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Commensalism in the fossil record: Eunicid polychaete bioerosion on Pliocene solitary corals

JORDI MARTINELL and ROSA DOMÈNECH



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Some solitary caryophylliid (*Caryophyllia*, *Trochocyathus*, and *Ceratotrochus*) and flabellid (*Flabellum*) scleractinian corals from Pliocene of Western Mediterranean exhibit long groove-shaped bioersional structures running along the surface of the thecae. They are epigenic structures produced by an episkeletozoan and therefore, they are described as Fixichnia. Here we propose *Sulcichnus* as a new ichnogenus, with three new ichnospecies (*Sulcichnus maeandriformis*, *S. helicoidalis*, and *S. sigillum*) to name this traces. *Sulcichnus* is attributed to the activity of polychaetes. Similar structures are recently produced by *Lumbrineris flabellicola*, a symbiotic eunicid which maintains a commensalistic relationship with solitary corals. In the fossil record, *Sulcichnus* occurs associated to shallow marine environments whereas their Recent counterparts are described on deep-marine corals. We interpret this as a consequence of a change in the environmental requirements of the coral/worm pair.

Key words: Scleractinia, Polychaeta, Eunicida, palaeoecology, bioerosion, commensalism, Pliocene, Mediterranean.

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Introduction

The study of bioerosion is a valuable tool to understand the biodiversity and ecological complexity of a given area at any point in Earth's history. As bioerosive organisms often lack a fossilizable hard skeleton, it is the trace they leave on the host what enables their existence to be determined and the biotic interaction established with the host to be interpreted.

The palaeontological marine record contains numerous examples of interspecific relationship. Many of them correspond to cases of exploitation (predation and parasitism) between invertebrates, in which one of the members of the pair benefits at the expense of the other. Kowalewski et al. (1998), Kowalewski and Kelley (2002), Leighton (2002), Kelley et al. (2003), Santos et al. (2003), and Zuschin et al. (2003) are examples of different approaches to the study of marine invertebrate predation in the fossil record among the most recent publications.

Although not so easy to identify as predation (except perhaps in the insects world), researchers have also published on parasitism evidences in fossil invertebrates. Mention should be made to the studies by Harries and Ozanne (1998), Martinell et al. (1999), Bates and Loydell (2000), Poinar (2001, 2003), Baumiller and Gahn (2002), Hoffmeister et al. (2003), Neumann and Wisshak (2006), and Zapalski (2007), among others.

Other types of biotic interactions, such as symbiosis (mutualism, commensalism) or competition, leave few traces on the host and so are more difficult to detect. Therefore, their identification in the fossil record always represents a significant contribution to our knowledge about how processes of biotic interaction and co-evolution have developed over time (Martinell 1989; Boucot 1990; Zapalski 2005). Taylor and Wilson (2003) reviewed the fossil record of hard substrate communities and provide examples of different types of exploitation and symbiosis. In the practice, symbioses can only be identified when the invader affected the host skeleton and some kind of structure was produced. Skeletal hosts belong to a great spectrum of groups (corals, molluscs, brachiopods, echinoderms, and others). Symbiotic fossil traces are represented by borings or by bioclaustrations (embedment structures) (Palmer and Wilson 1988; Taylor 1990; Tapanila 2005, 2006) in the host skeleton. In the Recent, symbionts frequently inhabit the host soft parts and no traces are evident.

Some examples of bioerosion evidences of commensalism in the geological past are described by Bałuk and Radwański (1997), Vermeij (1998), Nielsen (1999), García-Bellido Capdevila (2003), Tapanila (2004), and Wisshak and Neumann (2006), who generally attributed the role of symbionts to worm-like organisms. Oliver (1983) and Elias (1986) exposed some examples of symbiosis between rugose corals and worms in the North America Palaeozoic, some of them being attributed to a commensal behaviour but these symbiotic traces are better interpreted as bioclaustrations (embedments) rather than as bioerosion. Similarly, Tapanila (2002) described the relationship between soft-bodied organisms and tabulate corals in the Canadian Late Ordovician as a case of commensalism, although Zapalski (2007) interprets it mostly as a

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parasitic behaviour. Finally, Stolarski et al. (2001) described several bioclaustration structures as a result of symbiotic interaction between sipunculids and scleractinians from the Early Cretaceous to the present. Although the relationship among soft-bodied organisms and corals is known since the early Palaeozoic, few clear data exist on their taxonomy. Because that, some authors just use the term endosymbionts to refer to them (Tapanila 2002, 2005).

The present paper focuses on the identification, nomination, description, and interpretation of some characteristic bioerosion epigenic traces observed on several specimens of solitary ahermatypic corals collected in different Western Mediterranean Pliocene basins. These traces have already been mentioned both in the fossil record and in Recent specimens by other authors (see, i.e., Zibrowius 1977, 1987), but they have yet to be considered from the ichnosystematic point of view.

Institutional abbreviations.—JMC-UB, J. Martinell Neogene invertebrate collection at the Universitat de Barcelona, Barcelona, Spain; MGSC, Museu Geològic del Seminari Conciliar, Barcelona, Spain; MHNUT, Museo d'Historia Naturale de l'Università di Torino, Turin, Italy; MMPE, Museo Municipal Paleontológico de Estepona, Málaga, Spain; PCUG, Universidad de Granada, Granada, Spain, palaeontological collection.

