Palaeobiological and palaeonvironmental significance of the Pliocene trace fossil *Dactyloidites peniculus*

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The radial trace fossil *Dactyloidites peniculus* occurs in a deep tier in totally bioturbated shoreface sediments of Pliocene age in the Stirone Valley, N Italy, together with *Thalassinoides* isp. and *Ophiomorpha nodosa*. Long, narrow shafts running from centre of the radiating structure and abundant faecal pellets in the radial structure were discovered. The trace maker of *D. peniculus*, probably a polychaete, deposited the pellets deeply in the sediment, probably for reinforcement of the tubes and a gardening of microbes for feeding. This trace fossil exclusively occurs within a narrow horizon at the top of a shallowing-up section interpreted as a high-stand system tract, below a discontinuity surface capped by finer sediments. *D. peniculus* was formed in soft sandy sediments under stable conditions related to the latest phases of the high-stand system tract. Therefore, it is a candidate for indication of similar environmental situations having a soft sandy, but stable sea floor.

Key words: Trace fossils, *Dactyloidites*, gardening, sequence stratigraphy, marine flooding, foredeep, Neogene, Pliocene.

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Introduction

Dactyloidites peniculus, a radial trace fossil, has been described by D'Alessandro and Bromley (1986) from Pleistocene shallow marine sediments of southern Italy. New field observations of this trace fossil (second occurrence) from Late Pliocene sediments in Emilia Romagna, Italy, are reported in this study. This trace fossil occurs in a strictly defined horizon in a shallowing-up sequence, what implies a narrow ecological range. New morphological details, for instance a long vertical shaft or the presence of faecal pellets, and the palaeoenvironmental context shed new light on this poorly known ichnospecies. A morphological and palaeoenvironmental analysis of *D. peniculus* is the main aim of this paper.

The Stirone section was studied during campaigns in July and September 2005 and September 2006.

Institutional abbreviation.—INGUJ, Institute of Geological Sciences, Jagiellonian University, Krakow, Poland.

Geological setting

The Late Pliocene to early Pleistocene sediments in the Western Emilia Romagna (Parma and Piacenza provinces) were deposited in the northwestern extension of the palaeo-Adriatic Sea. They are part of the Po Plain-Adriatic Foredeep fill related to the Southern Alps and Apennines. The Late Pliocene sediments are interpreted as a regressive succession deposited in the transition from outer to inner shelf (Dominici 2001, 2004).

The Upper Pliocene–Lower Pleistocene sections along the Stirone river valley have been investigated since the sixties with regard to their sedimentology, palaeoecology, micropalaeontology, taphonomy and sequence stratigraphy (Pelosio 1960, 1964; Papani and Pelosio 1962; Pelosio and Raffi 1974, 1977; Iaccarino 1996; Mutti 1996; Molinari 1997; Mutti et al. 2000; Dominici 2001, 2004). However, there is not much information about ichnology, although Dominici (2001) mentioned some trace fossils.

The studied trace fossil occurs in the 48.8–51 m interval in the more than 75 m-thick Stirone section (Figs. 1, 2). This section can be subdivided in two units separated by a discontinuity at 51 m of the section. The lower part of the lower unit consists of very fine-grained sands and silty very fine-grained sands with intercalated layers containing molluscs, mainly bivalves in convex up orientation. The middle part of the unit displays similar grain sizes but is characterised by an increase of shell and plant debris. The upper part of the lower unit shows a slight coarsening and a decreasing silt content up to the discontinuity surface, which is covered by a thick silt interval (Fig. 3). Sediments below the discontinity are generally totally bioturbated, except for the upper part where a few layers show a primary lamination.

