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Recurrent constructional pattern of the crustacean burrow *Sinusichnus sinuosus* from the Paleogene and Neogene of Spain

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New occurrences of *Sinusichnus sinuosus* described in the Cenozoic of Spain evidence the almost continuous fossil record of this ichnospecies from the Upper Cretaceous to the Lower Pliocene. Morphological and size features of these highly regular sinusoidal burrows have been analyzed, showing a very recurrent constructional pattern through time. Such features are also constant along the ontogeny of the producer. The large number of similarities that this ichnogenus shares with fodinichnial burrow systems, such as *Thalassinoides*, *Ophiomorpha*, or *Spongeliomorpha*, point to a crustacean authorship. Since this sinusoidal architecture is also common among some graphoglyptids, other behavioral strategies are discussed. The ichnogenus *Sinusichnus* occurs commonly in shallow marine environments, in particular to deltaic depositional settings.

Key words: Decapoda, *Sinusichnus sinuosus*, bioturbation, Eocene, Miocene, Pliocene, Spain.

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Introduction

Decapods are among the most common burrowers in Mesozoic and Cenozoic shallow marine depositional settings as they are in modern environments. Their burrows include a variety of architectures, the most common being branching tunnel networks preserved in the fossil record as ichnofossils of the *Ophiomorpha–Thalassinoides–Spongeliomorpha* group (Bromley 1996), also referred to as "Ophiomorphids" (Seilacher 2007). Gibert (1996) added a fourth ichnogenus to this group, *Sinusichnus*, which was characterized by the sinuous geometry of the tunnels, which often exhibit high regularity (Gibert et al. 1999). This trace fossil was originally described from the Lower Pliocene of the NW Mediterranean, but later new occurrences were reported from the Upper Cretaceous of Germany (Kappel 2003) and Antarctica (Buatois et al. 2009), and the Oligo-Miocene of Venezuela (Buatois et al. 2009). In the present contribution, four new records are described from the Middle–Upper Eocene of the Ebro Basin (NE Spain), the Middle Miocene of the Camp de Tarragona Basin (NE Spain), and two localities of the Upper Miocene of the Guadalquivir Basin (SW Spain). These new occurrences allow having a more complete picture of the paleoenvironmental and stratigraphic record of the ichnogenus and demonstrate that it was more common than previously thought (cf. Gibert 1996). Previous paleobiologic interpretations of the sophisticated behavioral program that produced such regularly complex burrow networks are revised under the light of the new material and new hypotheses are discussed.

Abbreviations.—A, amplitude; Ø, diameter; λ, wavelength; R, correlation coefficient.

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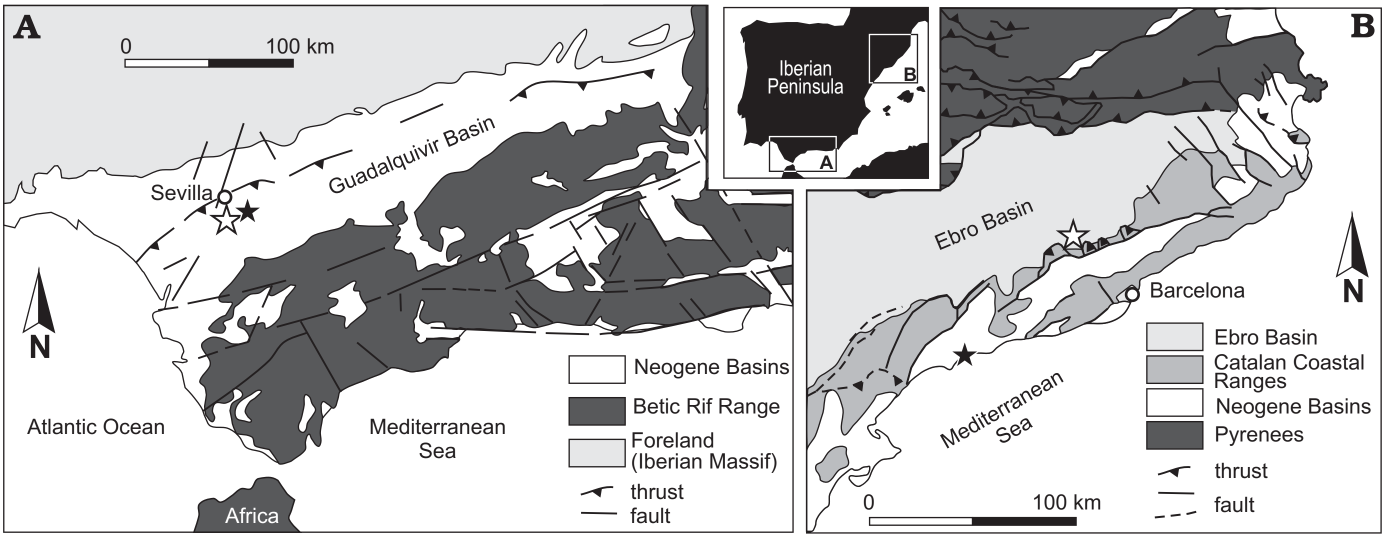

Fig. 1. Geographic and geologic setting. **A**. Synthetic geological map of the Guadalquivir Basin and surrounding areas. The black star shows the location of the Alcalá de Guadaíra outcrop, and the white star that of the Dos Hermanas locality. **B**. Synthetic geological map of Catalonia (NE Spain). The white star shows the location of the Vilomara outcrop in the Ebro Basin, and the black star that of the Waikiki Beach locality in the El Camp de Tarragona Basin. Inset map in between, displays the position of both areas in the Iberian Peninsula.

Geological setting

Eocene of the Ebro Basin (NE Spain).—The Ebro Basin is a triangular-shaped foreland basin bounded by three thrust-and-fold mountain belts: the Pyrenees to the north, the Iberian chain to the southwest and the Catalan Coastal ranges to the southeast (Fig. 1B). It represents the non-deformed part of the South-Pyrenean foreland basin. The South-Pyrenean foreland evolved from Late Cretaceous to Miocene times in response to flexural subsidence related to the growth of the mentioned mountain belts driven by convergence and collision between the Iberian and European Plates (Zoetemeijer et al. 1990; Vergés et al. 2002). The sedimentary infill of the basin can be subdivided into a lower stage (Ilerdian to Priabonian) including marine sedimentation and an upper endorheic stage (Priabonian to Miocene). The studied section in the Santa Creu valley near El Pont de Vilomara, hereafter called as Vilomara, corresponds to delta front and prodelta-slope facies belts of the Sant Llorenç del Munt fan-delta complex of López-Blanco (1993), developed on the SE Ebro Basin margin, attached to the Catalan Coastal ranges, during Bartonian to Priabonian times (Gómez-Paccard et al. 2012). The studied sections belong to the Vilomara T-R composite sequence in the regressive sequence set of the Milany megasequence (López-Blanco 1993; López-Blanco et al. 2000c). Paleoclimatic conditions deduced from pollen remains (Cavagnetto and Anadón 1996) were wet and warm related to tropical and subtropical conditions (López Blanco et al. 2000a).

Sub-aqueous facies belts defined in the detrital fan-delta complex by López-Blanco (1993) are: (i) fan-delta front sandstones and conglomerates deposited as mouth bars and subsequently modified by wave action and organic reworking and; (ii) fan-delta slope/offshore mostly constituted by prodelta marls which may include some sandy and conglomeratic sediment gravity flow deposits (turbidites and hyperpicnites).

Sinusichnus sinuosus occurs in different fan-delta front to slope horizons along the Vilomara sequence. Specifically, the ichnospecies is abundant in siltstone to fine-grained sandstone units located on the upper part of the sequence.

Middle Miocene of the El Camp de Tarragona Basin (NE Spain).—The El Camp de Tarragona Basin constitutes a tectonic depression located in the emerged sector of the Valencia Trough, an extensional system of grabens and horsts developed during the latest Oligocene and Miocene between the eastern part of the Iberian Peninsula and the Balearic promontory (Fontboté et al. 1990; Roca et al. 1999; Cabrera et al. 2004). The sedimentary infill of the El Camp Basin is constituted of Middle Miocene deposits belonging to the Garraf (Langhian) and Tarragona (Serravalian) Depositional Sequences (Cabrera et al. 1991). The best exposures are located along the coast and correspond to the Tarragona Sequence, which was deposited under shallow marine conditions in a mixed siliciclastic-carbonate platform. Facies include a variety of calcisiltites, biocalcarenites, coquinas and more rarely terrigenous sandstone beds. The fossil assemblage is characteristic of temperate (non-tropical) carbonates (Belaústegui and Gibert 2011).