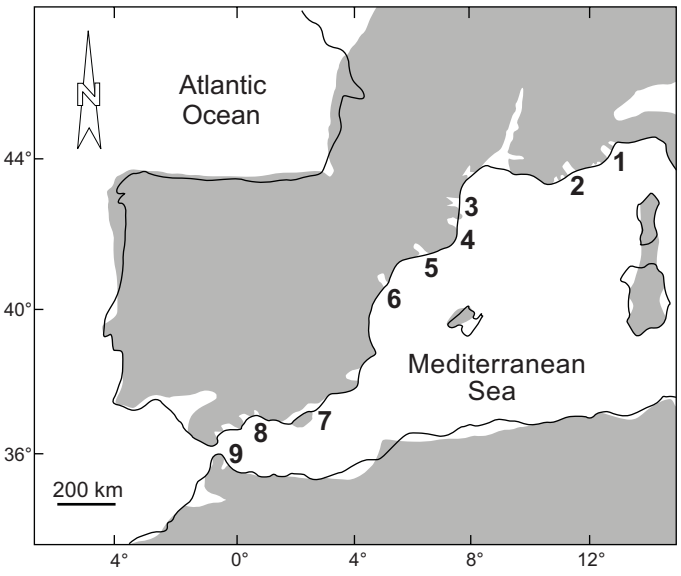


Fig. 1. Palaeogeographical map of the Western Mediterranean during the Piacenzian (Early Pliocene) showing the location of the basins that have provided the study material: 1, Liguria (NW Italy); 2, Alpes-Maritimes (SE France); 3, Roussillon (SE France); 4, Alt Empordà (Catalonia, NE Spain); 5, Baix Llobregat (Catalonia, NE Spain); 6, Baix Ebre (Catalonia, NE Spain); 7, Níjar-Almería (Andalusia, SE Spain); 8, Vélez-Málaga (Andalusia, SE Spain); 9, Estepona (Andalusia, SE Spain).

Geographical and geological setting

The Pliocene sediments from the Western Mediterranean appear in numerous basins along the coastline, from north-west Italy and south-east France to the south of the Iberian Peninsula. In descending order of latitude the main examples are those in Liguria (Italy); Rhône, Alpes-Maritimes, Orb and Roussillon (France), and Alt Empordà, Baix Llobregat, Baix Ebre, Murcia, Almería-Níjar, Vélez-Málaga, and Estepona (Spain) (Fig. 1). Their marine sedimentary filling is dated as Zanclean (Early Pliocene), only the Estepona Basin reaching to the early Piacenzian (Middle Pliocene) (Aguirre et al. 2005). All of them represent proximal shallow marine environments, except for the Liguria and Alpes-Maritimes basins, which also contain sediments deposited in deeper environments. Detailed descriptions of these basins can be found in Bernasconi and Robba (1994), Agustí et al. (1990), Clauzon et al. (1990), and Aguirre et al. (2002, 2005).

The coral fauna

Scleractinians in the Mediterranean Neogene basins.—The traces under study are identified on scleractinian corals, which are rather scarce in the Mediterranean Pliocene, but very important constituents of its Miocene basins. In fact, the particular climatic conditions of a good part of the Miocene favoured the development of significant coral reefs in the main Mediterranean basins. Well-known examples in the Western Mediterranean include the bioconstructions of Majorca (Balearic Islands), the Penedès region of Catalonia (NE Spain), Almería (SE Spain) and the Moroccan corridor. Studies such as those of Reuss (1872), Zuffardi-Comerci (1932), Chevalier (1961), Esteban (1979), Permanyer (1990), and Stolarski (1991) are examples of different approaches to these build-ups. Although these favourable conditions ceased as a result of the Messinian crisis, and coral reefs are no longer found in Pliocene series (Aguirre and Jiménez 1998), coral fauna was maintained, albeit to a much lesser extent.

As a consequence, neither hermatypic nor ahermatypic corals are characteristic elements of the Mediterranean marine Pliocene, although they can be locally significant. Due to their scarcity, bibliographic citations are also limited, but the presence of fossil scleractinian corals in these sediments has been well known since the end of the nineteenth century (Angelis 1894 a, b).

No doubt as a result of their scarcity, a detailed taxonomic review of this group has yet to be conducted. Indeed, although Montanaro (1931) published a detailed monograph on the Pliocene scleractinians there is a need for an up-to-date review of the members of this group in the Mediterranean. Other more concrete taxonomic studies of scleractinians from European basins include those of Simonelli (1895, 1896) for the Italian Neogene; Angelis (1894b), Osasco (1895), Cuif (1968), and Zibrowius and Placella

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(1981) for the Northern Italy Pliocene; Almera (1894) and Angelis (1894a) for the northeast Spain Pliocene; Marcopoulou-Diacantoni (2000) for the family Flabellidae from the Upper Pliocene of Crete (Greece), and Zibrowius (1977, 1987) for Mediterranean bathyal scleractinians from the Pliocene to the present day.

Coral taxa identified.—The study is based on material collected from the basins of Liguria (Italy); Roussillon (France), and Alt Empordà, Baix Llobregat, Vélez-Málaga and Estepona (Spain). We also reviewed the collections housed in the MMPE and the MGSC (Spain), and in the MHNUT (Italy). In the latter we also consulted material from Miocene deposits from the area around Turin. Finally, palaeontological information about the Almería-Níjar basin was also provided by Julio Aguirre and Antonio Jiménez (personal communication 2008).

Many of the distinguishing features of coral species are difficult to observe in fossil material, and thus we limited our taxonomy to the generic level, in the hope that other specialists will undertake a more detailed review.

Twelve scleractinian genera belonging to seven families were identified in the Pliocene basins of the Western Mediterranean. Of these, six are solitary and six colonial (hermatypic or not) (Table 1). The greatest taxonomic diversity was found in the Baix Llobregat basin, where all these genera, both colonial and solitary, are present. *Cladangia* and *Madracis* (both colonial) show the most limited geographical distribution, as they were identified only in the Baix Llobregat basin. The most cosmopolitan genus is *Flabellum*, which was identified in all the basins except the Baix Ebre. In the Alt Empordà and Baix Llobregatbasins, two species (minimum) of *Flabellum* are present, although they are scarce. Finally, the Estepona Basin yielded the greatest number of specimens, with nearly 200 corallites available for study.

Table 1. Check-list of the coral taxa identified in the Western Mediterranean Pliocene and their distribution in the different basins (see Fig. 1 for localities identification). Grey shading indicates solitary genera, the remaining ones being colonial forms.

