2092). Field observations were made
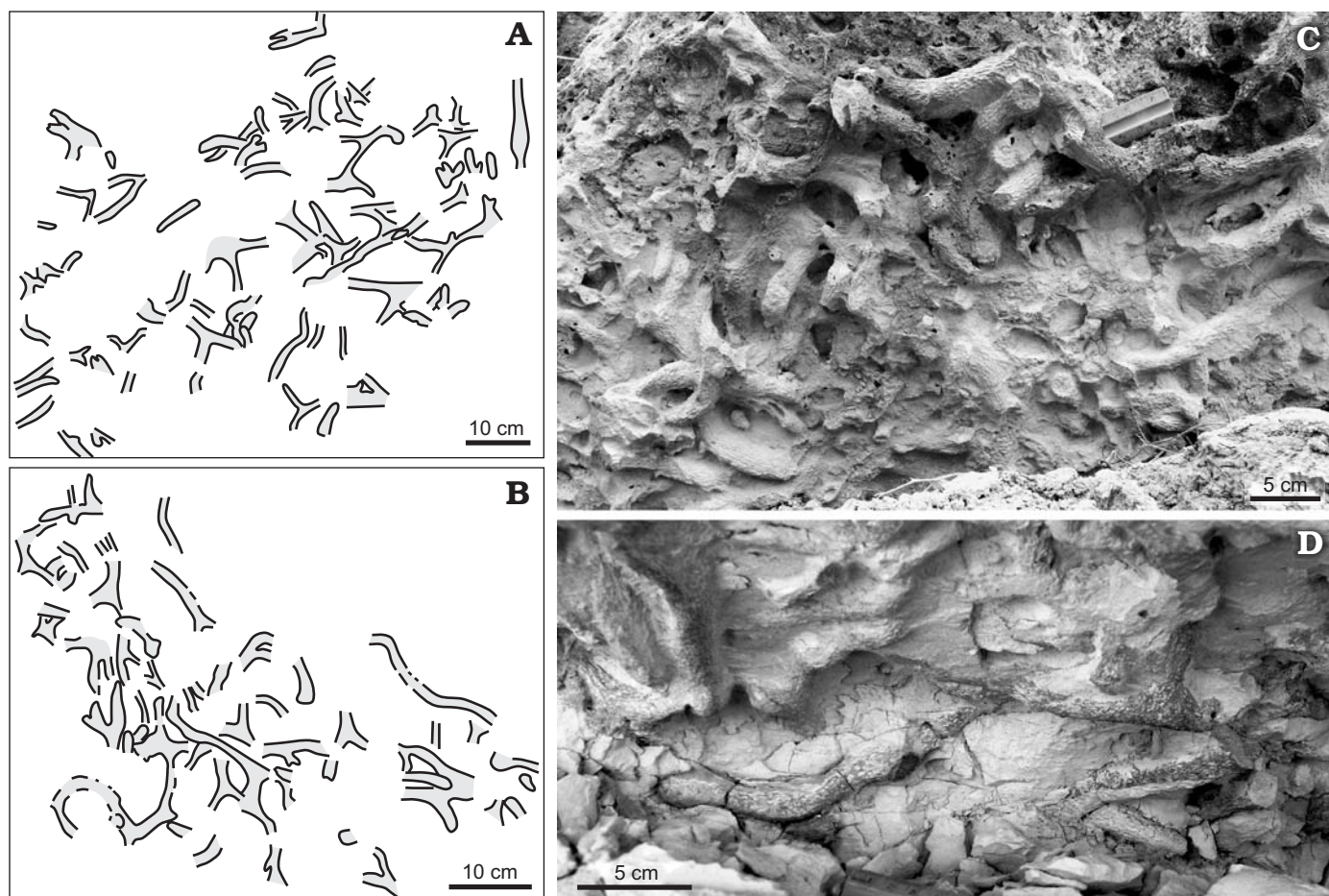
Fig. 2. Crustacean trace fossil *Spongeliomorpha iberica* Saporta, 1887 from the Miocene of La Muela de Maraón, Spain. **A**, **B**. Field sketches of burrow systems as seen in the sole of the limestone units. **C**. Sole of a limestone unit displaying a high density of burrows. **D**. Burrows penetrating into the underlying marls.

in overhangs that expose the sole of the limestone units and in loose boulders that display the same surface.

