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BIOEROSIVE STRUCTURES OF SCLEROZOAN FORAMINIFERA FROM THE LOWER PLIOCENE OF SOUTHERN SPAIN: A CONTRIBUTION TO THE PALAEOECOLOGY OF MARINE HARD SUBSTRATE COMMUNITIES

by A. SANTOS* *and* E. MAYORAL†

*Centro de Investigação Marinha e Ambiental, Faculdade Ciências do Mar e do Ambiente, Universidade do Algarve, Campus de Gambelas, 8000-139 Faro, Portugal; e-mail: aasantos@ualg.pt

†Departamento de Geodinámica y Paleontología, Facultad de Ciencias Experimentales, Universidad de Huelva, Campus de El Carmen, Av. de las Fuerzas Armadas s/n, 21071 Huelva, Spain; e-mail: mayoral@uhu.es

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Abstract: A palaeoecological study of sclerozoan foraminifera of the families Saccamminidae (aff. *Sagenina*), Lituolidae (*Placopsilina*), Cibicididae (*Cibicides*, *Dyocibicides*, *Cibicidella*) and Planorbulinidae (*Planorbulina* and *Planorbulinella*) that colonized epifaunal bivalves (ostreids and pectinids) during the early Pliocene in southern Spain has led to the recognition of two new boring ichnogenera: *Camarichnus* ichnogen. nov., with two ichnospecies, *C. subrectangularis* ichnosp. nov. and *C. arcuatus* ichnosp. nov., and *Canalichnus* ichnogen. nov., with one ichnospecies, *C. tenuis* ichnosp. nov. The first two ichnospecies were produced by adnate lituolids and cibicidids, the last by saccamminids. Their recognition is very important when quantifying populations of these organisms. Colonisation took place after death of the host bivalves, when they acted as very stable substrates whose topography probably controlled the initial settlement pattern of the foraminifera. The colonisation sequence started with the foraminifera (lituolids-saccamminids-cibicidids-planorbulinids) and was followed by vermetid gastropods, serpulids, spirorbids, cheilostome bryozoans and/or ostreids. Preferred orientations and overgrowth relationships between cheilostome bryozoans and serpulids have been detected in this material.

Key words: palaeoecology, encrusting foraminifera, bioerosion, trace fossils, Lower Pliocene, Spain.

BENTHIC foraminifera with encrusting habits are relatively abundant and well known, having been the subject of systematic (Adams 1962; Loeblich and Tappan 1964*a*, *b*; Wilson 1986) and ecological study (Langer 1993; Vénec-Peyré 1996). Their value as palaeobathymetric indicators and for determining the minimum exposure time of substrates on the sea-bed (Walker *et al.* 2001) has been demonstrated. They have also been studied with regard to establishing relationships between larval behaviour and the different topographic and hydrodynamic characteristics of the substrates that they encrust, which are almost always mollusc shells (Mayoral and Díaz-Estevez 1988) or bryozoan colonies (Zampi *et al.* 1997). Encrusting foraminifera (considered sclerozoans, *sensu* Taylor and Wilson 2003, i.e. animals colonising hard substrates) may also provide data for the study of possible competitive relationships, spatial distribution and orientation patterns, and ecological succession. Some of these foraminifera leave very characteristic marks on the substrate when they settle. These have hardly ever been mentioned in the literature, and have not been formally named as trace fossils. Santos and Mayoral (2003) made a preliminary study of the traces produced by encrusting foraminifera of the families Cibicididae and Planorbulinidae, in the lower Pliocene of southern Spain (Huelva and Málaga provinces), highlighting the palaeoichnological value of recognising these traces as well as the necessity of considering them formally as ichnotaxa. The aim of this paper is to present a palaeoecological study based on bivalve hard substrate communities, concentrating mainly on some encrusting foraminifera of the families Cibicididae, Planorbulinidae and Saccamminidae. Bioerosive structures resulting from their settlement are formally described for the first time, and their importance in palaeoecological studies is highlighted.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The material studied comes from Estepona (Malaga province), a village located on the Costa del Sol, southern Spain (Text-fig. 1A). The palaeontological site is located at a place known as Velerín pared, some 5 km north-east of Estepona (Text-fig. 1B). Rocks cropping out at Velerín pared belong to the upper part of the lower Pliocene, although they could extend up into the middle Pliocene (lower Piacenzian); they were included in the informal middle Pliocene unit of Guerra-Merchán *et al.* (2002) (Text-fig. 1C). This unit is 20–30 m thick and consists of two stratigraphic intervals. The material considered herein comes from the lower interval, which consists of 10–20 m of varying thicknesses of conglomerate, coarse-grained sand and gravel deposited by debris flow processes. Conglomerates deposited by channelized, tractive flows are more frequent at the top of this lower interval, where beds of sand become increasingly common. The upper stratigraphic interval (which is not considered further) is built up of metre-scale beds of cross-stratified sand with intense bioturbation and a very rich fossil content. The conglomeratic, lower stratigraphic interval contains the largest fossils, including a large number of bivalves (198 specimens) and gastropods (674 specimens) (J. L. Vera-Peláez, pers. comm. 2004), making this palaeontological site one of the most diverse in the Estepona Tertiary Basin (Vera-Peláez *et al.* 1995; Landau *et al.* 2003, Landau *et al.* 2004*a–c*). Bivalves (among which isognomonids, plicatulids, myids, pectinids, cardiids and ostreids dominate) are the group hosting the new bioerosive structures described in this paper. Epifaunal bivalves of the families Ostreidae and Pectinidae have been chosen because they are very abundant and representative of the fossil assemblage. Species of both families show clear indications of reworking and transportation, as well as a certain degree of abrasion (Lozano-Francisco *et al.* 1993; Vera-Peláez *et al.* 1995).

SYSTEMATIC PALAEOICHNOLOGY

All the material studied and illustrated here comes from the Velerín pared outcrop in Estepona, Málaga province (Spain) and belongs to the uppermost part of the lower Pliocene (Estepona Tertiary Basin), equivalent to the middle Pliocene unit of Guerra-Merchán *et al.* (2002). The material is housed in the palaeontological collections of the Geodynamics and Palaeontology Department of Huelva University, Spain.

Ichnogenus CAMARICHNUS ichnogen. nov.

Type ichnospecies. Camarichnus subrectangularis ichnosp. nov.

Derivation of name. Latin *camara*, chamber, cave, with reference to the origin of the trace.

Diagnosis. Very shallow depressions, slightly deeper in the central part, initially arranged in short, spiral series that either retain this pattern or develop into uniserial, more or less straight paths. Depressions subrounded in outline initially, and subrectangular to oval-arched in later stages. Outline marked by a very fine, shallow furrow. Depression interior is unornamented.

Remarks. Camarichnus ichnogen. nov. is quite markedly different from other ichnogenera such as *Leptichnus* Taylor *et al.*, 1999, *Podichnus* Bromley and Surlyk, 1973 and *Renichnus* Mayoral, 1987, which all form clusters of small pits in calcareous hard substrata. The groups of shallow pits of *Leptichnus* are subcircular, elongate or teardrop-shaped and all enter the substratum perpendicularly, whereas circular pits of *Podichnus* are centrifugally arranged, with some pits entering the substratum perpendicularly and others at oblique angles. On the other hand, *Renichnus* comprises kidney-shaped depressions in the form of a half moon, disposed in a crude row or coarsely coiled. In contrast, all the depressions of *C. arcuatus* are subrounded to subrectangular or oval-arched in outline and arranged in either spiral or uniserial series. The edges of the depressions exhibit a defined boundary consisting of a shallow, outer furrow, which is never observed in *Leptichnus* or *Podichnus*. A final difference between *Camarichnus* and these other ichnogenera is that the size attained by the former is substantially greater.