Localities	1	2	3	4	5	6	7	8	9
Family Rhizongiidae									
Cladangia					*				
Family Caryophylliidae									
Caryophyllia				*	*	*	*	*	*
Coenocyathus					*				
Trochocyathus			*	*	*			*	*
Ceratotrochus	*				*			*	*
Aplocyathus					*				*
Family Flabellidae									
Flabellum	*	*	*	*	*		*	*	*
Family Dendrophylliidae									
Dendrophyllia					*				*
Balanophyllia				*	*				
Family Astrocoeniidae									
Astrocoenia					*	*			
Family Pocilloporidae									
Madracis					*				
Family Faviidae									
Cladocora				*	*		*		

Material analysed

Traces of bioerosion on the solitary corals considered here were studied using both material gathered in the field and specimens housed in museums. The use of museistic material could entail a degree of bias favouring undamaged specimens. However, Hoffmeister et al. (2004), among others, show that observations can be equally valid in such cases. However, the quantification of bioerosion is here presented merely for the purpose of illustration.

In general, the studied skeletons are small (1–3 cm high and up to 1 cm wide). Only some corallites of *Flabellum* collected at the Alt Empordà and Liguria basins are larger than 4 cm high and 5 cm wide when complete.

The morphology of these corallites can be grouped into four categories, which we have named according to the classical nomenclature of Wells (1956): (i) flabellate form (fan shaped), here represented by *Flabellum*; (ii) trochoid form (with a basal angle of about 40°), represented by *Ceratotrochus*; (iii) conical or turbinate form (with a basal angle of 60° to 80°), represented by *Caryophyllia*; and d) turbinate to ceratoid form (with a basal angle only about 20°), represented by *Trochocyathus*.

Ichnological study

Entobia isp. and *Trypanites* isp. are the most usual bioerosion traces identified in the collected specimens, together with small *Oichnus* isp. found in the base of a few *Trochocyathus* corallites, and some *Maeandropolydora* isp. and *Pinaceocladichnus* isp. In general, these traces of bioerosion are scarce, as regards both the percentage of affected skeletons (around 2%) and the boring intensity. However, there is also a sixth meandroid epigenic trace that is not attributable to any previously described ichnotaxa, which constitutes the objective of this research.

This trace is present on the theca of four of the six solitary scleractinians identified: *Caryophyllia*, *Trochocyathus*, and *Ceratotrochus* (family Caryophyllidae), and *Flabellum* (family Flabellidae). It consists of a superficial meandroid groove, with a maximum width of 2–3 mm and a depth of 1–2 mm, which runs along the external side of the corallite theca and takes different forms. It should be noted that there is only one groove per single skeleton. The boring is well developed in the majority of bored specimens in all the basins, especially on *Caryophyllia* and on some *Flabellum*. The trace surrounds the

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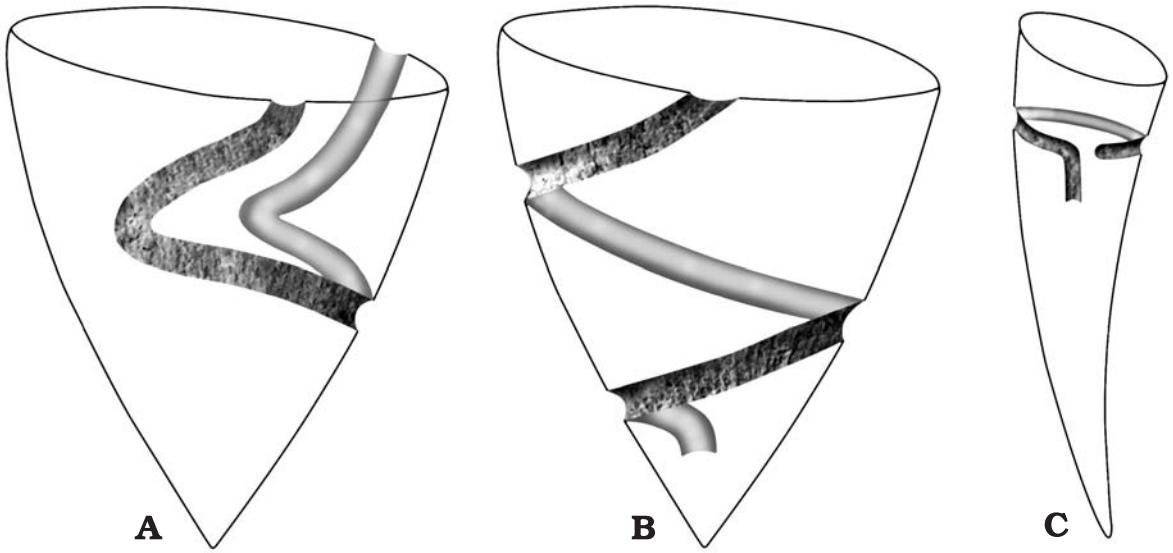


Fig. 2. Idealized models of *Sulcichnus maeandriformis* (**A**), *Sulcichnus helicoidalis* (**B**), and *Sulcichnus sigillum* (**C**).

skeleton from the base to the calyx. It is noticeable that the trace cuts cleanly through the coral skeleton although there is no evidence of reaction from the host; no deformation, defensive structures (i.e., overgrowths) or repairs (scars) were identified.

Ichnological study

Entobia isp. and *Trypanites* isp. are the most frequent bioerosion traces identified in the specimens, together with small *Oichnus* isp. found in the base of a few *Trochocyathus* corallites, and some *Maeandropolydora* isp. and *Pinaceocladichnus* isp. In general, these traces of bioerosion are scarce, as regards both the percentage of skeletons affected (around 2%) and the boring extent. However, there is also a sixth meandroid epigenic trace not attributable to any previously described ichnotaxon. This is the main object of the study.

This trace is present on the theca of four of the six solitary scleractinians identified: *Caryophyllia*, *Trochocyathus*, and *Ceratotrochus* (family Caryophyllidae), and *Flabellum* (family Flabellidae). It consists of a superficial meandroid groove, with a maximum width of 2–3 mm and a depth of 1–2 mm, which runs along the external side of the corallite theca and takes different forms. It has to be noted that there isis only one groove per single skeleton. The boring is well developed in most of bored specimens in all the basins, especially *Caryophyllia* and some *Flabellum*. The trace surrounds the skeleton from the base to the calyx. The trace cuts cleanly through the coral skeleton although there is no evidence of host reaction: no deformation, defensive structures (for example, overgrowths) or repairs (scars) were identified.