Configuration of the burrow systems.—*Spongeliomorpha iberica* is preserved as convex hyporeliefs on the soles of the limestone units (Fig. 2A–C) and full reliefs penetrating into the underlying marls (Fig. 2D). The density of burrows is very high (BPBI 5 of Miller and Smail 1997), which makes it difficult to identify individual burrow systems. Those exposed on the soles of the limestone beds are horizontal or subhorizontal tunnels, although some more oblique segments can be seen among those burrows that penetrate down into the marls. Cross-sectional shape of the burrows is subcircular to ovate. In the latter case the vertical axis may be twice as long as the horizontal one. Width of the tunnel varies from 8 to 20 mm with an average of 15 mm. Tunnels are commonly curved and may display an irregularly sinuous pattern. Branching is common, mostly displaying a "Y"-shaped morphology, although "T"-shaped branching points are also seen (Figs. 2, 3C). The maze is not anastomosed, but rather the tunnels branch without rejoining again. This results in a great abundance of blind tunnels, which typically display sharply tapering terminations (Fig. 3A). In some cases, twin blind tunnels are seen on top of

one another (Fig. 3G). Very short blind tunnels or alcoves are very common (Fig. 3B). Small chamber-like cavities sometimes occur at the base of the burrows. They have a bilobed sole and resemble those described by Gibert et al. (2008) from the Upper Miocene of southwest Spain. Another infrequent feature is the presence of *Rhizocorallium*-like connections between pairs of tunnels.