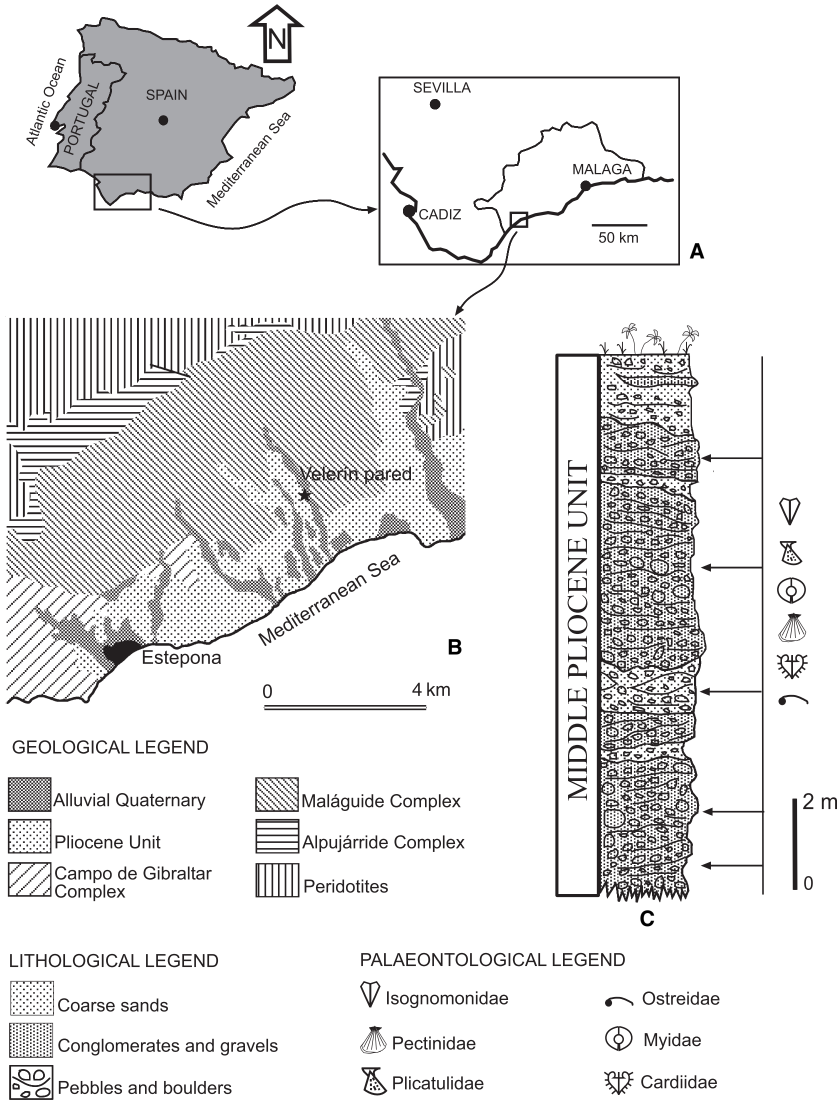
Camarichnus subrectangularis ichnosp. nov.
Plate 1, figures 3–6; Text-figure 2A

2003 Structure type 1, Santos and Mayoral; pp. A151–A152, fig. 2a.

Derivation of name. From subrectangular, alluding to the depressed outline.

Types. Holotype, VE/p/03/1 on fossil shells of *Ostrea* (*O.*) *edulis* Linné. Paratypes, VE/p/02/2, /03/2-4, /06, /20/1-7, /21/1-3, /23/1-9.

Diagnosis. Depressions subrectangular in outline during uniserial stage of development. Adjacent depressions



TEXT-FIG. 1. A, geographical location of the study area. B, geological map of the Estepona region (modified after Guerra-Merchán *et al.* 2002). C, simplified lithological log of the Velerín pared section.

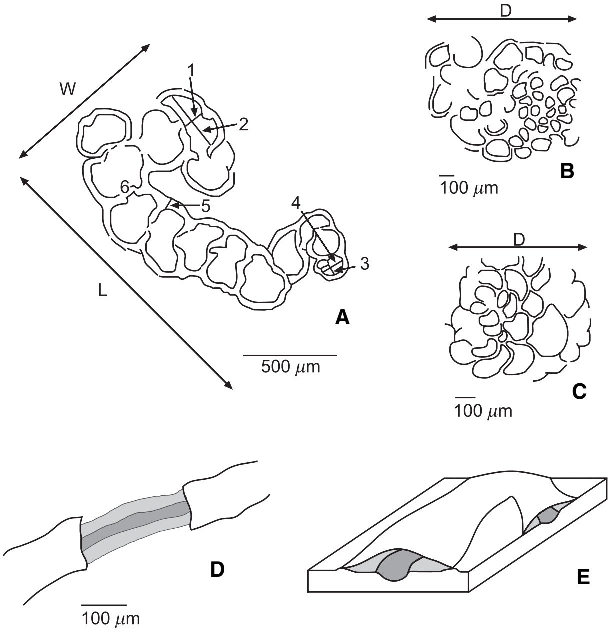
communicate through a very shallow, short but wide furrow located at centre of contact zone.

Description. Elongate in overall shape. In the very short initial stage (composed of a maximum of five depressions), depressions are subrounded and/or oval in outline and show a spiral arrangement (Text-fig. 2A; Pl. 1, figs 1–2). The latter stage (composed of 7–16 depressions, with a mean of 11) is uniserial, forms either a straight or a curved path, with depressions subrectangular in outline that progressively increase in size towards the end of the trace (Text-fig. 2A; Pl. 1, figs 1–3). The length of the uniserial stage ranges between 9 and 30 mm, averaging 18 mm. All depressions are wider than long, having a length/width ratio of 1 : 1·6. Width values vary from 0·1–0·2 mm for the smallest depressions to 0·1–0·4 mm for the largest. Depression length varies from 0·1–0·4 mm in the smallest to 0·1–0·6 mm in the largest examples. Depressions show no internal ornamentation and only communicate with one another through a very shallow, short and relatively wide furrow located in the centre of the contact zone and perpendicular to it (Pl. 1, figs 4–5). The width of this furrow is always less than 0·1 mm, ranging between 44 and 90 μm, with an average of 60 μm. The edges of the depressions are marked by a very shallow, outer furrow (Text-fig. 2A; Pl. 1, figs 5–6) having a maximum width of 0·1 mm, although normally narrower and ranging between 27 and 69 μm with an average of 46 μm.

Stratigraphical range. Lower Pliocene–Recent.

Camarichnus arcuatus ichnosp. nov.
Plate 1, figures 7–8; Plate 2, figures 1–4; Text-figure 2B–C

Derivation of name. Latin *arcus*, arco, alluding to the curved shape of the depressions.



TEXT-FIG. 2. A, sketch of *Camarichnus subrectangularis* ichnosp. nov. L, length; W, width; 1–2, minimum and maximum diameter of the largest depression; 3–4, the same for the smallest depression; 5, width of the exterior furrow; 6, width of the interior central furrow. B–C, *Camarichnus arcuatus* ichnosp. nov. D–E, *Canalichnus tenuis* ichnosp. nov. indicated in grey; dark grey, central, deepest furrow.

Types. Holotype, VE/p/02/1. Paratypes, VE/p/20/8, /21/4-6, /23/10, /23/11.

Diagnosis. Spiral and/or annular arrangement of depressions showing a characteristic arched or suboval outline. Furrows connecting depressions absent.

Description. Depressions either spiral or spiral-annular in arrangement (Text-fig. 2B–C, Pl. 1, figs 7–8). This makes the trace appear as more or less circular, isolated groups of depressions with a total diameter between 4 and 10 mm. During the initial stages, depressions are consistently arranged in spirals and show a subcircular outline. In later stages, they develop a very characteristic arched or suboval outline (Pl. 2, figs 1–4), and their arrangement either remains spiral or changes into annular. The centres of the depressions are deeper than the outer parts (Pl. 2, figs 3–4). Depression width varies from less than 0·1 to 0·1 mm in the smaller ones, and from 0·1 to 0·3 mm in the larger. In some instances, a very shallow and often indistinct, outer furrow is present, ranging from 40 to 60 µm in width.