The incidence of the trace in the various basins is highly variable and it has been quantified only when a minimum number of specimens were available. In the Estepona Basin, 10.7% of corallites (15 of 140 individuals) of *Caryophyllia* (from field samples) and 16% (19 of 119 individuals) of *Flabellum* (from MMPE) show the trace. In the Empordà basin, its presence rises to 50% in *Flabellum* (9 specimens out of 18) (from field samples). Finally, in the Liguria basin, 11 out of 29 individuals (39.3%) of the corallites of *Ceratotrochus* (MHNUT) were affected, while the groove does not appear in any of the 14 *Flabellum* specimens of this collection.

Detailed observation of the grooves led us to identify three patterns of growth (Fig. 2). These provided the basis for the systematic descriptions proposed in the next section: (i) meandering pattern, present in *Ceratotrochus*, *Flabellum*, *Caryophyllia*, and *Trochocyathus*; (ii) corkscrew pattern, present in *Caryophyllia*, *Ceratotrochus*, and *Flabellum*; and (iii) branding-iron pattern, present in *Caryophyllia* and *Trochocyathus*.

Examination of publications figuring Recent coral specimens bearing this groove revealed the presence of two of these growth patterns: meandering and branding iron.

Repository.—The types of the proposed ichnospecies are deposited in MMPE. The remaining material (paratypes included) is also housed there, as well as in MGSC, MHNUT, PCUG, and in JMC-UB.

Systematic ichnology

Ichnogenus *Sulcichnus* ichnogen. nov.

Etymology: After the Latin word *sulcus*, groove.

Ichnospecies type: *Sulcichnus maeandriformis* ichnosp. nov.

Diagnosis.—Long grooves, sometimes branched, running along the surface substrate sinuously or in a contorted fashion. Grooves never run in parallel, and loose or tight loops may occur.

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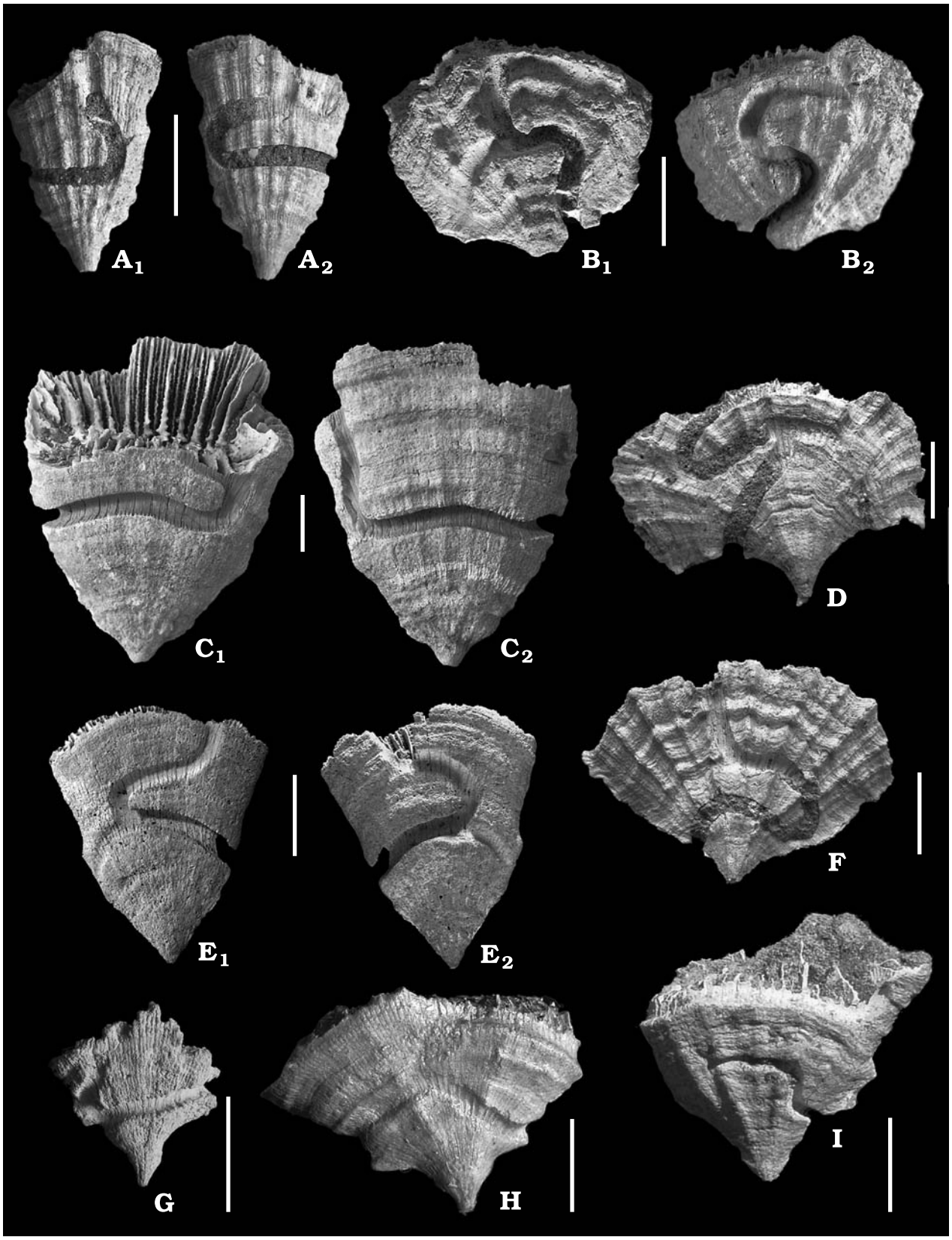


Fig. 3. Polychaete trace fossil *Sulcichnus maeandriformis* on *Flabellum* sp. from different Lower Pliocene sites. Pairs of pictures correspond to both sides of a single corallite and show the specular symmetry of the boring. **A**. Paratype, MMPE/Ic001.003.001, Bizcornil, Estepona. **B**. Paratype, MMPE/Ic001. 002.001, Velerín, Estepona. **C**. Holotype, MMPE/Ic001.001.001, Velerín, Estepona. **D**. Paratype, MMPE/Ic001.004.001, Velerín, Estepona. **E**. Paratype, MMPE/Ic001.005.001, Velerín, Estepona. **F**. Paratype, JMC-UB/I-0087, Vila-robau, Alt Empordà. **G**. JMC-UB/I-0130, Rio Torsero, Liguria. **H**. JMC-UB/I-0089, Vila-robau, Alt Empordà. **I**. UG-N-P-0117, Almería-Níjar. Scale bars 10 mm.