Sinusichnus sinuosus has been found only in one locality at Waikiki beach, east of the city of Tarragona (Fig. 1B). The outcrop exposes a well-developed coarsening-upward sequence in which basal calcisiltite levels gradually change to more and more coarse-grained calcarenite units (Belaústegui and Gibert 2009; Belaústegui et al. 2011, 2012). In particular, *S. sinuosus* occurs right on top of this sequence within a fine-to-medium-grained quartzitic biocalcarenite overlain by 2 m of grey marls with rare sandstone intercalations.

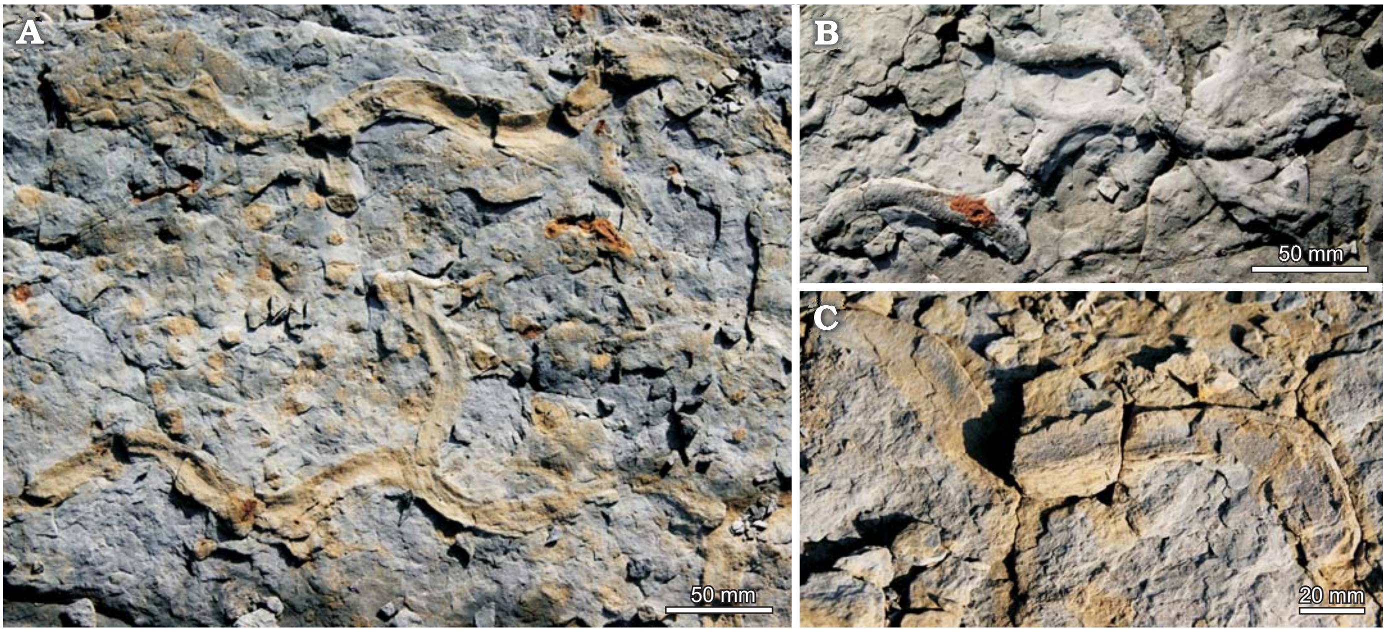

Fig. 2. The crustacean burrow *Sinusichnus sinuosus* Gibert, 1996 from the Eocene Vilomara outcrop in the Ebro Basin, Spain. **A**. System displaying the characteristic sinuous tunnels and Y-shaped branching. Upper part of the burrow is concave as only spreiten are preserved and the final passive infill of the tunnel is lacking. **B**. Two intersecting burrows. The one on the lower part of the picture displays a typical H-shaped geometry. **C**. Sinuous tunnel showing retrusive spreiten. Field photographs.

Upper Miocene of the Guadalquivir Basin (SW Spain).—The Guadalquivir Basin is a WSW-ENE depression extending from the Atlantic coast of Huelva to the surroundings of Jaén in south-western Spain. It constitutes a foreland basin located between the Betic Cordillera to the south and its passive margin of the Iberian Massif to the north (Sanz de Galdeano and Vera 1992; Vera 2000) (Fig. 1A). The upper Neogene sedimentary infill of the Guadalquivir Basin consists of five sequences (A–E) ranging from the early Tortonian to the Quaternary (Sierro et al. 1990, 1996; González-Delgado et al. 2004). In the southern sector of the basin, upper Tortonian(?)–Messinian to Pliocene deposits lie on top of olistostromic units derived from the front of the Subbetic External Zones (Riaza and Martínez del Olmo 1996; Braga et al. 2002).

The studied outcrops are located in the vicinity of the city of Sevilla, in the localities of Alcalá de Guadaíra and Dos Hermanas (Fig. 1A). At Alcalá de Guadaíra, *Sinusichnus sinuosus* occurs in the base of the calcarenites of the Guadaíra Formation (sensu Verdenius 1970), also known as "Caliza Tosca" (sensu Perconig 1966). This unit is composed of cross-bedded, fine- to medium-grained calcarenites with thin interbedded clay beds, containing abundant pectinid and oyster shells. The second locality, at Dos Hermanas, consists of a succession of interbedded greenish clay and sand with fossils of pectinids, oysters, gastropods, and plant remains. They are uncomformably deposited on a calcarenitic unit ("Caliza Tosca") and are referred to as "Formación Amarilla" in the local geologic map (Torres et al. 1977). Strata from both localities are dated as Messinian (upper Miocene) based on their foraminiferal content (Rico-García et al. 2008 and IB unpublished data).

Description of the trace fossils

The burrow systems studied herein bear the diagnostic features of *Sinusichnus sinuosus* as originally described by Gibert (1996). They constitute complex, predominantly bidimensional networks consisting of sinusoidal tunnels (Figs. 2–5). The tunnels are horizontal or only gently oblique (rarely more than 15°) to bedding, and display elliptical sections with constant width along the systems. They commonly bear branching. Tunnel junctions are typically Y-shaped (Figs. 2A, 3B, 4A, 5B), and often two adjacent branching points generate a characteristic H-shaped morphology (Fig. 2B), which was noted as a characteristic feature by Gibert (1996) and Gibert et al. (1999). Other forms of branching are much less common. Only in the Eocene specimens from Vilomara we observed multiple convergent tunnels, similar to those figured by Gibert et al. (1999: fig. 2G) and referred to as *Phycodes*-like branching by Buatois et al. (2009: fig. 2C). It is not clear how the burrow system was connected to the seafloor. We recognized neither a vertical shaft originating in a tunnel junction as the one described and figured by Gibert et al. (1999: fig. 2H) from a Pliocene specimen nor any other element that might have served as a burrow opening. Spreiten were not considered a diagnostic feature but a very common architectural element of *Sinusichnus sinuosus* by Gibert (1996). Nevertheless, such feature is present in all specimens studied herein from Paleogene and Neogene localities (Figs. 2C, 4B–D). They are vertical retrusive spreiten (not oblique as some from Pliocene examples; Gibert 1996) and although they are generally around 3.5–4 cm high, some specimens at Dos Hermanas may reach up to 9 cm. Spreiten consist of