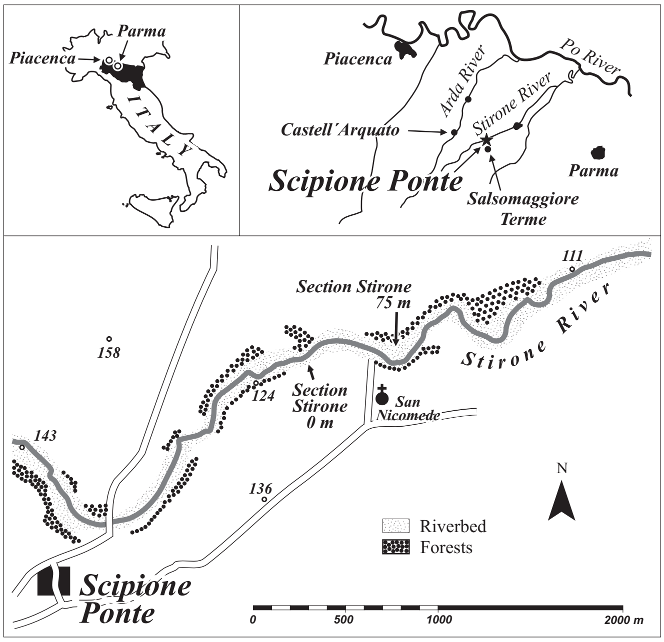


Fig. 1. Location of the study area in the Stirone river valley close to San Nicomede (Province of Parma, Italy). Arrows "Section Stirone 0 m" and "Section Stirone 75 m" point to the base and the top of the section shown in Fig. 2.

The interval with the trace fossil *Dactyloidites peniculus* (48.8–51.00 m) is exclusively composed of very fine, completely bioturbated sand. The deep-tier trace fossil *D. peniculus* is filled mainly with fine-grained pelleted material. *Ophiomorpha*, which occurs together with *Dactyloidites* displays a distinct wall, was produced in shifting sediment before formation of the discontinuity surface. The interval contains a *Thalassinoides* boxwork that reaches deep into the sediment below the discontinuity (Figs. 2, 3). The horizontal portions of *Thalassinoides* do not show any wall and they are only slightly compacted. These facts suggest that the *Thalassinoides* was produced in an already compacted sediment. It is very probable that the *Thalassinoides* boxwork was formed starting from the discontinuity surface. The boxwork was partially cemented during sedimentation of higher sediments. *Chlamys* layers, shell debris layers and a horizon with transported but well-preserved *Glycymeris* shells cover the discontinuity surface. More than 11 metres of overlying silt and sandy silt with *Pinna* characterize a rising sea-level of a new depositional sequence.

Systematic ichnology

Ichnogenus *Dactyloidites* Hall, 1866

Type ichnospecies: ?*Buthotrephis asteroides* Fitch, 1850; Lower Cambrian, New York State, USA.

Diagnosis.—Vertical radial spreiten structure having central shaft (Fürsich and Bromley 1985).

Remarks.—The ichnogenus *Dactyloidites* Hall, 1866 was reinterpreted by Fürsich and Bromley (1985). They included *Brooksella* Walcott, 1896 and *Haentzschelinia* Vialov, 1964 in this ichnogenus and recognized three ichnospecies of *Dactyloidites*: *D. asteroides* Fitch, 1850, *D. canyonensis* Bassler, 1941, *D. ottoi* (Geinitz, 1849). *D. peniculus* D'Alessandro and Bromley, 1986, and *D. cabanasi* (Meléndez in Cabanás, 1966) (see Gámez Vintaned et al. 2006 for the latter) were distinguished latter. Fürsich and Bromley (1985) interpreted *Dactyloidites* as a structure produced by worm-like organisms having a proboscis used for reworking sediment from a central shaft.

It seems that trace fossils described under *Dactyloidites* Hall, 1866 require a revision. First of all, the type material of the type ichnospecies (Lower Cambrian of New York State), which displays only a few rays of uneven width (see Häntzschel 1975: fig. W88.7), requires a revision, but this was never done. Vialov (1989) expressed his opinion that *Haentzschelinia* Vialov, 1964 should be excluded from *Dactyloidites* sensu Fürsich and Bromley (1985), foremost because of the fact that the radial elements of *Haentzschelinia*, in contrast to those of *Dactyloidites*, are numerous and of constant width. Vialov (1989) argued also that *Dactyloidites* is much larger and that its type material is confined to the Cambrian. Also Schweigert (1998) separated *Haentzschelinia* and *Dactyloidites* on the basis that *Dactyloidites* is a fully radial star-shaped trace fossil and *Haentzschelinia* forms commonly only a half or three quarters of a star. The diagnosis of *Dactyloidites* by Fürsich and Bromley (1985) accentuates spreiten, however in *D. peniculus* (see the diagnosis and description below) only spreite-like structures are present. It is not excluded that the diagnosis of *Dactyloidites* should be amended or *D. peniculus* should be ascribed to different ichnogenus. All these problems are, however, beyond the scope of this paper and cannot be resolved without re-evaluating the type material of *Dactyloidites*.

Dactyloidites peniculus D'Alessandro and Bromley, 1986

Figs. 4–6.

*1986 *Dactyloidites peniculus* isp. nov.; D'Alessandro and Bromley 1986: 79, pl. 12: 3; pl. 13: 3.