Bioglyphs.—The outer surface of the burrow casts is covered by bioglyphs, which appear as sharp ridges that form a rhomboidal pattern (Fig. 3). Bioglyph sculpture was examined with a binocular microscope. Artificial moulds were created by casting the burrows in plasticine, either by rolling cylindrical specimens or by pressing those with other morphologies on the casting material. This technique allowed us to recognize that the rhomboidal arrangement of scratches is mostly made up of individual "Y"-shaped scratches (Fig. 3F). They are 1 mm thick, 2–4 mm wide, and 5–8 mm long. In addition to the "Y"-shaped scratches, which constitute the most prominent part of the bioglyphs, a second group of smaller scratches is seen. They are sets of short, parallel, rectilinear ridges oriented perpendicularly to the axis of the burrow (Fig. 3D, E, G). These transverse marks are less deeply
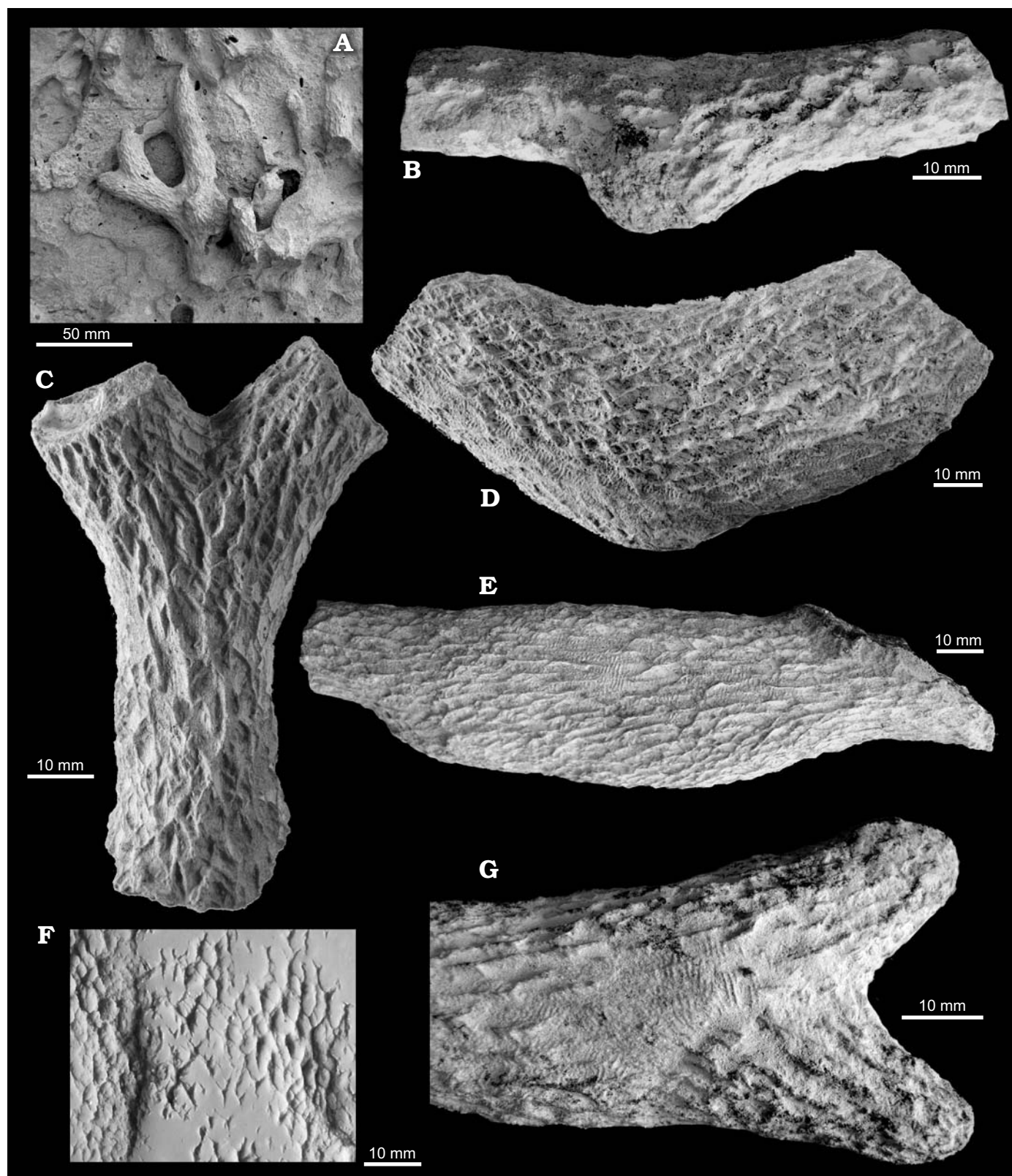
Fig. 3. Crustacean trace fossil *Spongeliomorpha iberica* Saporta, 1887 from the Miocene of La Muela de Maraón, Spain. **A**. Field photograph showing a typical burrow termination with multiple acuminate blind tunnels. **B**. Tunnel displaying the characteristic rhomboidal bioglyph and an enlargement or alcove (UB-IC522). **C**. Specimen with a "Y"-branching point (UB-IC533). **D**. Burrow with strongly marked rhomboidal bioglyphs and less impressed transverse scratch marks in the lower part (UB-IC530). **E**. Specimen with thick Y-shaped and thin transverse bioglyphs (UUIC-2089)). **F**. Plasticine cast of a burrow displaying how the rhomboidal bioglyph is constituted by "Y"-shaped individual marks (UB-IC194. **G**. Detail of a burrow termination with two blind tunnels and exhibiting both types of scratch marks (UB-IC520).

impressed and thinner (0.25 mm) than the larger "Y"-shaped scratches. They are fairly common but not seen in all specimens. Only occasionally, long longitudinal ridges also are observed.