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Remarks.—*Sulcichnus* have some similarities with the ichnogenera *Maeandropolydora* and *Caulostrepsis.* Bromley and D'Alessandro (1983: 293) amended the former description by Voigt (1965) and re-described *Maeandropolydora* as "Long cylindrical galleries having two or more apertures, running through the substrate sinuously or in irregular contortions. Galleries may run parallel in contact with each other in pairs, with or without fusion. Loose or tight loops may occur; the limbs of these may be connected by a vane or form a pouch".

Diagnosis of *Caulostrepsis* refers to U-shaped borings that have a vane connecting the limbs of the U-boring (Bromley 2004), with more or less complex designs (Bromley and D'Alessandro 1983).

Both traces correspond to complete endogenic tunnels made by endobionts, whereas *Sulcichnus* is an epigenic groove—never a tunnel—excavated on the solid substrate by an epibiont. *Maeandropolydora* often appears in the fossil record as a sinuous groove in the substrate due to breakage or weathering of the gallery roof. In such cases, misidentification may have occurred, and further revision is needed.

Sulcichnus maeandriformis ichnosp. nov.

Figs. 3, 4I–L.

Etymology: After the Latin words *maeander*, meander and *formis*, form.

Type material: Holotype, MMPE/Ic001.001.001 (Velerín, Estepona) (Fig. 3C). Paratypes, MMPE/Ic001.003.001 (Bizcornil, Estepona) (Fig. 3A), MMPE/Ic001.002.001 (Velerín, Estepona) (Fig. 3B), MMPE/Ic001.004.001 (Velerín, Estepona) (Fig. 3D), MMPE/Ic001.005.001 (Velerín, Estepona) (Fig. 3E), JMC-UB/I-0087 (Vila-robau, Alt Empordà) (Fig. 3F).

Type locality: Velerín, Estepona Basin, E Andalusia, Spain.

Type horizon: Upper Zanclean (Pliocene) silts, Estepona Basin, Málaga (SE Spain) (Aguirre et al. 2005).

Material.—Number of specimens: 9 from Rio Torsero, Liguria; 2 from Alpes-Maritimes; 5 from Vila-robau, Alt Empordà; 4 from Baix Llobregat; 1 from Níjar-Almería; 1 from Bizcornil, Estepona; 1 from Padrón, Estepona; 4 from Parque Antena, Estepona; up to 30 from Velerín, Estepona (Table 2).

Diagnosis.—Deep groove of relatively constant width that takes various sinuous forms.

Description.—Deep grooves (2 mm maximum) of relatively constant width in every specimen (between 1–2 mm) that describe various gentle undulations to tighter loops, although in the latter the opposite parts of the figure never parallel. The grooves normally begin and end at the edge of the calyx and sometimes show one or two short branches. The trace is often very symmetrical from one side of the corallite to the other in flabellate forms. In them, the central, lower part of the figure surrounds the corallite and the two extremes run more or less vertically to the calyx (Fig. 2).

Remarks.—This trace appears in specimens of all four coral morphologies considered: flabellate, trochoid, conical to turbinate, and turbinate to ceratoid (Table 3). It also appears on specimes of *Trochocyathus* coming from the Miocene of Turin (Italy) (MHNUT). Some Recent specimens sawn in the literature are also according with this pattern (Zibrowius et al. 1975).

Stratigraphic and geographic range.—Tortonian (Late Miocene) to Recent; worldwide.

Sulcichnus helicoidalis ichnosp. nov.

Fig. 4D–H.

Etymology: After the Greek word meaning helicoid.

Type material: Holotype, MMPE/Ic002.001.001 (Velerín, Estepona) (Fig. 4E). Paratypes, MMPE/Ic002.002.001 (La Lobilla, Estepona) (Fig. 4D), JMC-UB/I-0086 (Vila-robau, Alt Empordà) (Fig. 4F).

Type locality: Velerín, Estepona Basin, E Andalusia, Spain.

Type horizon: Upper Zanclean (Pliocene) silts, Estepona Basin, Málaga (SE Spain) (Aguirre et al. 2005).

Material.—Number of specimens: 1 from Rio Torsero, Liguria; 2 from Baix Llobregat; 1 from Padrón, Estepona; 2 from Velerín, Estepona (Table 2).

Diagnosis.—Helicoidal groove running around the corallite.

Description.—The trace consists of a groove that begins close to the base of the corallite and ends at the edge of the calyx, following an helicoidal, clockwise, sometimes irregular, pattern around the skeleton. Between one and two complete turns are made and it may present one or two short branches. Usually, the deepest part of the groove corresponds with the nearest to the coral calyx, and it is never deeper than 2 mm.

Remarks.—*S. helicoidalis* has been found in three of the four coral morphologies: flabellate, trochoid, and conical to turbinate (Table 3). It is also present on specimens of *Trochocyathus* from the Miocene of Turin (Italy) (MHNUT).

Table 2. Distribution of *Sulcichnus* ichnospecies in the different basins. Abbreviations: 1, Liguria (NW Italy); 2, Alpes-Maritimes (SE France); 3, Roussillon (SE France); 4, Alt Empordà (Catalonia, NE Spain); 5, Baix Llobregat (Catalonia, NE Spain); 6, Baix Ebre (Catalonia, NE Spain); 7, Níjar-Almería (Andalusia, SE Spain); 8, Vélez-Málaga (Andalusia, SE Spain); 9, Estepona (Andalusia, SE Spain).