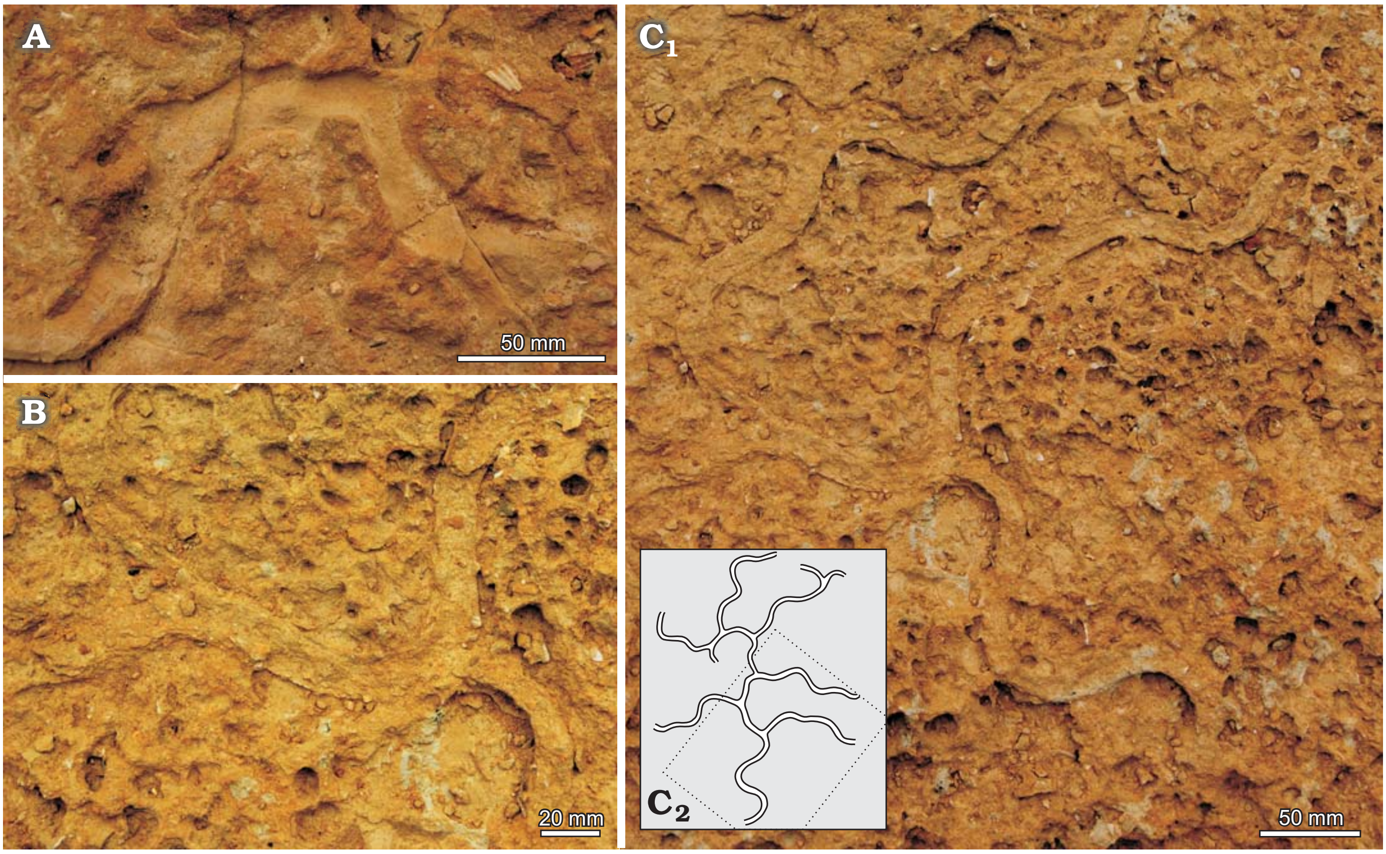

Fig. 3. The crustacean burrow *Sinusichnus sinuosus* Gibert, 1996 from the Middle Miocene of the Waikiki Beach outcrop in the El Camp de Tarragona Basin, Spain. **A**. Detail of a burrow partially filled with fine-grained sediment from the overlying marly unit. **B**. Detail of a Y-shaped branching point. **C**. Partial view of a more extensive network (C_1) showing variations in the sinuosity of tunnels and Y-shaped branching points; schematic drawing (C_2). Field photographs.

sediment of the same composition as the enclosing substrate and they may be topped by a string of sediment of different nature corresponding to the passive infill of the actual tunnel (Fig. 4D). This may be coarser- or finer-grained than the host rock, but generally better sorted.

The most striking characteristic of *Sinusichnus sinuosus* is the sinusoidal regularity of the path of the tunnels. Each one of the branches generally displays more or less consistent amplitude and wavelength values, although irregularities are partially seen along tunnels. Additionally, different sections in the same burrow systems may have different sinuosity. In order to characterize the geometry of the tunnels (Fig. 6), we measured amplitude (A), wavelength (λ), and diameter (Ø) of burrows from Vilomara (21 measurements), Tarragona (11), Dos Hermanas (19), and Alcalá de Guadaíra (18). Additionally, available material previously studied by Gibert et al. (1999) from the Pliocene localities of the Baix Ebre (23) and Baix Llobregat (17) were also measured for comparison.

Diameter and amplitude are comparable in all 6 trace fossil sites (Fig. 6). Average diameter varies from 0.95 to 1.9 cm among localities (Fig. 6). Nevertheless, the Vilomara specimens display a wide size distribution comparable to that seen in the Baix Ebre, because of the presence of very small specimens (less than 1 cm wide) coexisting with the most usual size of around 1.5 cm. Amplitude displays a wide dispersion of values in most localities with averages ranging from 1.4 to 2.4 cm and absolute values between 0.45 and 4.35 cm (Fig. 6). Average wavelength varies between 11.4 and 16.2 cm except in the Baix Ebre where the abundance of smaller specimens lowers down the value to 8 cm.

An interesting parameter to characterize the sinuosity of the tunnels is the relation between λ and A. This has been represented for each locality in a bivariate diagram (Fig. 7A) and also a λ/A ratio (Fig. 6) has been calculated. Although the Eocene and Pliocene specimens exhibit good correlation between both parameters (R coefficient between 0.7 and 0.88), *Sinusichnus* from the three Miocene localities exhibit much lower correlation coefficients. These differences might be pointing to a lesser regularity of the Miocene burrow networks or to a deficient database due to limited available material. When plotting specimens from all 6 localities together, correlation coefficient R is 0.75. A/λ ratio is very constant among all localities, ranging from 0.13 to 0.17 in average with relatively limited dispersion (Fig. 6). This ratio, that determines the geometry of the sinusoid, is not dependant on burrow size (i.e., ontogeny) as shown by the low correlation coefficients between both (Fig. 7B).

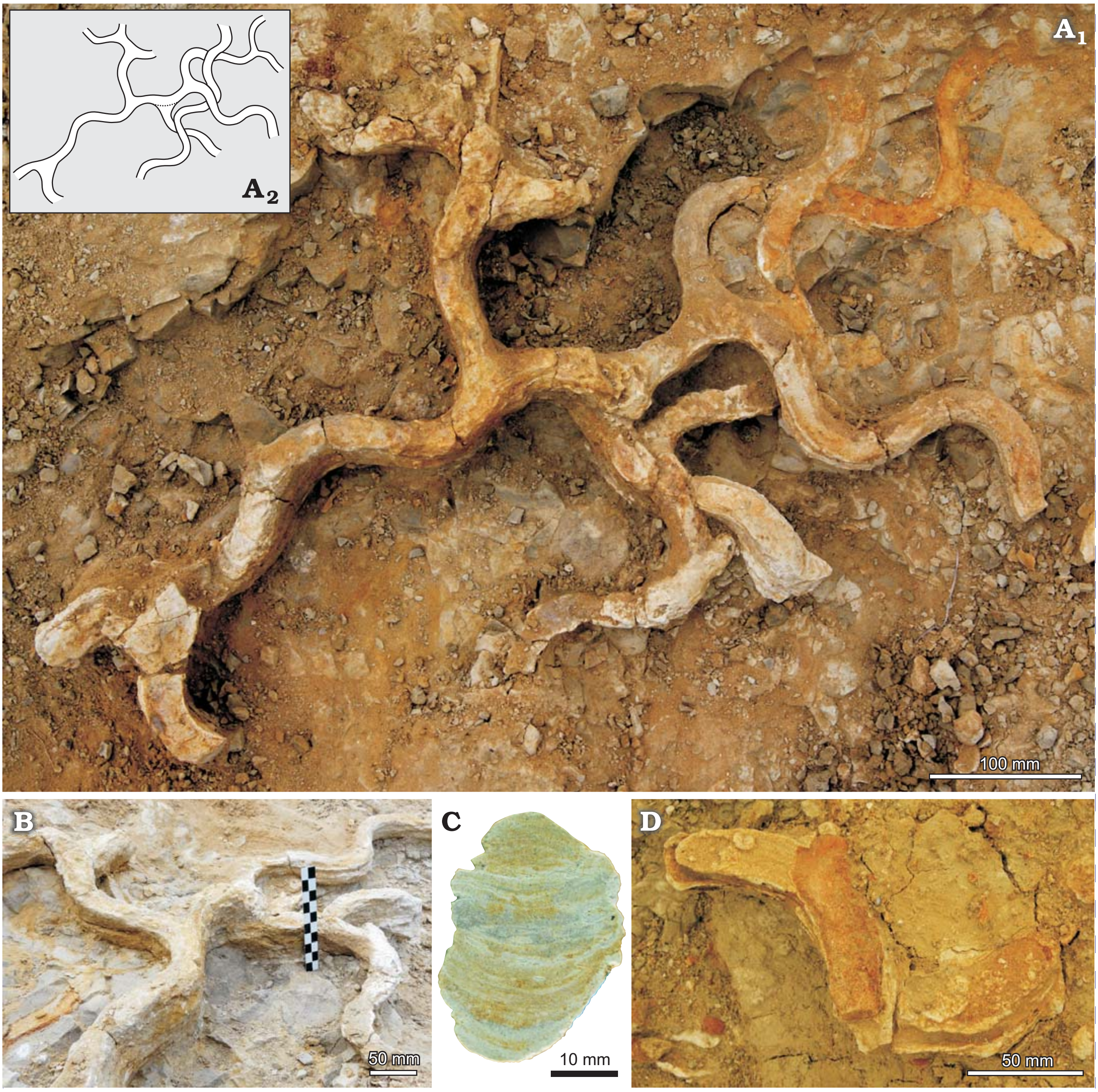

Fig. 4. The crustacean burrow *Sinusichnus sinuosus* Gibert, 1996 from the Upper Miocene Dos Hermanas outcrop in the Guadalquivir Basin, Spain. **A**. Plan view of two intersecting burrow systems (preserved as full-relieves) (A_1) and schematic drawing (A_2). **B**. Semi-lateral view of the same systems, where it is possible to observe the thick spreiten. **C**. Transverse burrow section, showing the heterolithic composition of the spreiten. **D**. Detail showing the spreiten and the coarser-grained passive infill of the tunnel. Field photographs.