Taphonomy.—*Spongeliomorpha* burrows are preserved as positive hyporeliefs on the soles of the limestone units or as full reliefs within the underlying marls immediately below the abrupt marl-limestone boundary. *Spongeliomorpha* is restricted to the horizons marking a lithologic change. They are filled by bioclastic calcarenite from the overlying unit. There is no evidence of *Spongeliomorpha* occurring in the sediment of the overlying unit. Although *Thalassinoides* and *Ophiomorpha* have been seen in the overlying limestone units, no connections between them and *Spongeliomorpha* have been recognized. The *Spongeliomorpha* preserved as hyporeliefs seem to be casts rather than 3-D burrows. The upper parts of the burrow systems were not preserved, as they probably were truncated before deposition of the calcarenitic limestones.

Thus, we consider the *Spongeliomorpha* burrow systems as pre-depositional trace fossils that formed on a mud firmground prior to the deposition of the shallow-water carbonates, as evidenced by the preservation of bioglyphs and the absence of any compaction of the burrows. Despite a high burrow density, tunnels rarely cross each other, but rather they seem to avoid one another, suggesting that the entire *Spongeliomorpha* burrow system remained open during occupation, which would be consistent with the interpretation of a firm substrate.

Ichnotaxonomic remarks.—Several authors (Fürsich 1973; Schlirf 2000) have suggested that *Thalassinoides* Ehrenberg, 1944 and *Ophiomorpha* Lundgren, 1891 should be considered junior synonyms of *Spongeliomorpha* Saporta, 1887, because all three ichnogenera are branching burrow systems, which are differentiated only by wall features that may reflect differences in substrate consistency. Although Bertling (2007) has argued that wall ornament features must have an ichnotaxonomic value of "low to none", we recommend that these three ichnogenera remain separate and valid, albeit closely related. *Ophiomorpha* bears a pelleted lining, which represents a very specialized wall-construction behavior seen today in the burrows of some callianassid shrimp (Gibert et al. 2006 and references therein). *Spongeliomorpha* and *Thalassinoides* never possess pelleted walls. *Thalassinoides* may have a similar geometric configuration as the other two ichnogenera, but it has smooth, unlined or only thinly lined walls.

Thus, bioglyphs clearly allow us to differentiate *Spongeliomorpha* from *Thalassinoides*. Nevertheless, two other features also are characteristic of, at least, some *Spongeliomorpha* occurrences (Marcinowski and Wierzbowski 1975; Muñiz and Mayoral 2001; Gibert and Robles 2005). These are: (i) the abundance of short, blind tunnels with a very characteristic tapering termination and (ii) the apparent absence of an anastomosing-tunnel geometry as seen in *Thalassinoides*. Including those features as additional ichnotaxobases at an
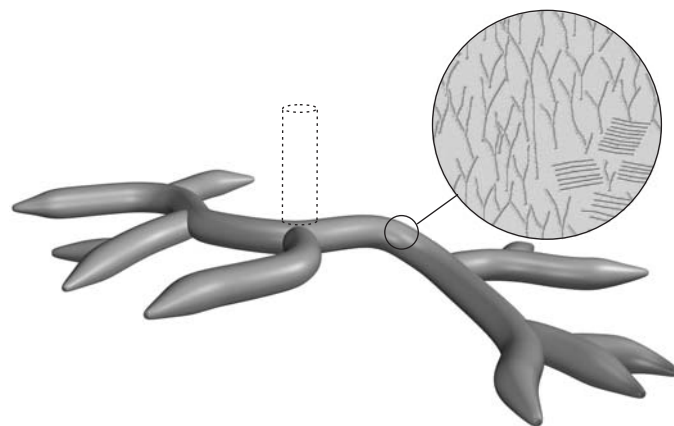

Fig. 4. Interpretative reconstruction of a *Spongeliomorpha iberica* burrow system. The morphology of the apertures is not known, here they are shown as a simple vertical shaft. Inset shows the bioglyph pattern with "Y"-shaped and transverse scratch marks.

ichnogeneric level would require revision of all ichnospecies, an objective which is beyond the scope of this paper.