Remarks. The spiral or spiral-annular arrangement of depressions distinguishes *C. arcuatus* from *C. subrectangularis* in which the depressions are in a uniserial series.

Stratigraphical range. Lower Pliocene–Recent.

Ichnogenus CANALICHNUS ichnogen. nov.

Type ichnospecies. Canalichnus tenuis ichnosp. nov.

Derivation of name. Latin *canalis*, channel, alluding to the shape of the trace.

Diagnosis. Superficial, very shallow furrows, subtriangular in cross-section, organised into more or less isolated or parallel series that branch at acute angles.

Canalichnus tenuis ichnosp. nov.

Plate 2, figures 5–8; Text-figure 2D–E

Derivation of name. Latin *tenuis*, tenuous, delicate, referring to its aspect.

Types. Holotype, VE/p/03/5. Paratypes, VE/p/21/7, /23/11.

Diagnosis. Superficial furrows of more or less straight path, either occurring in isolation or in dense populations. In both cases the furrows are distinct, although very shallow. Ichnospecimens in dense groups branch in

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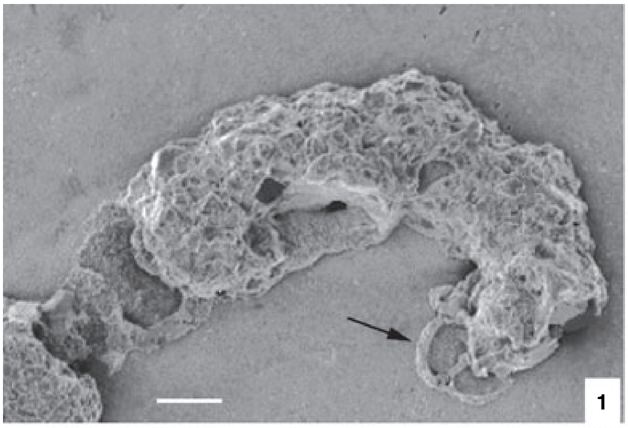
EXPLANATION OF PLATE 1

Figs 1–2. Arenaceous *Placopsilina*, the producer of *Camarichnus subrectangularis*, at different stages of conservation. 1, VE/p20/5, basal remnants of *Placopsilina* test partially eroded; black arrow shows the coiled early stage. 2, VE/p06, basal remnants of *Placopsilina* test eroded; white arrows shows incipient *Camarichnus subrectangularis*; black arrow shows the coiled early stage. Scale bars represent 500 µm in 1; 100 µm in 2.

Figs 3–6. *Camarichnus subrectangularis* ichnosp. nov. VE/p03/1, holotype. 3, uniserial stage of significantly eroded *Placopsilina*. 4, enlargement of the rectangle in 3; right arrow points to the depression related with the chamber; left arrow points to the central interior furrow. 5–6, VE/p20/1, arrows show the lateral furrow. 6, enlargement of the rectangle in 5. Scale bars represent 100 µm in 3–4; 50 µm in 5–6.

Figs 7–8. *Camarichnus arcuatus* ichnosp. nov. 7, VE/p23/12; 8, VE/p23/13. Scale bars represent 100 µm.

PLATE 1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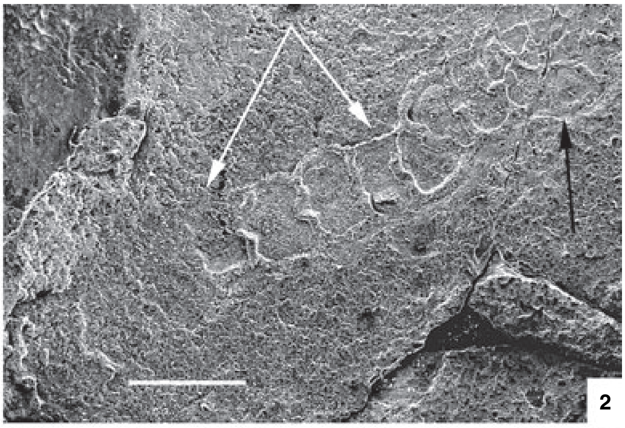
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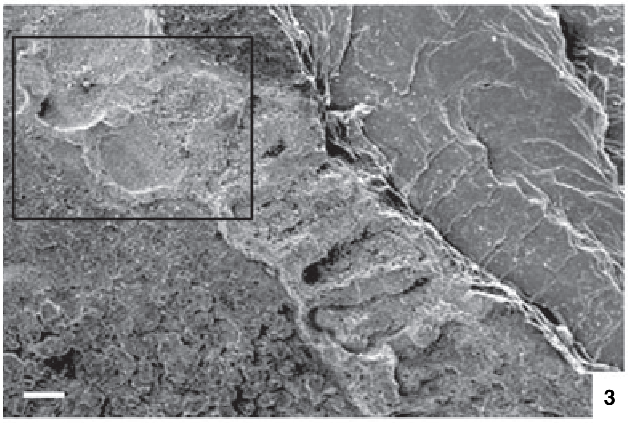
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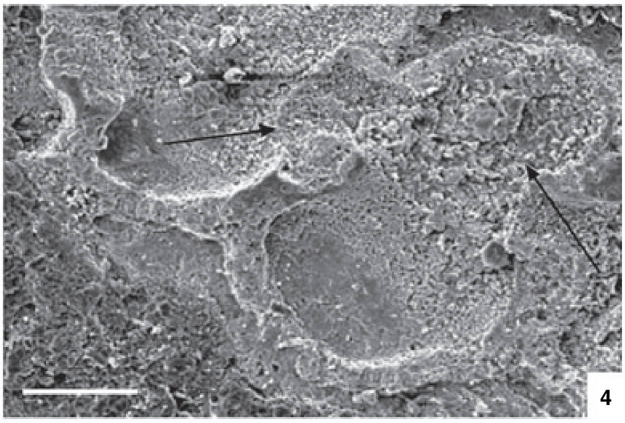
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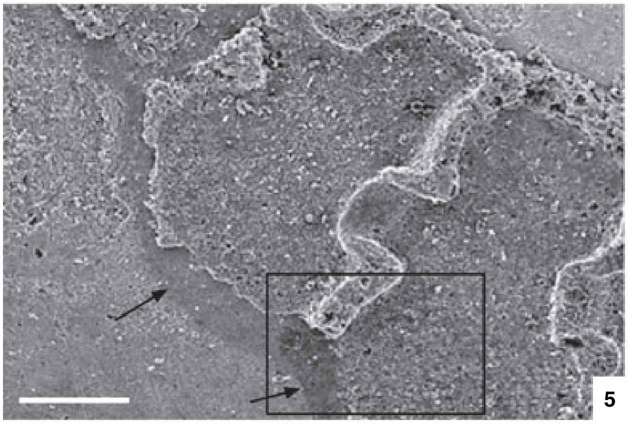
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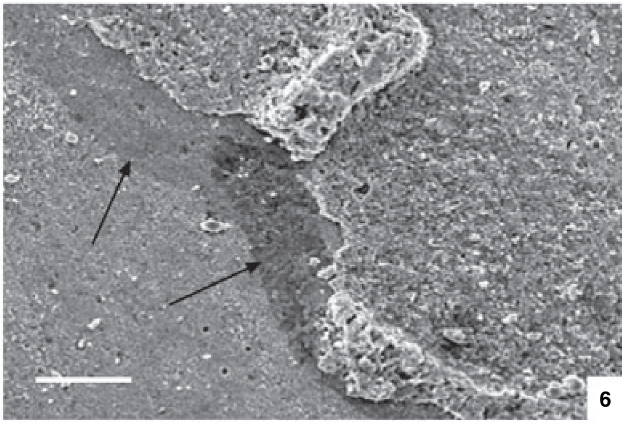
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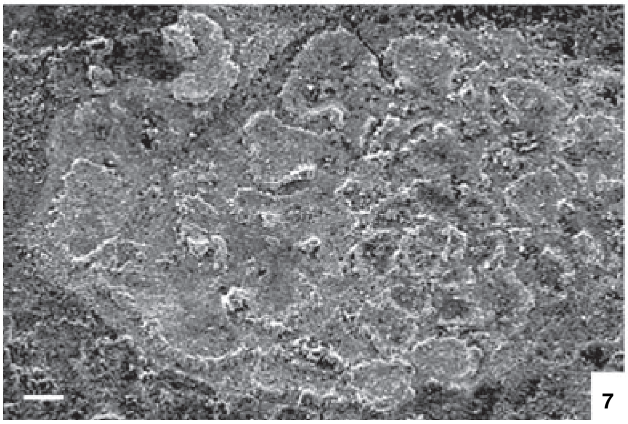
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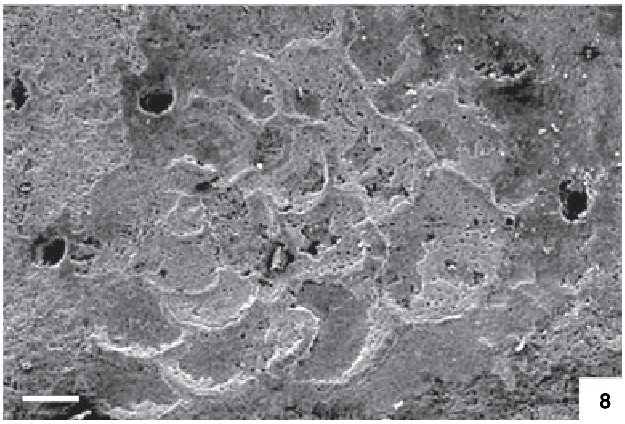
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SANTOS and MAYORAL, *Camarichnus*, *Placopsilina*