Localities	1	2	3	4	5	6	7	8	9
Sulcichnus helicoidalis	*				*				*
Sulcichnus maeandriformis	*	*		*	*		*		*
Sulcichnus sigillum									*

Table 3. Presence of *Sulcichnus* ichnospecies on the solitary ahermatypic coral taxa: *Sulcichnus helicoidalis* (1), *Sulcichnus maeandriformis* (2), and *Sulcichnus sigillum* (3).

Ichnospecies	1	2	3
Family Caryophylliidae			
Caryophyllia	*	*	*
Trochocyathus		*	*
Ceratotrochus	*	*	
Family Flabellidae			
Flabellum	*	*	

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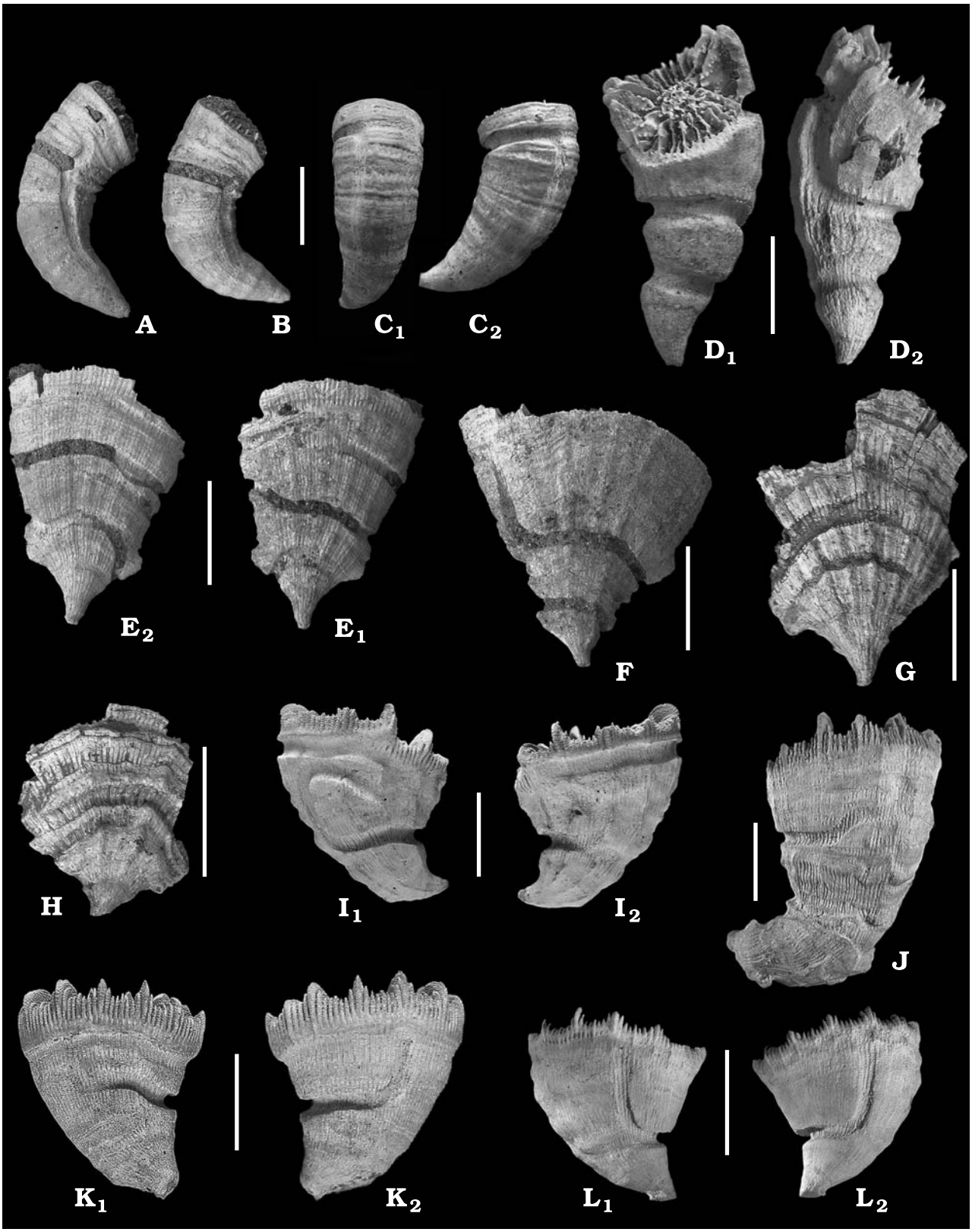


Fig. 4. Examples of the three *Sulcichnus* ichnospecies. *Sulcichnus sigillum* on *Trochocyathus* sp. Pairs of pictures correspond to both sides of a single corallite, showing the specular symmetry of the groove. **A**. Paratype, MMPE/Ic003.002.001, Arroyo Vaquero, Estepona. **B**. Paratype, MMPE/Ic003.003.001, Velerín, Estepona. **C**. Holotype, MMPE/Ic003.001.001, Parque Antena, Estepona. *S. helicoidalis* on *Trochocyathus* sp. **D**. Paratype, MMPE/Ic002.002.001, La Lobilla, Estepona. *S. helicoidalis* on *Flabellum* sp. **E**. Holotype, MMPE/Ic002.001.001, Velerín, Estepona. **F**. Paratype, JMC-UB/I-0086, Vila-robau, Alt Empordà. **G**. MGSC-3523, Baix Llobregat. **H**. MGSC-3524, Baix Llobregat. *S. maeandriformis* on *Ceratotrochus* sp., Rio Torsero, Liguria. **I**. MGPUT-I-001. **J**. MGPUT-I-002. **K**. MGPUT-I-003. **L**. MGPUT-I-004. Scale bars 10 mm.

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Stratigraphic and geographic range.—Tortonian (Late Miocene) to early Piacenzian (Middle Pliocene); Mediterranean area.