Schlirf (2000) suggested that *S. iberica* should be considered a junior synonym of *Spongeliomorpha sudolica* (Zaręczny 1878) from the Cretaceous of Poland, which is a trace fossil that originally was interpreted as a sponge under the genus *Spongia* but later identified correctly as a burrow (Marcinowski and Wierzbowski 1975). Although this approach was accepted provisionally by Gibert and Robles (2005), examination of type material of *Spongia sudolica* at the Muzeum Geologiczne Instytutu Nauk Geologicznych PAN in Kraków now strongly suggests that the two ichnospecies are distinctly different. *S. sudolica* bears a rhomboidal bioglyph similar (but not identical) to that of *S. iberica*, but there are several features that clearly distinguish between the two ichnospecies: (i) the rhomboidal interspace left between scratches is smaller in respect to burrow diameter in *S. sudolica* than in *S. iberica*, (ii) blind tunnels terminate in a blunt, rounded end in *S. sudolica* rather than tapering to an acute point as in *S. iberica*, and (iii) bioglyphs in type material of *S. sudolica* are seen only on one side of the burrow, probably in the floor as interpreted by the presence of "draft" fills (see Seilacher 1968, 2007) in the unornamented (upper?) side.

Discussion

Tracemaker identity.—Large branching burrow systems like those represented by *Spongeliomorpha iberica* (Fig. 4) are typically assigned to decapod crustacean producers. The bioglyphs on the *Spongeliomorpha* walls support the hypothesis that the tracemaker had to be an animal with rigid appendages capable of scratching the firm mud. Among modern crustaceans, several groups construct and inhabit underground open burrows (Bromley 1996). They include alpheids (pistol shrimps), thalassinideans (ghost shrimps), astacideans (lobsters and crayfish), and brachyurans (crabs) among the decapod crustaceans (Atkinson and Taylor 1988),

and also stomatopod crustaceans (mantis shrimp) (Myers 1979). Of these burrowing taxa, alpheids and thalassinideans (e.g., Shinn 1968; Swinbanks and Luternauer 1987) construct the most geometrically complex burrow systems, which may compare favorably to the multiple branching burrow systems of *Spongeliomorpha* at Muela de Maraón. Stomatopods and marine astacideans (e.g., Rice and Chapman 1971; Myers 1979) construct simpler burrows with limited branching. Most brachyuran crab burrows have been described in supratidal and intertidal areas (e.g., Braithwaite and Talbot 1972), and they are typically vertical to steeply inclined with a "J"- or "Y"-shaped morphology. Rice and Chapman (1971) described the burrow of the brachyuran *Goneplax rhomboides* from a sublittoral setting as a horizontal maze, which is comparable to *Spongeliomorpha* or *Thalassinoides* in the fossil record. Nevertheless, as pointed by Seilacher (2007), crabs burrow by moving sideways, and because of their characteristic crawling behavior they do not need turnaround chambers. The enlargements seen in the burrows at Muela de Maraón can be interpreted as turnarounds, thus pointing to a shrimp-like morphology for the tracemaker. Therefore, alpheid or thalassinidean shrimps are the most likely candidates for the tracemakers of the Miocene *Spongeliomorpha iberica* burrow systems from Muela de Maraón.

Construction.—Atkinson and Taylor (1988) reviewed the excavating techniques used by burrowing decapods. They reported that modern astacideans, thalassinideans, and alpheids excavate their burrows in a similar manner by using their first three pairs of pereiopods and the third maxilliped in digging and transporting sediment loads. The same authors remarked that the first pair of pereiopods (the large, pinching chelipeds) may play a major role in the excavation, or they may be used only for sediment transport away from the excavation site.

Analysis of the bioglyphs in *Spongeliomorpha iberica* helps us to understand the constructional mechanisms used by the tracemaker. Seilacher (2007) examined the bioglyphs of *S. iberica* and concluded that the tracemaking animal would have made headway by using the claws (chelipeds), while the other walking legs (pereiopods) would have widened the tunnel by scraping the wall in posterior directed motions.