Y-shaped patterns; isolated examples branch at acute, almost orthogonal angles (Pl. 2, figs 7–8).

Description. C. tenuis is most easily identified by the calcareous remains of the tubular shell of the producers, which are often preserved. When shell remains are absent, the path of the trace is defined by one or several shallow furrows that smooth out the microtopography of the substrate, erasing any surface ornamentation (Pl. 2, figs 7–8). Furrow width ranges from 26 to 40 μm and their depth scarcely reaches 2 μm. Uneroded marginal areas are parallel to each side of the furrow; the width of these areas is usually greater than the furrow itself, ranging from 20 to 66 μm (Text-fig. 2D–E; Pl. 2, figs 5–6).

Where ichnospecimen density is relatively high (Pl. 2, fig. 5), the furrows branch at acute angles between 40 and 45 degrees and are organised into more or less parallel series. When density is much lower, furrows branch off at almost orthogonal angles (Pl. 2, figs 7–8).

Stratigraphical range. Lower Pliocene–Recent.

DISCUSSION AND INTERPRETATION

The origins of the bioerosive structures described here are not problematic because they are closely associated with their producers. Thus, *Camarichnus* is linked with encrustation by orbitoid foraminifera of the families Lituolidae, Cibicididae and Planorbulinidae. More precisely, *C. subrectangularis* is a trace left by different species of the genera *Placopsilina*, *Cibicidella* and *Dyocibicides*, while *C. arcuatus* was produced by Cibicididae (*Cibicides*, *Cibicidella*) and Planorbulinidae, certainly by *Planorbulinella* and *Planorbulina*.

On the other hand, interpretation of the producer of *Canalichnus tenuis* is more uncertain. The morphology of shell remains attached to specimens of *C. tenuis* is identical to the textulariid foraminifera *Sagenina* within the family Saccamminidae. However, *Sagenina* has a micro-agglutinated test whereas the shell remains here are calcareous, imperforate, and show fibrous or prismatic structure. For this reason, we refer to the producer as aff. *Sagenina* until a more precise systematic determination is possible. In both cases, the possibility that at least some of these structures are artefacts related to erosion and pressure solution (Lescinsky and Benninger 1994) is rejected due to their preservational state.

PALAEOECOLOGICAL CONSIDERATIONS

The presence of encrusting organisms on skeletal remains is very common in Cenozoic rocks, but as Taylor and Wilson (2003) pointed out, published studies are surprisingly scarce. In particular, encrusting foraminifera are seldom mentioned in the literature (Adams 1962, middle Eocene of Hauteville and Frésville, France; Mayoral and Díaz Estévez 1988, lower Pliocene of Huelva, Spain; Santos *et al.* 2003, lower Pliocene of Málaga, Spain). Thus, very little is known about recruitment pattern and post-larval development of these organisms and, of course, also about the traces produced in the substrates as a result of their activities. As a consequence of taphonomic processes (especially during biostratinomy), encrusting foraminifera can easily become free from the substrates on which they were fixed, and also be destroyed mechanically or chemically (through dissolution) due to the fragility of their tests. For this reason, trace fossils are often the only evidence for the past existence of encrusting foraminifera.

Hence the bioerosive structures identified in this paper are of palaeoecological value: they can be used in the determination and quantification of populations of encrusting foraminifera. If we quantify encrusting foraminiferan populations on ostreid and pectinid substrates (Text-fig. 3A) taking into account the ichnogenera *Camarichnus* and *Canalichnus* and ignoring them, the difference can reach 14 per cent (Text-fig. 3B).

Spatial distribution

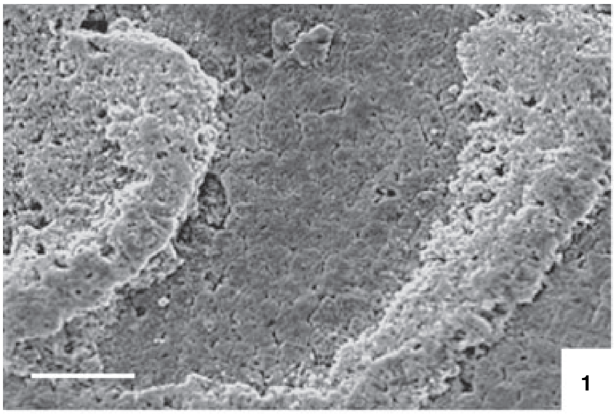
In order to investigate the spatial distribution of encrusting foraminifera, a total of 77 valves of *Ostrea* (*O.*) *edulis*

EXPLANATION OF PLATE 2

Figs 1–4. *Camarichnus arcuatus* ichnosp. nov. 1, VE/p23/13, arcuate depression with remains of the *Planorbulinella* shell. 2–3, VE/p02/1, holotype; spiral arrangement of depressions (arrows) related to the encrustation of a *Cibicides* specimen. 3, detail of 2; arrows point to the depressions. 4, VE/p23/12, depressions partially recrystallized (arrows) corresponding to an early stage of the trace fossil. Scale bars represent 100 μm in 2; 50 μm in 1, 3–4.

Figs 5–8. *Canalichnus tenuis* ichnosp. nov. 5–6, VE/p03/5, holotype; trace fossil preserved together with shell remains of aff. *Sagenina*. 6, detail of 5; arrow shows the central furrow. 7–8, VE/p03/2, general view of *C. tenuis* aff. *Sagenina* pathway partially covered by a serpulid annelid. 8, detail of 7; shallow furrows are shown by the arrows. Scale bars represent 500 μm in 7; 100 μm in 5–6, 8.