Two of the four localities with *Sinusichnus* studied herein correspond to detritic siliciclastic facies (Vilomara and Dos Hermanas), while in the other two, facies are dominantly carbonate (Alcalá de Guadaíra) or mixed terrigenous-carbonate (Tarragona). Eocene *Sinusichnus* from Vilomara, which are preserved as semirelieves and full-relieves, occur in silt to fine-grained sandstone layers. Tunnels generally have a coarser infill (medium- to coarse-grained sandstone) than the host substrate, while spreiten may be heterolithic as the host sediment substrate. *Sinusichnus* may be very abundant in some levels. It co-occurs with other trace fossils such as common *Planolites* and less common *Asterosoma* and *Thalassinoides*.

The Messinian occurrence at Dos Hermanas shows some similarities with that of Vilomara. *Sinusichnus* abound all along a succession of interbedded silty clays and silty fine-

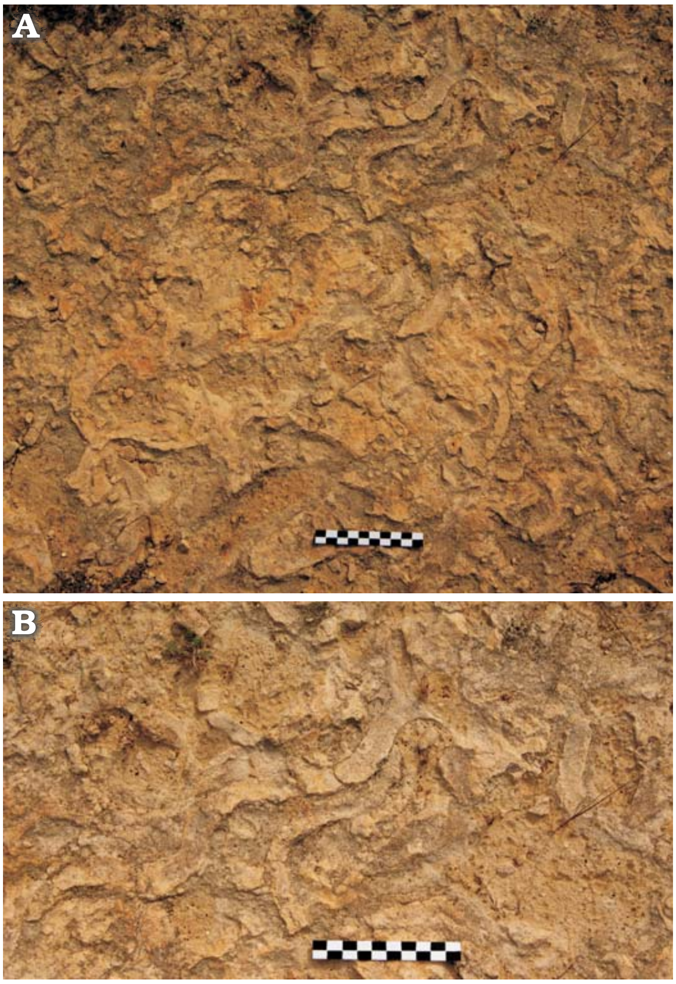

Fig. 5. The crustacean burrow *Sinusichnus sinuosus* Gibert, 1996 from the Upper Miocene Alcalá de Guadaíra outcrop in the Guadalquivir Basin, Spain. **A**. General view of an intensely bioturbated horizon, mostly consisting of numerous intersecting *Sinusichnus* networks. **B**. Detail of a Y-shaped branching point. Field photographs. Scale bars correspond to 10 cm.

grained sands, generally preserved as full reliefs below sand layers. Tunnels are filled with the overlying sediment, while spreiten consist of various sizes of sediment grains. Other trace fossils in this locality are common *Thalassinoides*, *Teichichnus*, spatangoid burrows (cf. *Bichordites*), and rarer *Planolites*, as well as frequent straight and robust (more than 10 cm in diameter), unbranched burrows.

At Alcalá de Guadaíra *Sinusichnus* occurs in a skeletal biocalcarenitic unit, mainly associated to thin clay-silt intervals. Bioturbation intensity due to *Sinusichnus* burrows is higher than in any other locality, reaching ichnofabric indices of 4 or 5 (sensu Droser and Bottjer 1986). Tunnel infill and spreiten usually bear the same sediment composition as that of the surrounding rock. A few *Thalassinoides* and spatangoid burrows (cf. *Bichordites*) are the only other trace fossils in this locality.

Finally, the Tarragona occurrence is limited to a single bioturbated horizon located on top of a bioclastic calcarenite unit overlain by an interval of terrigenous clays. Traces are preserved as negative epirelieves as tunnel infills are mostly eroded away. Occasionally, the infills consist of clays from the overlying unit indicating that *Sinusichnus* colonization is genetically related to the terrigenous unit. This is the only locality where *Sinusichnus* does not occur associated to other trace fossils.

Discussion

Tracemaker, construction, and function.—Some of the architectural features of *Sinusichnus sinuosus* are comparable to those of common Mesozoic and Cenozoic, including modern, crustacean burrows. Thus, *Thalassinoides, Ophiomorpha*, and *Spongeliomorpha* (the "Ophiomorphids" of Seilacher 2007) correspond to large tunnel networks with characteristic Y-shaped branching points, which are often horizontally-developed and occasionally may bear retrusive spreiten (e.g., Bromley and Frey 1974; Ekdale 1992; Gibert and Ekdale 2010) (Fig. 8). Such general burrow architectures are well known in modern crustaceans, particularly among thalassinidean and alpheid decapods (e.g., Atkin-

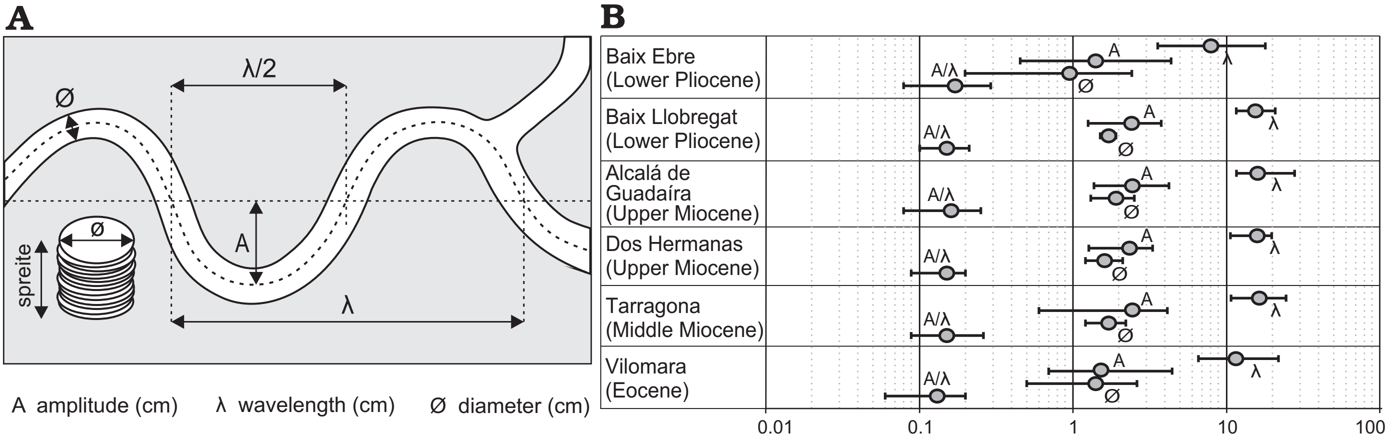

Fig. 6. Geometric parameters of the crustacean burrow *Sinusichnus sinuosus* Gibert, 1996. **A**. Schematic drawing showing the parameters that have been measured. **B**. Diagram comparing the amplitude (A), wavelength (λ), diameter (Ø), and A/λ ratio for the four occurrences studied herein and from two of the Lower Pliocene localities in NE Spain described by Gibert et al. (1999). Circle indicates average and bar expresses dispersion of the values.