Sulcichnus sigillum ichnosp. nov.

Fig. 4A–C.

Etymology: After the Latin word *sigillum*, mark, brand, referring to the branding iron morphology of the groove.

Type material: Holotype, MMPE/Ic003.001.001 (Parque Antena, Estepona) (Fig. 4C). Paratypes, MMPE/Ic003.002.001 (Arroyo Vaquero, Estepona) (Fig. 4A), MMPE/Ic003.003.001(Fig. 4B).

Type locality: Parque Antena, Estepona Basin, E Andalusia, Spain.

Type horizon: Upper Zanclean (Pliocene) coarse-grained sand levels within conglomerates, Estepona Basin, Málaga (SE Spain) (Aguirre et al. 2005).

Material.—Number of specimens: 1 from Arroyo Vaquero, Estepona; 1 from Padrón, Estepona; 1 from Parque Antena, Estepona; 8 from Velerín, Estepona (Table 2).

Diagnosis.—Shallow groove parallel to the columella and bending 90° close to the calyx, to form a deeper, ring-shaped groove.

Description.—Shallow grooves (1 mm maximum in depth) that run more or less in parallel to the axis of the columella from close to the base of the corallite. They turn a sharp 90° to the left when reaching a point a few millimetres from the edge of the calyx, where they deepen (to some 2 mm) and run almost the whole of the perimeter of the corallite, thus taking on the appearance of a branding iron.

Remarks.—This trace has only been identified in the turbinate coral morphologies (*Caryophyllia* and *Trochocyathus*) (Table 3). Some Recent specimens seen in the literature also follow this pattern.

Stratigraphic and geographic range.—Zanclean (Early Pliocene) to Recent; worldwide.

Reports of *Sulcichnus* in the literature

There are numerous reports in the literature that show *Sulcichnus* to be common in the fossil record on solitary corals since the Miocene, although authors do not always describe the presence of the trace.

Reuss (1872) reported and figured different Miocene caryophylliids with these grooves, collected in the central Europe Miocene basins.

Angelis (1894b) illustrated a specimen of *Flabellum* from the Ligurian Pliocene (Italy) which appears to show a groove. Two authors reported corals from various Pliocene locations in the north of Italy and also figured specimens with grooves: Osasco (1895) (*Ceratotrochus*) and Simonelli (1895) (*Flabellum* and *Ceratotrochus*). Roger (1943, 1944) figures several species of *Flabellum* from the Lower Pliocene of Dar Bel Hamri (Atlantic coast of Morocco) that show *Sulcichnus*. Posteriorly, Chavan (1952) re-described one of the forms identified as *F. avicula* by Roger (1944), and also pointed out the presence of the groove. This author also refers to the same type of groove shown by specimens of *Ceratotrochus* found in this Moroccan location, as well as in *Flabellum* from the Malacitan Mediterranean Pliocene.

Cuif (1968) studied caryophylliids from Liguria and Djebel Hammamet (Tunisia), two areas a considerable distance apart, and in both found specimens with the grooves.

Chevalier (1961) studied European Miocene corals but none of his plates show specimens with *Sulcichnus*. However, Zibrowius et al. (1975) pointed out that in Chevalier's collection, which is housed in the Natural History Museum of Paris, they saw several Pliocene solitary scleractinians from the Atlantic Morocco and from Liguria (Italy), all of them showing the excavation. They also detected the groove in Miocene and Pliocene specimens from the British Museum collections: for example, in some *Flabellum* from Los Tejares (Málaga, Andalusia), Pisa and Bussana (Liguria, Italy), in many specimens of *Ceratotrochus* from Tunisia, the north of Italy and the Alpes-Maritimes (France), and in *Trochocyatus* from the Miocene of Tortona (Italy).

The majority of traces seen in the literature (Recent and fossil forms) resemble *S. maeandriformis*, and a few seem to better fit with *S. sigillum* pattern. Nevertheless, a clear identification is not always feasible from the pictures, as previously noted.

Sulcichnus tracemaker

Generally speaking, traces of bioerosion offer palaeontologists a first-hand source of ecological information. Despite of this, information about such traces is not commonly reported in studies of modern biota. However, in the specific case of *Sulcichnus* neontologists have shown particular interest in identifying the trace and attributing it to examples from the fossil record (Zibrowius et al. 1975).

Fage (1936) was the first to describe these grooves on Recent Flabellidae, and he attributed them to the activity of the worm *Lumbrineris flabellicola* (Fage 1936) (Polychaeta: Eunicida: Lumbrineridae). Zibrowius et al. (1975) undertook the study of biotic relationships between *L. flabellicola* and various contemporary species of deep-water ahermatypic corals. However, they went a step further and attributed to this same annelid similar traces observed in numerous Neogene specimens, both via the literature and museum collections (see previous section). Given the small number of changes undergone by Polychaeta over time, Zibrowius et al. (1975) concluded that the same association currently observed between *Lumbrineris* and certain ahermatypic corals could be extended as far back as the Miocene.

In contemporary seas this association has been mainly, although not exclusively, observed on solitary skeletons of deep-water ahermatypic corals (azooxanthellates) (Fig. 5). Zibrowius et al. (1975) described this association on the basis

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of samples from the NE Atlantic, the SW Indian Ocean (South Africa), Madagascar, the China Sea and Japan. Samples were dredged at depths between 125 and up to 1,100 m. As observed by these authors, the eroding polychaete *L. flabellicola* inhabits a self-secreted membranous tube exteriorly attached to the host and causes a superficial to deep groove on the coral skeleton, a Recent equivalent of *Sulcichnus* being described here. Following the terminology of Taylor and Wilson (2002), *Lumbrineris* can be considered an episkeletozoan.

The worm seems to be almost eurytopic, following the distribution of its potential hosts. Thus, it has been detected as far afield as the Philippines, Japan, and the NE Atlantic. Zibrowius et al. (1975) report several Recent species that act as hosts for the worm, belonging to the genera *Caryophyllia*, *Flabellum*, *Rhizotrochus*, and *Balanophyllia* (all of which are solitary), as well as ahermatypic colonial species of the family Dendrophylliidae.