PLATE 2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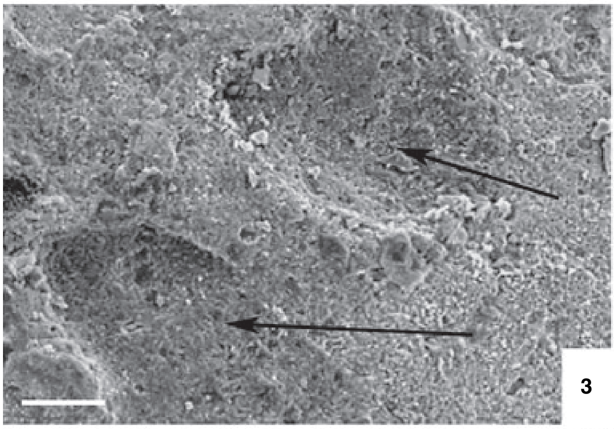
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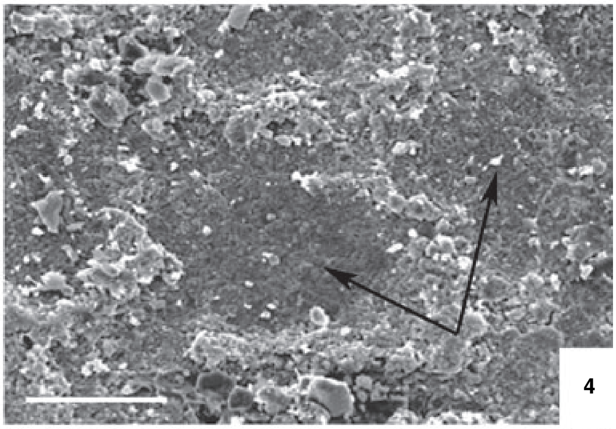
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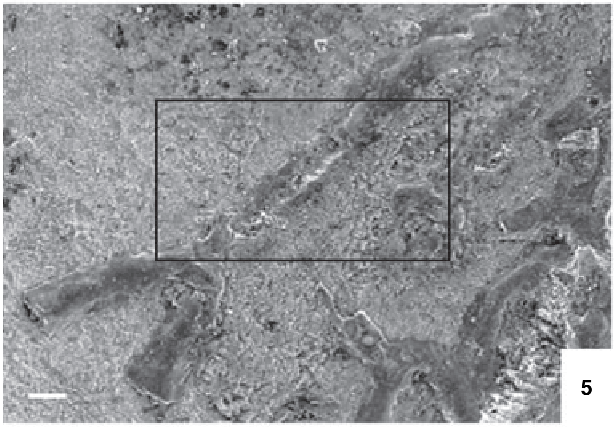
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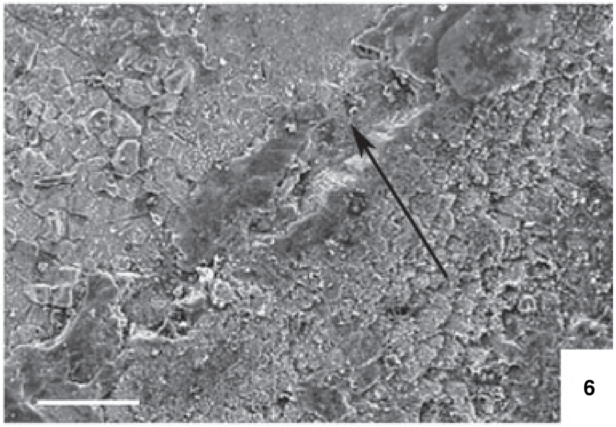
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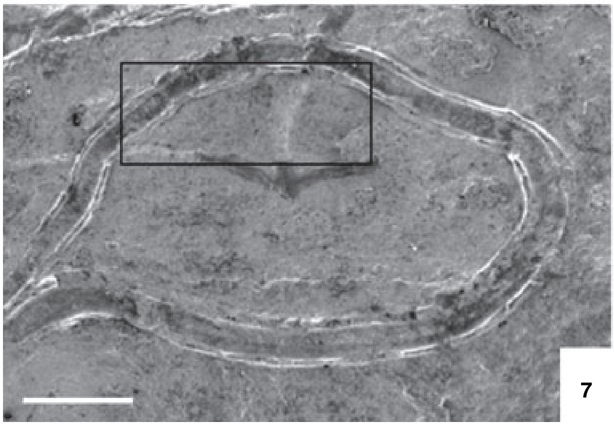
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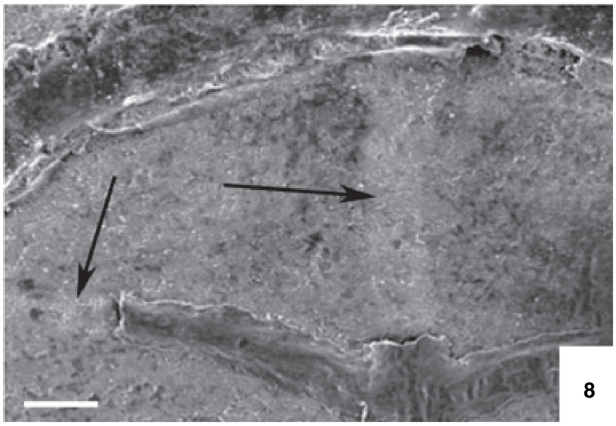
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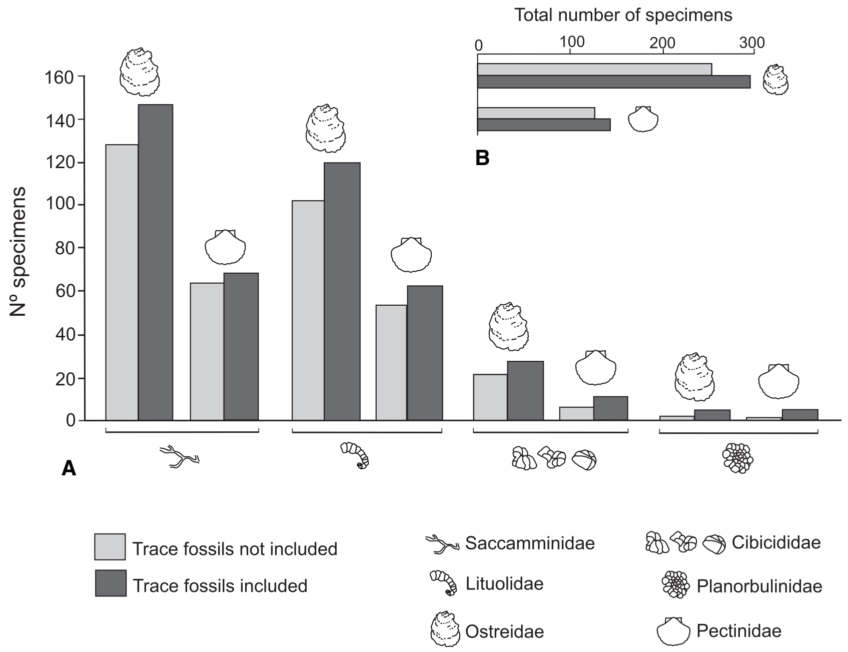
SANTOS and MAYORAL, *Camarichnus*, *Canalichnus*