Amended diagnosis.—Simple, numerous and crowded cylindrical elements radiating laterally from a central shaft. They form a radial pile arranged in a part or full circle brush-like structure. The radial elements consist of tubes that can overlap and form spreite-like structures. The tubes can be lined and irregularly coated with pellets.

Material.—7 specimens, 5 thin sections, and numerous field observations documented by 88 photographs.

Description.—A radial structure, which appears as an oblate ellipsoid of revolution in outline. It is 82 to 270 mm wide (mean value 115.6 mm) and 42 to 120 mm high (mean value 77.3 mm). The radiating elements are thin, 4–5 mm thick, straight to curved, unbranched tubes. The tubes can coalesce, especially in their proximal parts (Figs. 4B, 5A). In vertical section, the tubes may overlap partially and appear as indistinct spreiten. The tubes run from the common centre. Some

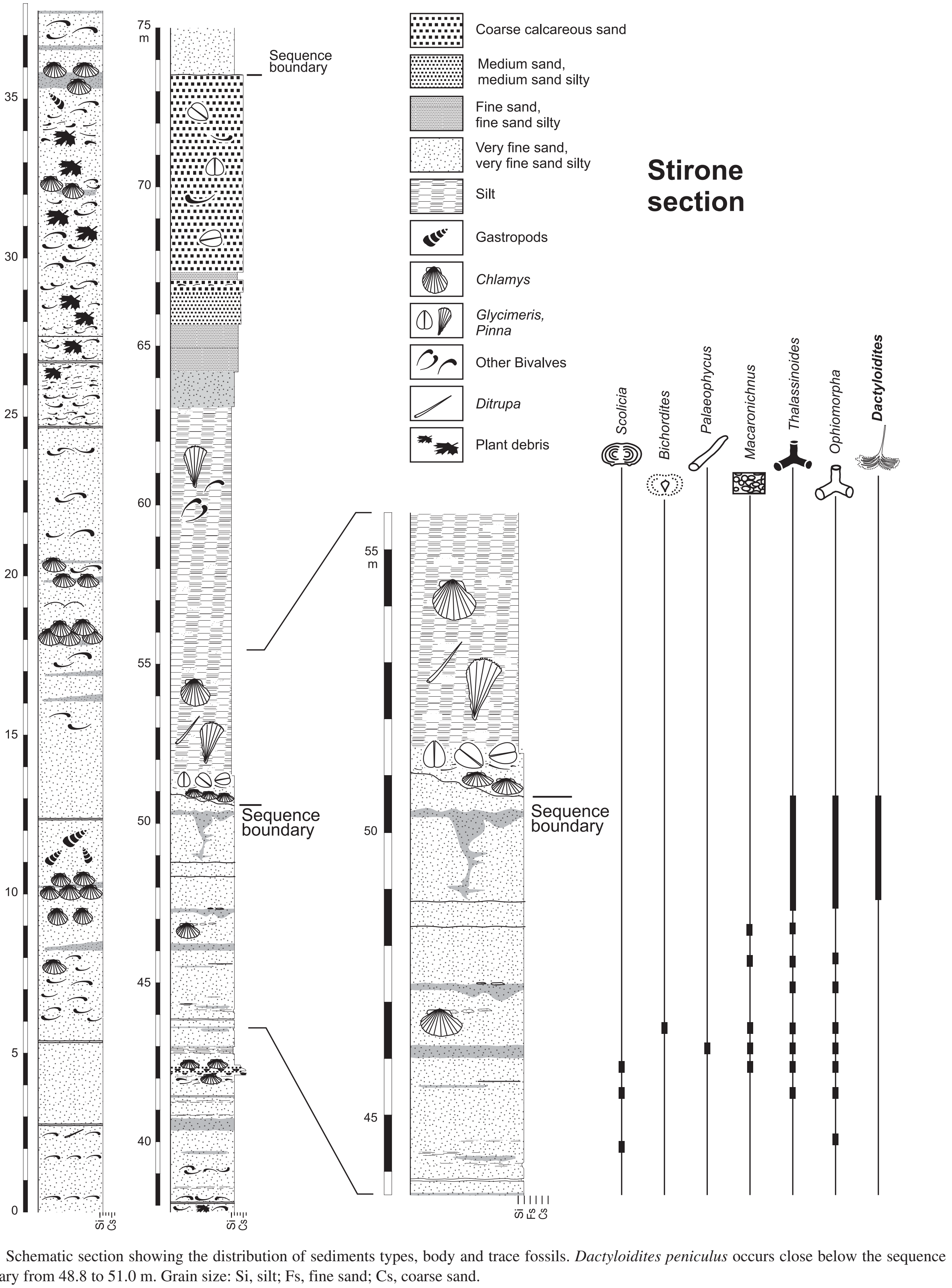


Fig. 2. Schematic section showing the distribution of sediments types, body and trace fossils. *Dactyloidites peniculus* occurs close below the sequence boundary from 48.8 to 51.0 m. Grain size: Si, silt; Fs, fine sand; Cs, coarse sand.