At present, the relationship established between *L. flabellicola* and the coral host is clearly obligatory and permanent for the worm (Zibrowius et al. 1975; Cairns and Zibrowius 1997; Martin and Britayev 1998). It may correspond to a case of parasitism (- +), commensalism (0 +), mutualism (+ +) or amensalism (00). In the former the relationship would be negative for the host, while the others would not. Studies on Recent material (Martin and Britayev 1998) strongly suggest a relationship based on commensalism. In the current specimens the anterior part of the worm is always found close to the calyx of the coral, and may even stretch beyond it. This would enable the eunicid to place its proboscis inside or around the mouth of the cnidarian and obtain food. It would then return to its tube (Miura and Shirayama 1992, Martin and Britayev 1998) with no detriment to the host. However, much remains to be known about symbiotic relationships between worms and other groups, and commensalism may have received undue emphasis.

Martin and Britayev (1998) described 292 species of commensal polychaetes belonging to 28 families. Therefore, commensals would be found in 31% of the known families of polychaetes. In addition, these authors state that majority of commensal polychaetes (67%) are obligatory symbionts, and among these, 59% are found exclusively on a single type of host. This figure rises to 87% when considering those which appear on two or three hosts. These data fit well with our observations in the fossil record.

Maeandropolydora and *Caulostrepsis* are mainly attributed to the activity of spionids (Polychaeta: Spionida: Spionidae), which infest a variety of skeletal and non-skeletal substrates. Among the most recent papers, Wielgus et al. (2002, 2006) report numerous genera of colonial corals infested and bored by spionid polychaetes in the Red Sea. Worms activity modify the colonial morphology in polluted water, thus acting as parasites. Rodrigues (2007) and Rodrigues et al. (2008) discuss the ecological significance of spionid traces from an example of infestation in Recent brachiopod shells. They conclude that these traces may represent either comensalism or parasitism, so further studies are needed to determine the dominant symbiotic interaction.

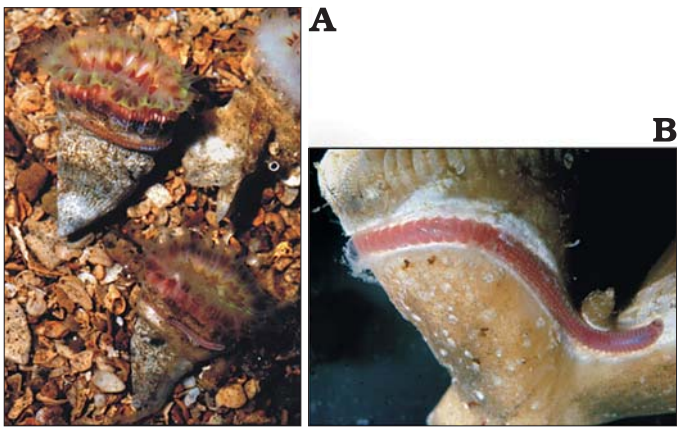


Fig. 5. Recent polychaete *Lumbrineris flabellicola* (Fage, 1936) infesting alive caryophyllids. Pictures by Alan and Eve Southward, from the Marine Biological Association, UK; reproduced with permission.

Discussion and concluding remarks

Although there are descriptions of symbiosis between Recent *L. flabellicola* and colonial corals, *Sulcichnus* has only been observed on solitary forms in the fossil record. To date, it has not been identified in colonial forms from the Mediterranean Neogene (ahermatypic or not), and no examples have been observed in the bibliography or in museum collections.

One notable aspect is that the skeletons of Neogene corals infested by what were probably eunicid polychaetes show no signs of the host having rejected or protected itself against the symbiont, as no overgrowths or deformation structures indicating a biological response from the host have been observed. This lack of skeletal response provides support to the actualistic hypothesis of a symbiotic relationship based on commensalism (Martin and Britayev 1998). In this case, the host would be neutral and the worm would be benefited: it would gain a substrate to live on, protection against possible predators (the coral's cnidoblasts would serve as a good defence), and a reliable place to obtain food.

It should also be noted that the Recent record of this worm-coral symbiosis is mostly found on deep-sea forms. However, the fossil specimens studied generally come from sediments considered as being of shallow water (the exception being those from the most northerly basins: Liguria and Alpes-Maritimes) origin. This suggests a possible shift on the environmental preferences of the ecological pair. Further actualistic and palaeontological studies are required to clarify this issue.

If we consider *Sulcichnus* within the field of the ethological classification of trace fossils, it should be included in the

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Fixichnia class (Gibert et al. 2004) as it represents an anchoring structure where the supposed membranous tube of the producer was fixed. It cannot be considered as a Domichnia, because traces of this class are cavities produced by endobionts, and *Sulcichnus* is actually an epigenic structure produced by an epieskeletozoan.

Seven scleractinian families and twelve genera have been identified in the main Pliocene basins of Western Mediterranean. From them, only four solitary genera (*Caryophyllia*, *Ceratotrochus*, *Trochocyathus*, and *Flabellum*) belonging to two families (Caryophyllidae and Flabellidae) exhibit these bioerosive grooves.

Sulcichnus has a quite variable morphology but three main models can be distinguished. Thus, three ichnoespecies have been described and nominated. Only *S. maeandriformis* appears in the four affected genera; *S. helicoidalis* is only present in three of them (all except *Trochocyathus*), and *S. sigillum* is restricted to two caryophyllids (*Caryophyllia* and *Trochocyathus*). In other words, the meandering model does not seems to be conditioned by the corallite morphology as it is present in the four basic skeleton morphologies, whereas the branding iron model was only developed in the morphologies with a clear circular section (conical and turbinate ones).

Finally, regarding the geographical distribution of *Sulcichnus* in the Western Mediterranean (Table 3), *S. maeandriformis* appears to be the most common and it is present in almost all the basins from Liguria (NE) to Estepona (SE). *S. helicoidalis* is not so constant, but it also occurs in both the northern and southernmost basins. *S. sigillum* has been only identified in Estepona.

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