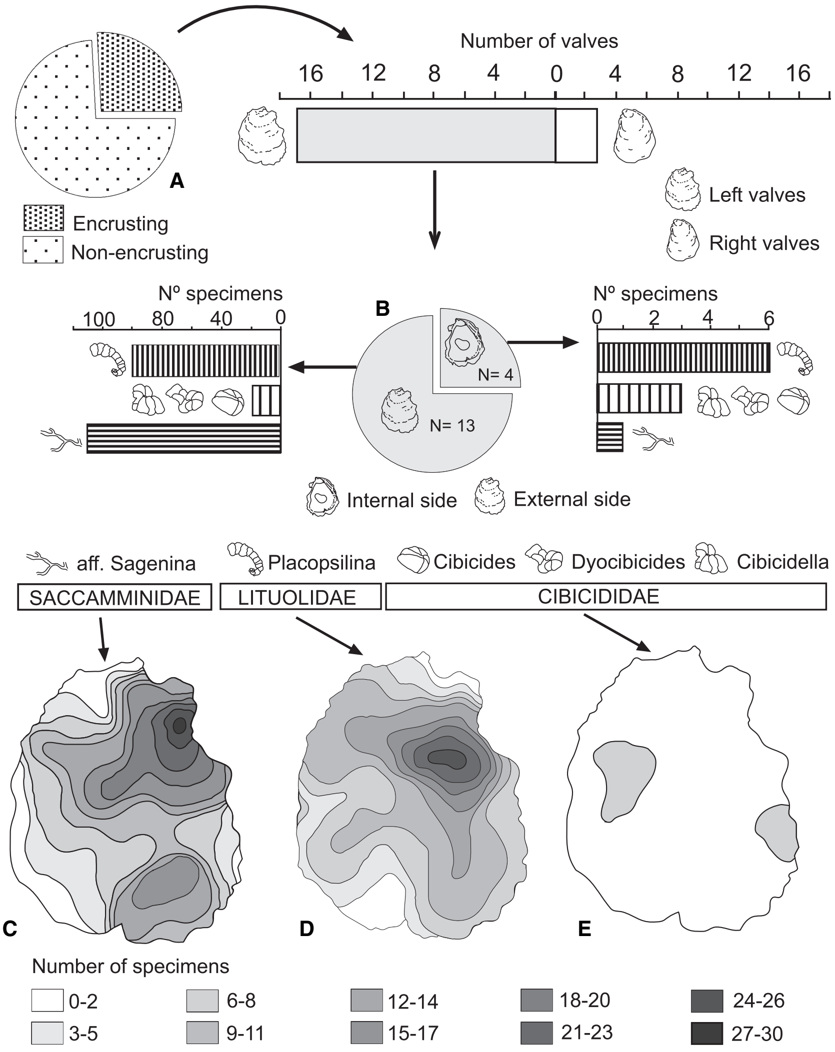
TEXT-FIG. 3. Comparison between population sizes of sclerozoan foraminifera with and without trace fossils considered. A, histograms for each family of foraminifera. B, histograms for the total number of foraminifera.

Linné, 1758, 30 valves of *Pecten* (*P.*) *jacobaeus* (Linné, 1758) and 27 valves of *Pecten* (*P.*) *benedictus* Lamarck, 1819 from the lower (conglomeratic) interval of the middle Pliocene unit of Guerra-Merchán *et al.* (2002) were studied. Contour diagrams were prepared to identify areas of highest foraminiferan density, and the areas of distribution of foraminifera in relationship to the pitch of the pectinid and ostreid shells.

Twenty (26 per cent) of the ostreid valves were encrusted, 17 left valves and three right valves (Text-fig. 4A). Right valves show only two examples of foraminiferal recruitment; thus, they were not considered in our analysis. Among the left valves, the external surface is colonised preferentially (76% of cases, 13 specimens), the internal surface less often (14% of the cases, four specimens) (Text-fig. 4B). The number of foraminiferan individuals is also substantially different, with a total of 233 individuals on the external surface and ten individuals on the internal surface. On the external surface, saccamminids (50%) dominate over lituolids (42%) and cibicidids (8%), whereas on the internal surface, lituolids are dominant (60%) over cibicidids (30%) and saccamminids (10%) (Text-fig. 4B). Planorbulinids have not been considered here because they are very scarce on both surfaces (< 2% of the total). Considering distribution and population density, saccamminids show two maxima, one on the posterior dorsal margin of the valves and the other on the posterior ventral margin (Text-fig. 4C); lituolids peak on the posterior, dorsal zone of the valves (Text-fig. 4D), and cibicidids next to the anterior and posterior margins (Text-fig. 4E), although this location is not very significant because there are only three individuals. (Planorbulinids were not analysed because there was only one individual.)

In order to analyse the relationship between population density and the pitch of the substrate, a standardised external side of a valve of *Ostrea edulis* was divided into three regions showing average pitch values of 10–20, 21–60 and > 60 degrees (Text-fig. 5A). Counting the total number of foraminifera, it was observed that the maximum (105 specimens) occupied the 21–60 degree pitch region, followed closely by the 10–20 degree region (100 specimens) (Text-fig. 5B). Maximum occupation is actually located very close to the maximum gradient zone (70–90 degrees), which usually coincides with the posterior, dorsal margin of the valves. Additionally, there are two relatively subsidiary regions of high density at 21–60 degrees, at the anterior, dorsal margin (next to the beak) and near the posterior, ventral margin (Text-fig. 5C).

For pectinid substrates, incidence of encrustation is similar to that of ostreids, with 25 per cent of the valves founded by encrusting foraminifera (Text-fig. 6A). Right valves host the majority of encrusting foraminiferans (13 valves) (Text-fig. 6B). Colonisation is confined almost entirely to the external surfaces of the valves (99% of cases); only one specimen has been observed with foraminiferans on the internal surface. Saccamminids (47% of cases, 57 specimens) and lituolids (46% of cases, 54 specimens) have a similar incidence whereas cibicidids are in the minority (7% of cases, eight specimens), repeating the pattern seen in ostreids (Text-fig. 6C–E).

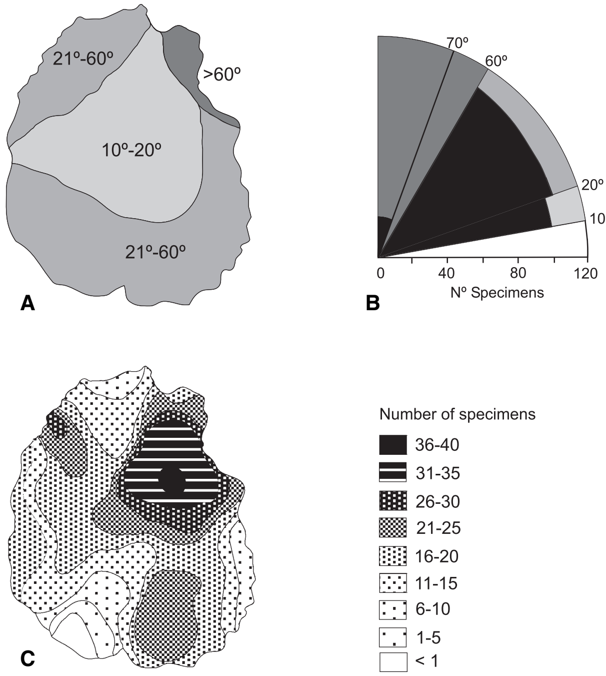


TEXT-FIG. 4. Distribution of sclerozoan foraminifera on Ostreidae. A, percentage of valves with encrusting foraminifera and their distribution between left and right valves. B, quantification of the three main families of foraminifera on the external/internal surfaces of the valves. C–E, contour diagrams showing the spatial distribution on the external left valves: C, Saccamminidae; D, Lituolidae; E, Cibicididae.

Regarding the pitch of the substrate, a standardized external surface of a valve of *Pecten* was divided into six regions showing average pitch values of < 5, 5–30, 31–40, 41–50, 51–60 and > 60 degrees (Text-fig. 7A). The greatest number of specimens (79) is located in the pitch region of 5–30 degrees (Text-fig. 7B), while the global maximum of occupation lies in the central, middle part of the shell (Text-fig. 7C).

Orientation

Generally, the foraminifera studied are randomly orientated, a pattern found frequently in sclerobionts (Taylor and Wilson 2003). Nevertheless, some foraminifera show preferred orientations that are basically controlled by substrate topography, such as radial costae in pectinids, and costae and irregular folds in ostreids. In this manner, saccamminids (and, to a lesser extent, other foraminifera) usually settled on intercostal areas in pectinids and, as a consequence, grew between the costae (Pl. 3, figs 1–2). They accommodate to the free space available, either by orientating their tests parallel or perpendicular to the valley; in the latter case specimens may be ‘compressed’ between two costae (Pl. 3, fig. 5). In other instances, orientation is controlled by the presence of sclerozoans that were there previously, such as serpulids, which restrict or limit the space available for settlement of foraminifera (Pl. 3, fig. 7). It is possible that the observed concentration of forams in intercostal areas of pectinid shells could be due to loss by abrasion (biological or physical) of those on the prominent costae. However, this argument is not supported because there is no evidence of any kind of abrasion on the prominent costae of the specimens studied.