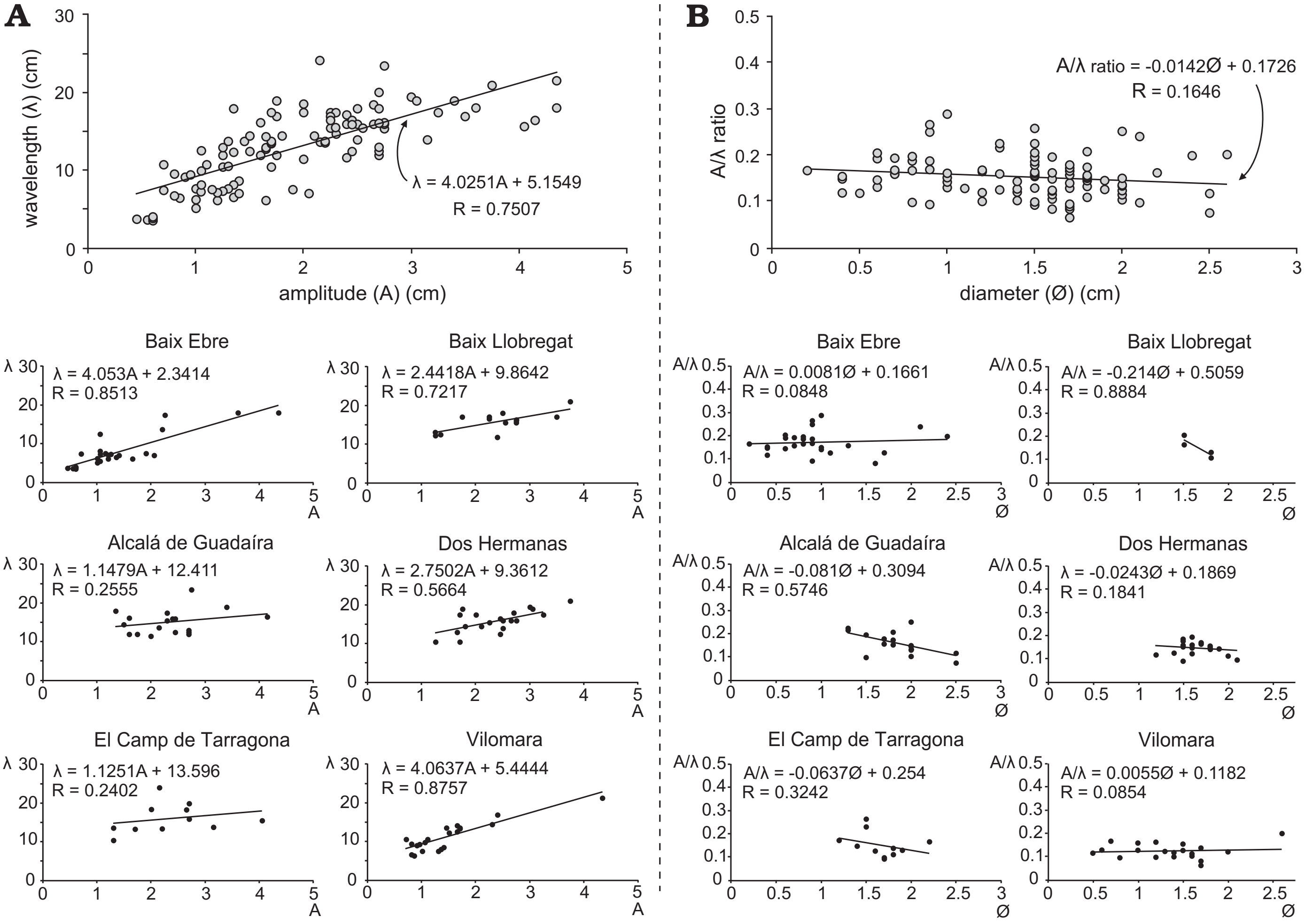

Fig. 7. Graphics illustrating the relation between some measured parameters of the crustacean burrow *Sinusichnus sinuosus* Gibert, 1996. **A**. Above, correlation plot of amplitude (A) versus wavelength (λ) for all the specimens measured in the six localities. Below, same diagram for each one of the six localities individually. **B**. Above, correlation plot of diameter (Ø) versus A/λ ratio for all the specimens measured in the six localities. Below, same diagram for each one of the six localities individually.

son and Taylor 1988; Bromley 1996). Nevertheless, none of the previously reported crustacean burrow systems exhibit any geometry comparable to the sinusoidal regularity of *Sinusichnus*. The closest resemblance is that found in some burrow networks of the varunid brachyuran *Eriocheir sinensis* (Chinese mitten crab), reported by Rudnick et al. (2005). In their figure 3, they show a complex maze with multiple branching and sinuous tunnels. Nevertheless, this architecture does not display the regularity seen in *Sinusichnus* (Fig. 8). Additionally, the authors underlined the large morphological variability of the dwellings of the crab, while the geometric pattern of *Sinusichnus* is very consistent among specimens. The absence of modern analogues for *Sinusichnus* burrows may be due to the fact that casting of modern burrows have been mostly limited to intertidal or very shallow subtidal environments (e.g., Belaústegui et al. 2010; Pemberton et al. 1976; Pervesler and Dworschak 1985). Recent recovery of burrow casts from the deep sea (Seike et al. 2012), although expensive, may offer a future opportunity to have a better picture of the architectural diversity of decapod crustaceans.

Gibert et al. (1999) also contemplated the possibility of other invertebrates as possible *Sinusichnus* tracemakers. Some worm species construct open branched networks with irregularly sinuous tunnels (Fig. 8). Such is the case of the polychaete *Nereis virens* (Hertweck 1986), or the enteropneust *Stereobalanus canadensis* (Romero-Wetzel 1989; Bromley 1996). Nevertheless, this option seems less likely as worm burrows are generally smaller than those produced by decapods.

Bioglyphs (Ekdale and Gibert 2010) are a common feature in crustacean burrows useful for tracemaker identification (Gibert and Ekdale 2010). Although no evidence of scratching on the walls of *Sinusichnus sinuosus* has been recognized, Kappel (2003) erected a second ichnospecies, *S. priesti*, from the Upper Cretaceous of Germany with closely similar architecture to *S. sinuosus* but characterized by the presence of bioglyphs. Although his figures are not very clear, this author describes the bioglyphs as forming a crisscrossed pattern of scratches, similar to that of the crustacean burrow *Spongeliomorpha iberica* (e.g., Gibert and Ekdale 2010).