Our analysis of the rhomboidal mesh of scratches has revealed that in most cases the bioglyph consists of individual "Y"-shaped imprints. The "Y"-morphology likely records the plucking action of the chelipeds. "Y"-shaped scratches occur in blind tunnels oriented preferentially with the two-branched side pointing to the burrow end. Although more observations may help to confirm our hypothesis, this orientation suggests that the animal would have pinched the substrate to remove a parcel of sediment. The tapering and acute termination of the tunnels is consistent with the chelipeds playing a major role in digging ahead, as the claws could reach farther away anteriorly than the walking limbs. Long

longitudinal ridges that are occasionally observed in some specimens may correspond to the action of walking legs expanding the burrow as suggested by Seilacher (2007).

Fine transverse scratches, much smaller than the more prominent longitudinal scratches, are visible at several places inside the burrows. These are unlikely to have been produced during initial burrow excavation, but rather they are the result of subsequent (post-excavation) activity of the inhabitant. They must have been produced by a small, rigid appendage with numerous protruding elements capable of producing parallel grooves. Seilacher (2007) suggested that these fine "brushings" were made by tail appendages (uropods) in order to ventilate the tunnel. However, the transverse orientation of these fine scratches does not seem to support that hypothesis. We suggest instead that they could have been produced by maxillipeds (or other mouth parts) in order to graze on bacterial films growing on the tunnel wall (as discussed in the next section).

It is interesting to note how the bioglyph pattern of *S. iberica* is markedly different from that of other *Spongeliomorpha* ichnospecies (Muñiz and Mayoral 2001), the analysis of which may reveal different excavating mechanisms and even different tracemakers.

Function of the burrow systems.—Atkinson and Taylor (1988) listed several possible functions that may be attributed to the burrows of fossorial decapds: (i) providing protection and concealment, either from predators or from adverse environmental conditions, (ii) providing of a territorial center, (iii) providing a site for molting, mating, egg incubation or juvenile recruitment, (iv) providing a site for feeding.

Griffis and Suchanek (1991) categorized thalassinideans in three general trophic groups: (i) deposit feeders, which ingest and process burrowed sediment, (ii) drift catchers, which collect plants and other organic material to store in their burrow for ingestion at a later time, and (iii) suspension feeders, which feed on particles filtered from the water circulating throughout the burrow. They proposed a classification of burrow systems based on architecture, considering that this was derived from different trophic behavior of different taxa. Some of the features that they considered are rarely seen in the trace fossil record (e.g., presence of mounds at the openings and number of openings) and they are certainly not seen in the trace fossils at Muela de Maraón. Thus, it is difficult to apply their burrow classification in the trace fossil record, especially when it is difficult to isolate individual burrow systems. Marine decapod burrowers may exhibit some additional trophic habits, such as seen among some astacideans and crabs that are scavengers or predators outside their burrows.

We will analyze several hypotheses for *Spongeliomorpha iberica*:

(1) Deposit feeding (sediment-mining). The high density of the burrows, which rarely crosscut, and the branching pattern may suggest intense exploitation of the food resources contained in the sediments. Nevertheless, the extensive pres-

ence of bioglyphs indicates that the substrate was very firm after dewatering by compaction, and so it is doubtful that the sediment would contain a sufficient amount of organic matter to sustain a population of deposit-feeding animals.

(2) Suspension feeding (filter-feeding). This scenario would require a burrow with several openings and well-connected tunnels in order to allow for water circulation. Although we have not been able to reconstruct the upper parts of the *Spongeliomorpha iberica* burrow system, the abundance of blind tunnels does not seem to represent any benefit for an animal that obtained its nutritional resources primarily from suspension-feeding.