TEXT-FIG. 5. Spatial distribution according to substrate topography in *Ostrea*. A, schematic division of a valve into gradient zones. B, number of foraminifera specimens occurring on each gradient zone. C, contour diagram showing the distribution on the valve of all specimens of foraminifera.

Competition and succession

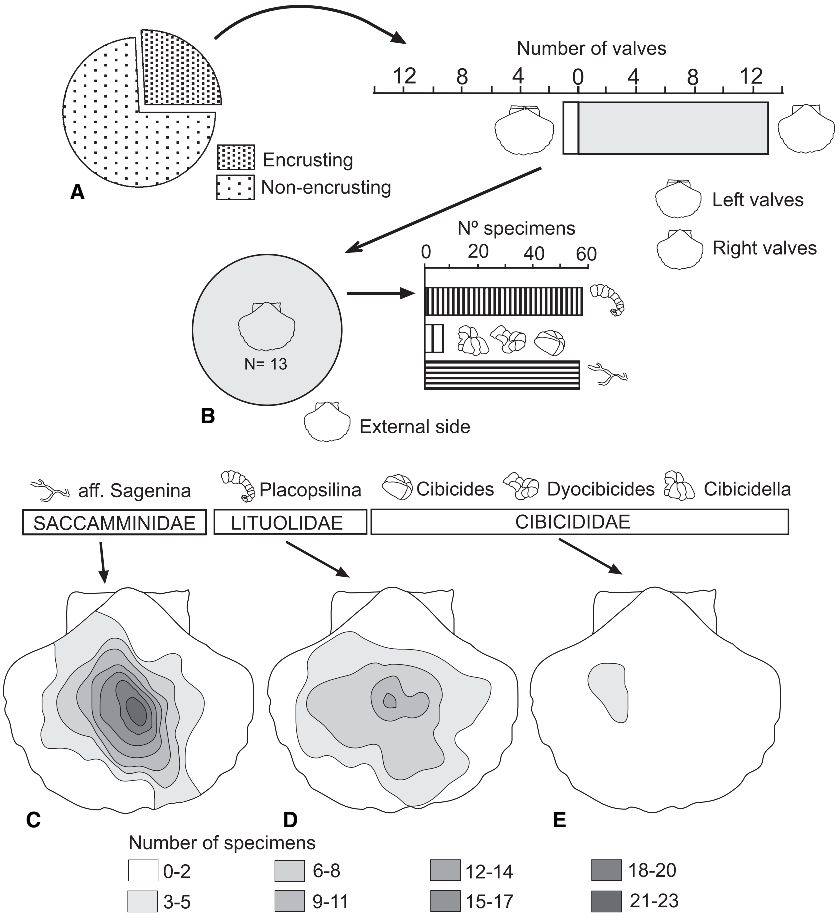
Encrusting organisms are a group of sclerobionts that permit, in many instances, inference of competitive relationships between individuals, as generally they occupy substrates that have important spatial restrictions. This gives rise to various patterns of spatial occupation, such as overlapping growth and changes in direction of growth. Thus, colonisation sequences can be recognised. The foraminifera in this study show a clear colonisation sequence, starting with pioneering establishment of lituolids (*Placopsilina*; Pl. 3, fig. 5), followed by saccamminids (aff. *Sagenina*; Pl. 3, fig. 3) and finally by cibicidids (*Cibicides*, *Dyocibicides*, *Cibicidella*; Pl. 3, fig. 2) and planorbulinids (*Planorbulinella* and *Planorbulina*). The fact that all of these occupy similar substrate space, together with evidence of individuals overgrowing others and adapting their growth to neighbouring foraminifera, may be indicative of competition during the life of the encrusting organisms. Other competitive relationships in this encrusting community are evident from reciprocal overgrowth of serpulid tubes and bryozoan colonies (Pl. 3, fig. 11).

Colonisation sequences on a larger scale (considering the entire encrusting biota, not only the foraminifera) are related to autogenic succession, given that sclerobionts (*sensu lato*) are always preserved *in situ* on the substrate on which they lived. Previous studies of such successions are relatively numerous, but concern Palaeozoic (Ager 1961; Wilson 1985) or Mesozoic (Bottjer 1982; Hattin and Hirt 1986; Rakús and Zitt 1993; Klikushin 1996) communities. For the Cenozoic, Mayoral and Reguant (1995) inferred several phases during the life and post-mortem colonisation of *Glycymeris insubrica*, an infaunal bivalve from the lower Pliocene of the southern Iberian Peninsula.

For the ostreid and pectinid bivalves studied here there is evidence of several colonisation episodes. As indicated above, the sequence always begins with foraminifera (following the order previously described) settling on the outer surfaces of the most convex parts of the valves, this location being related to maximum hydrodynamic stability. Clearly, colonisation took place post-mortem, after the valves were disarticulated. Larval settlement of foraminifera had to be controlled by substrate topography, with preference for areas protected from fast flow. For this reason, larvae colonised *Ostrea* in areas under the growth lines and costae, and other depressed areas, in regions of strong to moderate gradient. As for *Pecten*, larvae (especially the larvae of aff. *Sagenina*) colonised intercostal areas of low to moderate gradient, most probably related to the availability of free areas at the time of settlement.

This phase may not have been very long-lasting, as foraminifera usually show only minor evidence of bioerosion. Furthermore, the fact that foraminifera are almost never found on the inner surfaces of the valves may imply that these were totally or partially buried, convex-up, giving little chance for being inverted and colonised. In other instances, valves show signs of having been exposed on the sea-bed for a longer time, displaying numerous bioerosive ichnogenera (Pl. 3, fig. 12) such as *Entobia*, *Pinaceocladichnus*, *Maeandropolydora*, *Caulostrepsis*, *Gastrochaenolites* and *Oichnus*. During these later phases, the internal and external surfaces of the valves were colonised indiscriminately. The typical order of settlement of encrusting organisms in late stages began with vermetid gastropods (Pl. 3, figs 6–8), often above the pioneering foraminifera (especially aff. *Sagenina*; Pl. 3, fig. 9), preserved as shells or traces (*Renichnus*; Pl. 3, fig. 8). Annelids came later, almost always serpulids with spirorbids on top of them (Pl. 3, fig. 4). Either later or at the same time as annelids, colonies of cheilostome bryozoans developed, normally membraniporids (P. D. Taylor, pers. comm. 2004) (Pl. 3, fig. 11), together with ostreid (Pl. 3, fig. 4) or anomiid bivalves (Pl. 3, fig. 10).

TEXT-FIG. 6. Distribution of sclerozoan foraminifera on Pectinidae. A, percentage of valves with encrusting foraminifera and their distribution between left and right valves. B, quantification of the three main families of foraminifera on the external surface of the valves. C–E, contour diagrams showing the spatial distribution on the external right valves: C, Saccamminidae; D, Lituolidae; E, Cibicididae.



CONCLUSIONS

Our study of the record of sclerozoan organisms on epifaunal bivalves of the families Ostreidae and Pectinidae from the lower Pliocene of southern Spain focused mainly on encrusting foraminifera belonging to the families Saccamminidae, Lituolidae, Cibicididae and Planorbulinidae, and provides new information on bioerosion. It has been found that these organisms leave, as a result of their encrusting activity, a series of marks on the substrate surface that must be considered as true trace fossils. These traces are described here as *Camarichnus*, with two ichnospecies that are related to settlement processes of lituolids and cibicidids, and *Canalichnus*, with one ichnospecies related to the saccamminids. The importance of taking these trace fossils into account when quantifying the populations of encrusting foraminifera is highlighted. Substrate colonisation started with the settlement of encrusting foraminifera, first the lituolids, followed by the saccamminids and then by the cibicidids-planorbulinids. This occurred in one or more stages after death of the host ostreid or pectinid, when substrates underwent long-term exposure on the sea-bed under conditions of great stability. The highest level of colonisation occurred on external surfaces of the most convex valves. Larval settlement may have been controlled by substrate topography. On the ostreid shells, larval settlement took place under growth lines and costae, and on depressed areas of either strong or moderate gradient. In pectinids, it occurred over the intercostal areas of low to moderate gradient, giving rise to preferred orientations during the development and growth of populations.