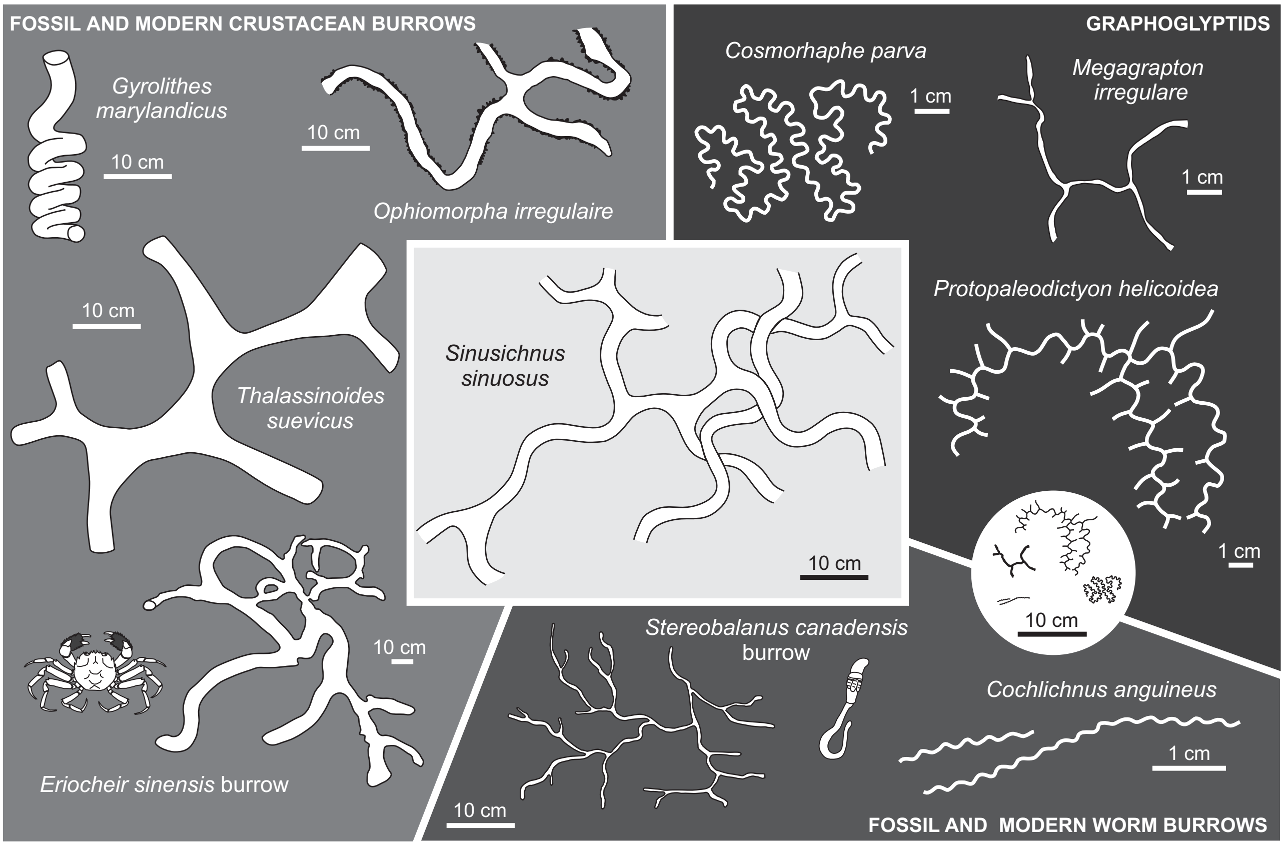

Fig. 8. Trace fossils and modern burrows that render some similarities to *Sinusichnus* crustacean burrow networks. Circle on the right shows grapholglyptids and *Cochlichnus* at the same scale as the others, except for the burrows of the Chinese mitten crab, *Eriocheir sinensis*. Likewise, all drawings are plan views, except for *Gyrolithes* which is lateral view. *Megagrapton irregulare* after Häntzschel 1975; *Stereobalanus* burrow from Romero-Wetzel 1989; *Ophiomorpha irregulaire* after Bromley and Ekdale 1998; *Eriocheir* burrow from Rudnick et al. 2005; *Gyrolithes marylandicus*, *Thalassinoides suevicus*, *Cosmorhaphe parva*, and *Protopaleodictyon helicoidea* after Seilacher 2007; *Cochlichnus anguineus* from Gibert and Sáez 2009.

The absence of scratches in *S. sinuosus* could be related with taphonomic processes that would prevent its preservation.

Once established the crustacean nature of the *Sinusichnus* tracemaker, it is worth comparing the architecture of this trace fossil with that of other well-known ichnogenera and ichnospecies. Thus, *Thalassinoides suevicus* (Rieth, 1932) consists of horizontal burrow systems with common Y-shaped branches as *Sinusichnus*, but its tunnels are always straight or only gently curved (Ekdale 1992) (Fig. 8). Greater sinuosity is seen in the tunnels of *Ophiomorpha irregulaire* Frey, Howard, and Pryor, 1978 although they are meandering rather than regularly sinuous as in *Sinusichnus* (Frey et al. 1978; Bromley and Ekdale 1998) (Fig. 8). Irregular sinuous spreiten burrows characterize *Teichichnus flexuosus* Schneider, 1962 (Fillion and Pickerill 1990; Gibert and Ekdale 1999), but they show no branching. A geometric regularity comparable to that of *Sinusichnus* can only be found among crustacean trace fossils in *Gyrolithes* Saporta, 1884. This vertically helicoidal ichnogenus (Fig. 8) is often connected to complex burrow systems and has a perfect modern analogue in the burrows of the thalassinidean shrimp *Axianassa australis* (Dworschak and Rodrigues 1997). Although the spiral morphology of *Gyrolithes* is constructionally very different to the sinusoids of *Sinusichnus*, it shows the capability of decapods to develop sophisticated behavioral programs resulting in regularly curved architectures.

Regular sinuous morphologies are found in other trace fossils. The best known is probably the ichnogenus *Cochlichnus* Hitchcock, 1858, which is an unbranched sinusoidal trace (Fig. 8). Such morphology results from the locomotory movement of the tracemaker, probably a nematode worm (Gibert and Sáez 2009). *Cochlichnus* is not an open burrow but rather a trail, and thus the result of a very different constructional behavior from *Sinusichnus*. Gibert et al. (1999) compared the sinuosity of both ichnogenera to conclude that they were different as a result of these different behavioral strategies. In the trace fossil record, the geometrical regularity of *Sinusichnus* can only be compared with that of graphoglyptids (Fig. 8). Graphoglyptids are open burrow networks, interpreted to be produced for farming purposes in deep sea settings (Agrichnia of Ekdale et al. 1984). They bear a variety of regularly patterned architectures (Seilacher 1977, 2007). Some of them consist of regularly sinuous tunnels, including from simple unbranched forms such as *Cosmorhaphe* Fuchs, 1895 to more complex branched systems such as *Belorhaphe* Fuchs, 1895, *Megagrapton* Książkiewicz, 1968, or *Protopaleodictyon* Książkiewicz, 1970. These burrows, and in particular the last one, exhibit some remarkable resemblances