(3) Extra-burrow feeding (surface-feeding). Although thalassinideans do not usually leave their burrows, other decapods do emerge in order to obtain their food resources from the substrate surface outside their dwellings, either as scavengers, predators or detritus-feeders. In this case, the burrow would have no particular trophic function, and it would act only as a refuge. S*pongeliomorpha* from the Cretaceous of Poland and the Miocene of northeastern Spain may exhibit "draft" fills (authors' observations), which have been interpreted as an indication of constricted burrow openings (Seilacher 1968, 2007). Such narrow apertures are common in the burrows of thalassinidean shrimp and they prevent the dweller from leaving the burrow. In the *S. iberica* material from Muela de Maraón, no such feature has been seen, nor the burrow openings have been preserved.

(4) Gardening. Blind tunnels are a characteristic feature in *Spongeliomorpha iberica* burrow systems. Although it is possible that they may simply represent unfinished tunnels, their abundance and the fact that many of them are very short may indicate that they were constructed for a specific purpose. Many thalassinideans collect plant material, which is stored in cul-de-sac chambers to mature into food that may be edible by the shrimp (e.g., Griffis and Suchanek 1991; Dworschak et al. 2006). No distal chambers have been recognized in the *Spongeliomorpha iberica* at Muela de Maraón, but alcoves and blind tunnels may have played this role. On the other hand, the fine transverse scratches commonly seen in burrow walls may have been produced by the latero-medial movement of maxillipeds or other mouth appendages. Such a scratching on the walls maybe interpreted as a result of the grazing activity of the animal upon microbial food resources found on the burrow margin. Such behavior has been recognized among several modern taxa of thalassinideans (Griffis and Suchanek 1991).

We conclude that the *Spongeliomorpha iberica* burrow systems from Muela de Maraón were not deposit-feeding or suspension-feeding burrows. Instead, they served the combined purposes of dwelling and feeding for thalassinidean or alpheid shrimps that obtained their food by gardening, i.e., by grazing on microbial growths accumulating on the tunnel walls. Additionally, the shrimps also may have obtained organic detritus from outside their burrows and stored it in the alcoves and blind tunnels for later consumption.

Paleoenvironmental significance.—The *Spongeliomorpha* horizons at Muela de Maraón occur at the sharp boundaries between the underlying marls and the overlying limestones. Each burrowed horizon exhibits an important continuity, and it is observable wherever the lithofacies contact is well exposed.

The marls were deposited below wave base in a circalittoral shelf setting, as indicated by the abundance of benthic foraminifera. Subsequently, the bioclastic limestone units were formed in a shallower, shoreface setting that was affected by storm and wave action. The shallow marine conditions are indicated by the coarse-grained calcarenitic lithofacies and by the overall body fossil assemblage. In particular, pectinids, which are among the most abundant fossils, have thick, inflated, strongly ribbed shells and belong to the genera *Chlamys*, *Pecten*, and *Aequipecten*. Such an assemblage is typical of inner shelf settings in the Neogene throughout the Mediterranean region (Aguirre et al. 1996).

Thus, the surface that is marked by a *Spongeliomorpha* horizon represents an abrupt facies change that correlates with a rapid shift from deeper- to shallower-water facies, and it constitutes an erosional regressive surface. The burrow systems were formed when crustaceans colonized an exhumed firmground after sea level fell and before sandy shoreface sediments were introduced.

This example from the Fortuna Basin of southeastern Spain conforms to the so-called "*Glossifungites* Ichnofacies" (Pemberton et al. 2004, and references therein), which commonly occurs in association with major stratigraphic surfaces. Gibert and Robles (2005) described *Spongeliomorpha* horizons in the Middle Miocene of the Vallès-Penedès basin in northeastern Spain as examples of the *Glossifungites* ichnofacies. However, the Vallès-Penedès occurrences were linked to flooding (transgressive) events, while the interpretation for the occurrences at La Muela that are described in this paper are linked to a sea level fall (regression). Thus, the main control on the formation of extensive *Spongeliomorpha* horizons seems to be the availability of submarine firmgrounds for crustacean colonization in shallow marine settings.

Acknowledgements

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