The colonisation sequence was completed by the recruitment of vermetid gastropods, serpulids, spirorbids, cheilostome bryozoans and/or ostreids. Throughout this sequence, competitive overgrowth relationships between cheilostome bryozoans and serpulids can be detected.

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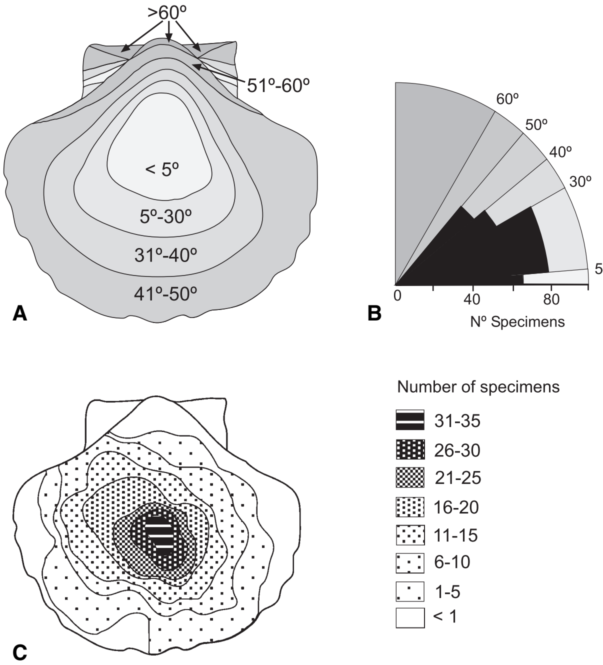

TEXT-FIG. 7. Spatial distribution according to substrate topography in *Pecten*. A, schematic division of a valve into gradient zones. B, number of foraminifera specimens occurring on each gradient zone. C, contour diagram showing the distribution on the valve of all specimens of foraminifera.

ment) contributed a grant to the Research Group RNM 316 ('Tectonics and Palaeontology') and to Project B023258SE29 BC, 'Palaeobiology of the Pliocene marine basins of Estepona, Málaga and Vélez-Málaga'. We thank P. D. Taylor and one anonymous reviewer for detailed reviews of the manuscript and valuable comments and suggestions that considerably improved this paper, and M. P. Smith and D. J. Batten for their editorial guidance and work.

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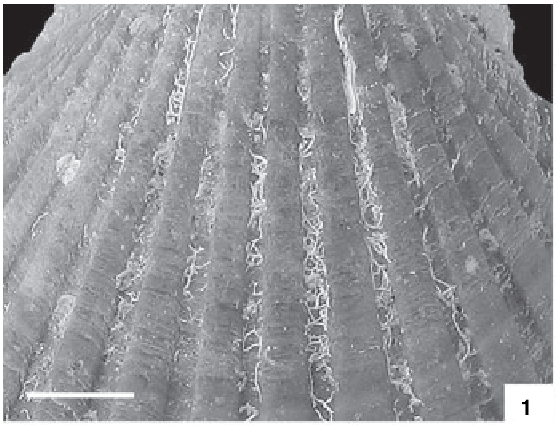
EXPLANATION OF PLATE 3

Figs 1–3, 5. VE/p300, *Pecten* (*P.*) *jacobaeus* (Linné, 1758) with sclerozoan foraminifera. 1, aff. *Sagenina* disposed along the intercostular zones. 2, detail of 1 with a *Cibicides* specimen superimposed above several shells of aff. *Sagenina*. 3, aff. *Sagenina* superimposed on a specimen of *Placopsilina*. 5, *Placopsilina* specimen compressed and adapted to the intercostular valley of a pectinid. Scale bars represent 1 cm in 1, 4; 1 mm in 2–3, 5.

Figs 4, 6–12. Different kinds of sclerozoans on *Ostrea* (*O.*) *edulis*. 4, VE/p02/2, *Ostrea* (*O.*) *edulis* Linné with an sclerozoan assemblage composed of serpulid and spirorbid annelids, cheilostome bryozoans and ostreids. 6, VE/p02/6, *Ostrea* (*O.*) *edulis* Linné colonised by vermetid gastropods and aff. *Sagenina*. 7, VE/p190, specimen of *Placopsilina* surrounded by a serpulid annelid. 8, VE/p22/1, vermetid gastropods (to the left) and their trace fossil *Renichnus arcuatus* Mayoral (to the right). 9, VE/p02/6, detail of 6, with vermetid gastropods superimposed on an assemblage of aff. *Sagenina*. 10, VE/p22/2, *Centrichnus eccentricus* Bromley and Martinell (centre) with serpulid and spirorbid annelids (top left). 11, VE/p13, reciprocal overgrowth between serpulid annelid and a colony of a membraniporid cheilostome (?*Acanthodesia*). 12, VE/p401, *Ostrea* (*O.*) *edulis* Linné highly bioeroded (*Entobia* ichnosp. indet). Scale bars represent 1 cm in 4, 11–12; 1 mm in 6–10.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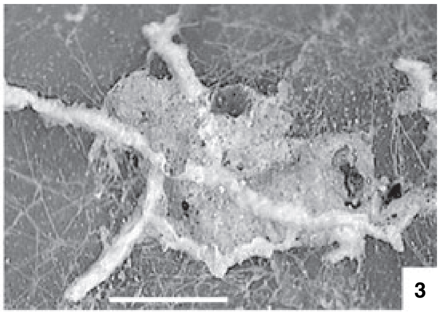
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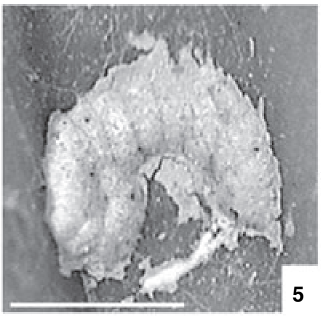
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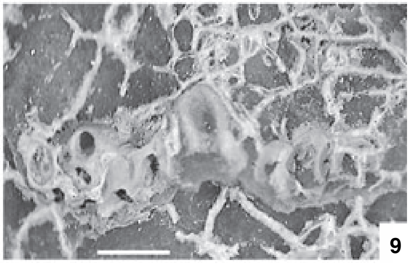
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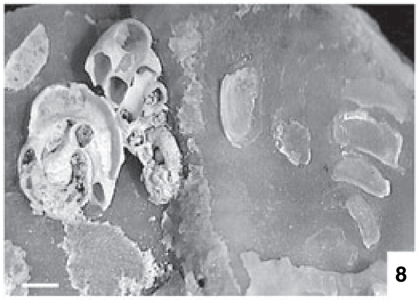
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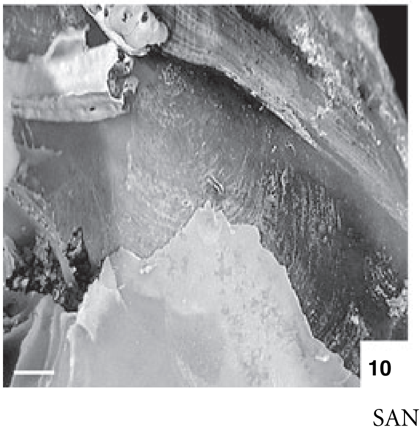
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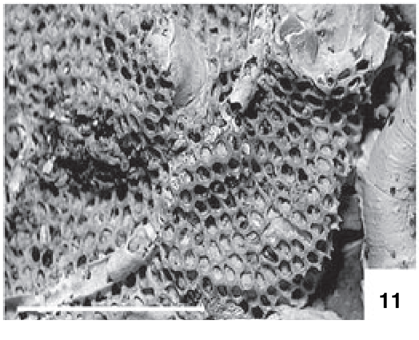
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