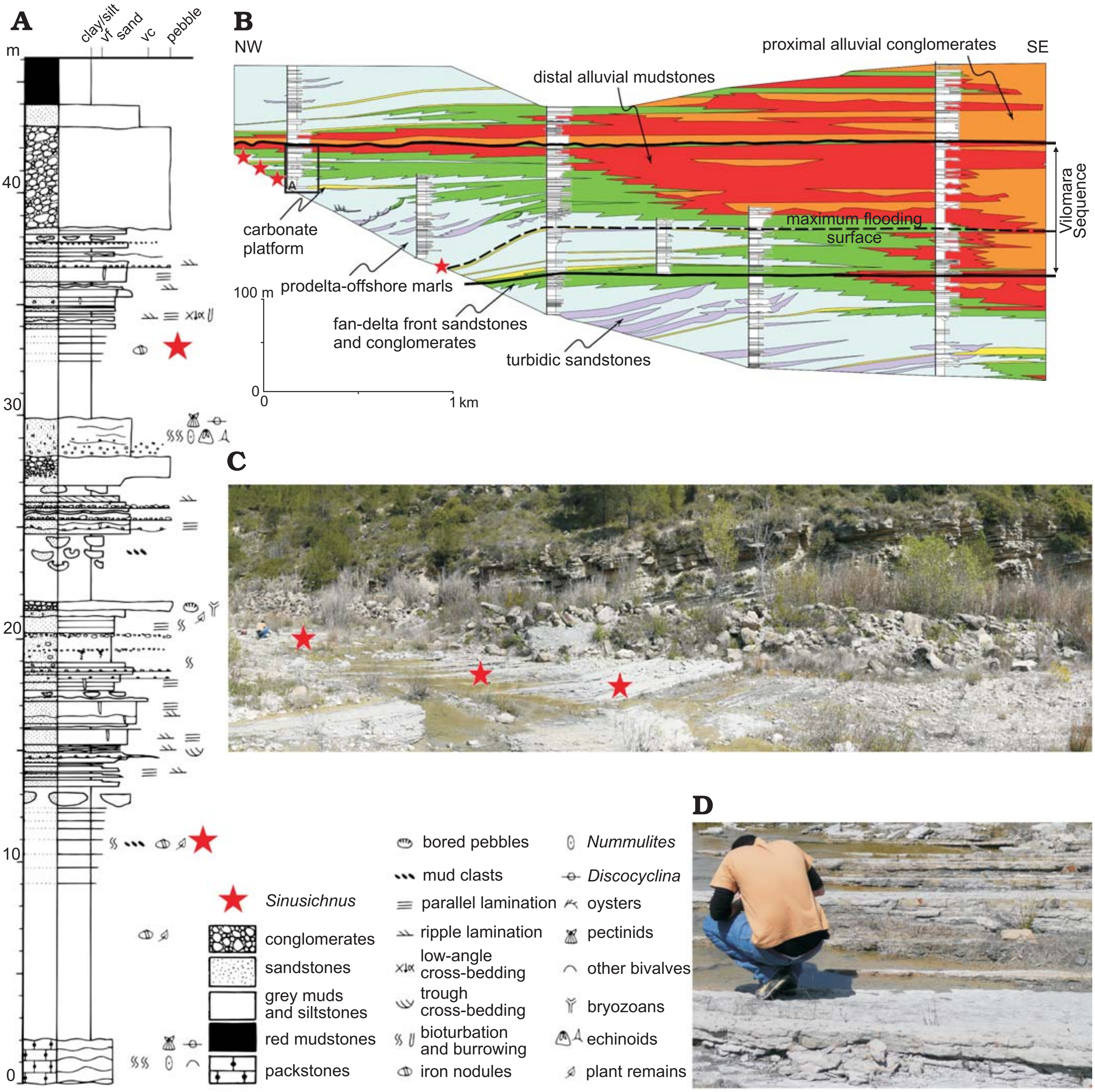

Fig. 9. Depositional setting of the crustacean burrow *Sinusichnus sinuosus* Gibert, 1996 bearing outcrops in the Vilomara area, Spain. **A**. Stratigraphic log showing the location of *Sinusichnus* (indicated by stars) (vf, very fine-grained sand; vc, very coarse-grained sand). **B**. Correlation panel (from López-Blanco et al. 2000c) showing *Sinusichnus* occurrences in relation to facies belts on the Sant Llorenç del Munt fan-delta complex and within the regressive sequence set of the Vilomara Composite sequence. Location of A is indicated. **C**. Panoramic view of the transition from delta front (sandstone beds on the SE) to prodelta (siltstone and mudstone beds on the NW) including *Sinusichnus* horizons (stars). **D**. Detail of the tabular alternation of sandstones and siltstone beds on the transition from delta front to prodelta that bears *S. sinuosus*.

with *Sinusichnus*, although they are considerably smaller and characteristic of deep sea turbidites. This similarity was already noted by Gibert (1996) and Gibert et al. (1999), who suggested a possible agrichnial function for, at least, the smaller *Sinusichnus* burrows. Although graphoglyptids have been recognized in modern deep sea floor (Ekdale and Berger 1978; Ekdale 1980), the tracemaker remains unknown despite huge efforts to find out its identity (Rona et al. 2009).

Thus, *Sinusichnus* has remarkable affinities with other crustacean burrow networks such as *Thalassinoides* and *Ophiomorpha*, often considered as fodinichnial burrows (Ekdale 1992). On the other hand, the highly regular construc-

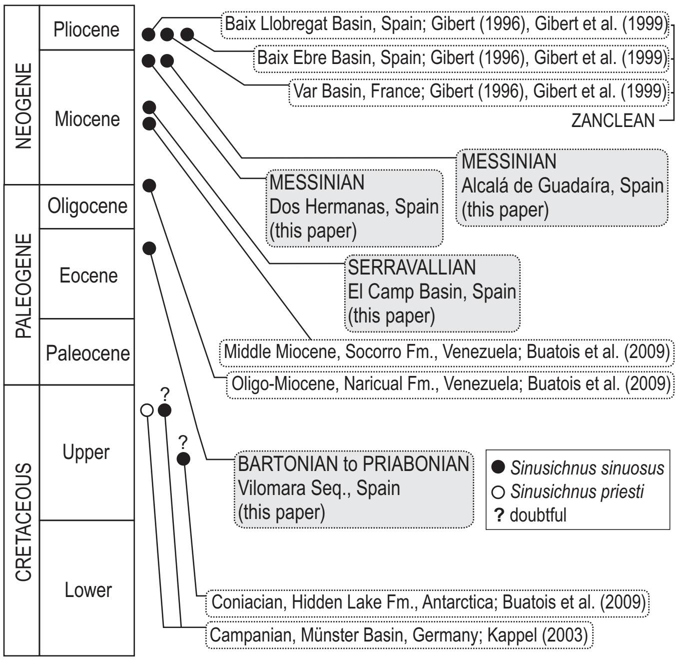

Fig. 10. Stratigraphic distribution of known fossil occurrences of the ichnogenus *Sinusichnus*.

tional pattern of *Sinusichnus* is only comparable to that of graphoglyptids, commonly interpreted as agrichnial burrow systems (Seilacher 1977), which are always much smaller than *Sinusichnus* and found in very different paleoenvironmental settings. On this basis, discussing about the functionality of *Sinusichnus*, Gibert et al. (1999) combined the two scenarios: deposit-feeding and farming. Deposit-feeding was also supported by the presence of spreiten. They discussed that in most cases retrusive spreiten were not perfectly vertical but rather oblique and thus pointing to sediment exploitation rather than simple vertical adjustment to sedimentation. In the cases we studied herein, such lateral displacement has not been observed. On the other hand, some material from the Baix Llobregat described by Gibert et al. (1999) lacks spreiten. Thus, the fodinichnial nature of those spreiten is unclear. Although it is likely that the animal processed sediment for feeding purposes when shifting upwards the tunnel, it seems more straightforward that spreiten resulted from reorganization of sediment entering the burrow and adjustment to sedimentation. The slight obliquity of spreiten in some Baix Ebre material must have been an unintentional consequence of the variation in the sinuosity of the tunnel through time. *Phycodes*-like structures described by Buatois et al. (2009) and observed by the present authors in Vilomara may support deposit-feeding activity of the tracemaker. Modern burrowing thalassinideans exhibit a variety of trophic modes, mainly deposit-feeding, suspension-feeding and farming in chambers, either equally combined or with one dominant over others (e.g., Griffis and Suchanek 1991). Even an agrichnial behavior, similar to those inferred for graphogliptids (i.e., growing of microbes on mucus-lined walls; Seilacher 1977), has been observed in some modern thalassinideans (e.g., Kinoshita et al. 2008). The farming interpretation of graphoglyptids has not been fully demonstrated yet but it has become the most accepted hypothesis for explaining their complex geometry as an adaptation to environments low in food resources. Although *Sinusichnus* occurs in shallow marine settings, presumably rich in food, the similarity in the architectural patterns points out to a similar functionality. Gibert et al. (1999) suggested that the agrichnial behavior could have been only effective for the smaller (younger) individuals as food necessities would have increase faster with size than burrow surface. Different feeding behaviors between juveniles and adults of some modern deposit-feeding species have been also described by Jumars et al. (1990). Small networks, of comparable diameter to graphoglyptids, occur associated to large burrows in Vilomara (Eocene) and Baix Ebre (Pliocene), indicating that juveniles did burrow networks with the same architecture as adults.

The agrichnial hypothesis was also supported by Buatois et al. (2009) who established a comparison with the farming interpretation of *Gyrolithes* proposed by Seilacher (2007). Significance of crustacean spiral burrows (mainly *Gyrolithes*) has been widely discussed (e.g., Toots 1963; Linsenmair 1967; Farrow 1971; Beynon and Pemberton 1992; Schober and Christy 1993; Dworschak and Rodrigues 1997; Felder 2001; Clayton 2005; Netto et al. 2007; Gibert et al. 2012). In an attempt to understand the meaning of modern and fossil spiral burrows, different possibilities have been suggested: (i) deterrence and/or protection against predation, (ii) courtship, (iii) adaptation to salinity changes, (iv) facilitation of in-burrow locomotion, (v) microbial farming, (vi) exploitation of food resources, (vii) providing porewater exchange, and (viii) symmetric or asymmetric producers (unequal handedness). This plethora of hypothesis evinces that, as Atkinson and Taylor (1988) pointed out, despite the good knowledge of the architectural diversity of crustacean burrows, at least in intertidal and shallow subtidal settings, much further information about their physiological ecology is needed.

The fact that *Gyrolithes* and *Sinusichnus* are both geometrically regular, curved crustacean burrows does not necessarily imply that they must share a similar functionality but rather may be a consequence of the anatomical and navigational capabilities of decapods to develop such sophisticated constructional behaviors. Thus, helicoidal burrows generally constitute only a part of a more complex burrow system and they may represent a strategy to exploit a localized resource and thus, a facultative behavior. On the contrary, the sinuous regularity of *Sinusichnus* constitutes the obligatory architectural behavior of the tracemaker. So, according to this difference between facultative or obligatory behaviors, among the hypotheses mentioned above to explain the functionality of *Gyrolithes*, only two seem to be adequate for *Sinusichnus*: microbial farming and predator deterrence. The first has been discussed above. The second option is linked with the "housekey" analogy proposed by Seilacher (2007; see also Rona et al. 2009), who suggested that the different geometric complexity of graphoglyptids could perhaps have evolved as a mechanism to allow access into the burrow only to the tracemakers of each particular architecture, and to dissuade, mislead or warn possible intruders.

Paleoenvironmental significance.—The four new occurrences of *Sinusichnus sinuosus* described herein come from strata deposited in shallow marine settings. Among them, the Eocene locality at Vilomara has the best sedimentological and stratigraphic control thanks to previous detail study of extensive outcrops of the Sant Llorenç de Munt fan delta complex along the Santa Creu valley and neighboring areas (López-Blanco 1993, 1996; López-Blanco et al. 2000a–c; Cabello et al. 2010, 2011). *Sinusichnus* is particularly abundant in several outcrops in the upper regressive sequence set of the Vilomara composite sequence (Fig. 9A, B). These outcrops correspond to thin (centimetric) alternation of siltstone and fine-grained sandstone (Fig. 9C, D) deposited below mean fair-weather wave base, at the transition between distal sandy delta front and offshore-prodelta mudstone beds. *S. sinuosus* traces are preserved in the interface between sand and silt. The well-exposed outcrops allows estimating a horizontal distance of less than 1 km from the paleocoastline and a paleodepth not deeper than few tens of meters (Fig. 9B) indicating the delta front to prodelta (nearshore to offshore) transition habitat preference of the tracemakers. Occurrences in deeper prodelta muddy facies associated to sandy turbidites are much less common. In this more distal setting, *Sinusichnus* is a secondary constituent of an *Asterosoma*-dominated ichnofabric.

The locality of Dos Hermanas constitutes an isolated Messinian outcrop, which has not been yet studied in detail. The succession is constituted by interbedded silty clay and silty sandstone. *S. sinuosus* is abundant all along the section. Macrofauna and microfauna are indicative of shallow-marine nearshore conditions, which is consistent with the ichnological assemblage accompanying *S. sinuosus* (*Thalassinoides*, *Teichichnus*, cf. *Bichordites*). The nearly 20-m thick section does not show any particular organization of sedimentary facies, what together with the absence of a more detailed knowledge of other neighboring localities, only allow to interpret the depositional setting as a coastal terrigenous system. In contrast, *S. sinuosus* from the other Messinian locality in the Guadalquivir Basin at Alcalá de Guadaíra occurs in bioclastic calcarenites (Guadaira Formation). These facies, which contain pectinid, oysters, cirripeds, and echinoids, were studied by Clauss (1991) who concluded that they were deposited in a mixed siliciclastic-carbonate platform, under shallow, open marine conditions. Bajo et al. (2008) suggested a shallow marine infralittoral depositional environment characterized by coarse detritic bottoms with variable hydrodynamic energy. *S. sinuosus* is abundant in relation to thin muddy horizons in the lowermost part of the calcarenitic unit. Finally, *S. sinuosus* from the Serravalian of Tarragona also occurs in units interpreted as deposited in a mixed silicilastic-carbonate platform (Cabrera et al. 1991). Nevertheless, although they are found on top of a quartzitic biocalcarenite, the traces are genetically related to the overlaying unit of grey marls, as its infill is predominantly marly. Thus, in this locality *S. sinuosus* is linked to a surface indicative of a major depositional change due to the entry of terrigenous sediment during a regressive pulse. The poor outcropping conditions of the terrigenous unit prevent any further interpretation.

These new occurrences confirm the predominantly shallow-marine character of *S. sinuosus* already indicated by most previous findings. Thus, Buatois et al. (2009) interpreted the strata containing *S. sinuosus* in the Upper Cretaceous of Antarctica and the Oligo-Miocene of Venezuela as deposited in fan delta or delta settings. On the other hand, Lower Pliocene occurrences described by Gibert (1996; Gibert et al. 1999) come from marginal marine embayments or "rias" produced as a result of flooding of Messinian canyons in the NW Mediterranean. In two of them, the Baix Ebre and Baix Llobregat Basins (NE Spain), deposition took place in shallow marine coastal systems with occasional salinity stressed conditions (Gibert and Martinell 1993, 1996). In contrast, *Sinusichnus* from the Var Basin (SE France) was related to distal facies of a deep Gilbert-type-like delta at depths estimated between 100 and 200 m (Gibert and Martinell 1998). Gibert et al. (1999) tried to explain this unusual occurrence by speculating that the producing organisms may have been displaced alive by turbiditic flows from their original shallow habitats to deeper environments, a scenario previously proposed as "doomed pioneering" by Grimm and Föllmi (1994) for deep-sea occurrences of *Thalassinoides* and *Gyrolithes* in the Oligo-Miocene of Mexico. Occurrence of *Sinusichnus* in Campanian deep sea deposits from the Münster Basin could also be explained by a similar mechanism (Kappel 2003).

Temporal distribution.—Gibert (1996) considered to be feasible that *Sinusichnus sinuosus* was the trace fossil of a single decapod taxon inhabiting the western Mediterranean during the Pliocene after taking into consideration its limited geographic and temporal distribution. Later publications have greatly expanded both (Fig. 10). The presence of the ichnospecies in the Neogene is well established with undisputable occurrences in the Upper Oligocene–Lower Miocene of Venezuela (Buatois et al. 2009), Middle Miocene of Venezuela (Buatois et al. 2009) and Spain, and Upper Miocene of Spain. The new occurrence described herein from Vilomara (Ebro Basin) clearly extends the range of *Sinusichnus* to the Eocene. Older records of the ichnogenus are not so clear. Kappel (2003) recorded *Sinusichnus sinuosus* and a second ichnospecies, *S. priesti*, in the Upper Cretaceous (Campanian) of Germany. Although the specimen figured as *S. sinuosus* (Kappel 2003: fig. 11.5.4) is much less regular than typical for the ichnospecies and lacks any branching, pictures of *S. priesti* provided by the author (Kappel 2003: fig. 11.5.5, table II: fig. 2, table III: fig. 1) display very similar architectural features (branching, regular sinuosity, spreiten) to those of *S. sinuosus*. The only difference between both ichnospecies is the presence of bioglyphs in *S. priesti*. Another Upper Cretaceous occurrence was reported by Buatois et al. (2009) from the Coniacian of Antarctica. The specimen of *S. sinuosus* figured by these authors (Buatois et al. 2009: fig. 2A) displays some branches but renders some doubts because of its irregular sinuosidal pattern and low amplitude/wavelength ratio compared to other occurrences. Only one older possible occurrence is known to the present authors. Gibert and Ekdale (1999) described one single burrow network bearing sinuous tunnels from the Middle Jurassic of Utah, which showed some similarities with *Sinusichnus*. Nevertheless, without access to further material the authors preferred to describe it as *Thalassinoides*? isp., an option that is followed herein.

Being the Jurassic record doubtful and clearly insufficient, we can avow that the ichnogenus *Sinusichnus* has a known stratigraphic record extending from the Upper Cretaceous to the Pliocene. The new occurrences demonstrate that this trace fossil is not so uncommon as previously thought (cf. Gibert 1996) and hopefully its adequate recognition should expand even more this database in the future. Nevertheless, the suggestion of Gibert (1996) that the ichnogenus could be produced by a single decapod taxon or, to put in different words, that it is a "monophyletic" ichnogenus, may still hold. Gibert (2003) addressed the problem of monophyly and polyphyly in trace fossils, and based on previous work done by modern ethologists proposed a series of criteria to recognize behavioral homology and homoplasy in the ichnological record. While the more or less continuous stratigraphic record supports monophyly ("stratigraphic criterion"), the consistent, complex, and highly patterned architecture of *Sinusichnus* complies with the "ichnocomplexity criterion", which may be stated as "the more complex is a behavior recorded by one or several ichnotaxa, the more likely the behavior is homologous". Thus, the constructional and functional behavior recorded by *Sinusichnus* very likely records the work of a particular decapod taxon, which may still exist today and have yet to be recorded in modern settings. The evolution of this sophisticated behavior took place in the Upper Cretaceous, if not earlier, in the framework of the Mesozoic diversification of decapods, which was particularly important during the Cretaceous (Carmona et al. 2004). This diversification led to the increasing abundance and diversity of crustacean trace fossils as part of the evolution of new life strategies in the context of the Mesozoic Marine Revolution (Carmona et al. 2004; Buatois et al. 2009).

Conclusions

- The new occurrences of the ichnogenus *Sinusichnus* described herein demonstrate that this trace fossil is not so uncommon as previously thought and complete its known record from the Upper Cretaceous until the Lower Pliocene.
- The sinusoidal regularity of *Sinusichnus* evidences a sophisticated behavior whose functional significance is not clear. In addition to the previous hypothesis proposed for this trace fossil, according to which *Sinusichnus* is the result of a combination of fodinichnial and agrichnial behavior, this complex geometry may have been also evolved as a defensive mechanism to deter the entrance of intruders into the burrow.
- *Sinusichnus* is most characteristic of shallow marine, offshore to nearshore transition environments, particularly deltaic settings. Nevertheless, it may occur in deeper water settings.
- *Sinusichnus* records the work of an unknown group of decapod crustaceans, which developed complex burrow architecture as a result of a successful highly-sophisticated behavioral program. The evolution of such behavior has to be framed within the Cretaceous diversification experimented by decapods.

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