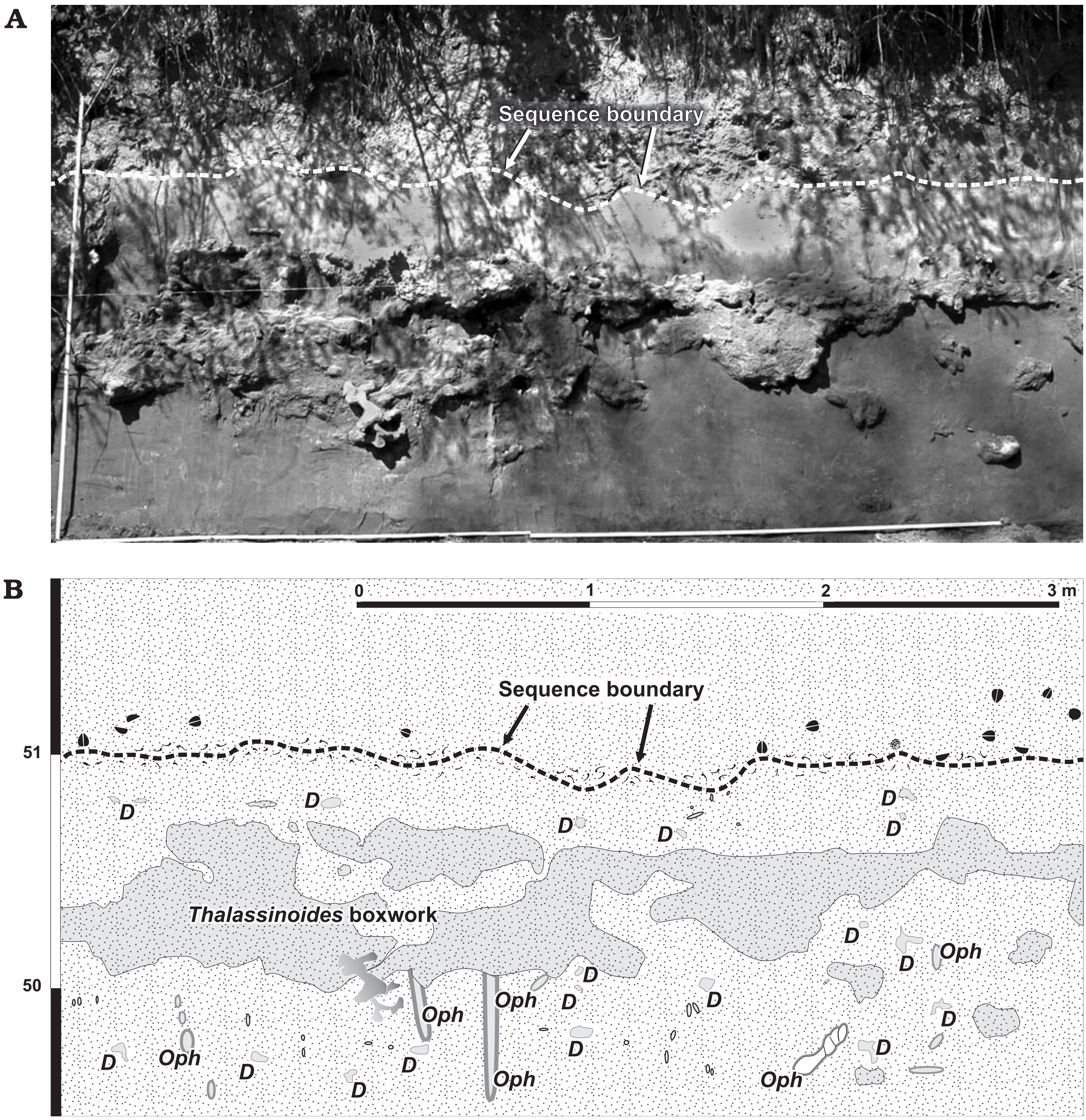
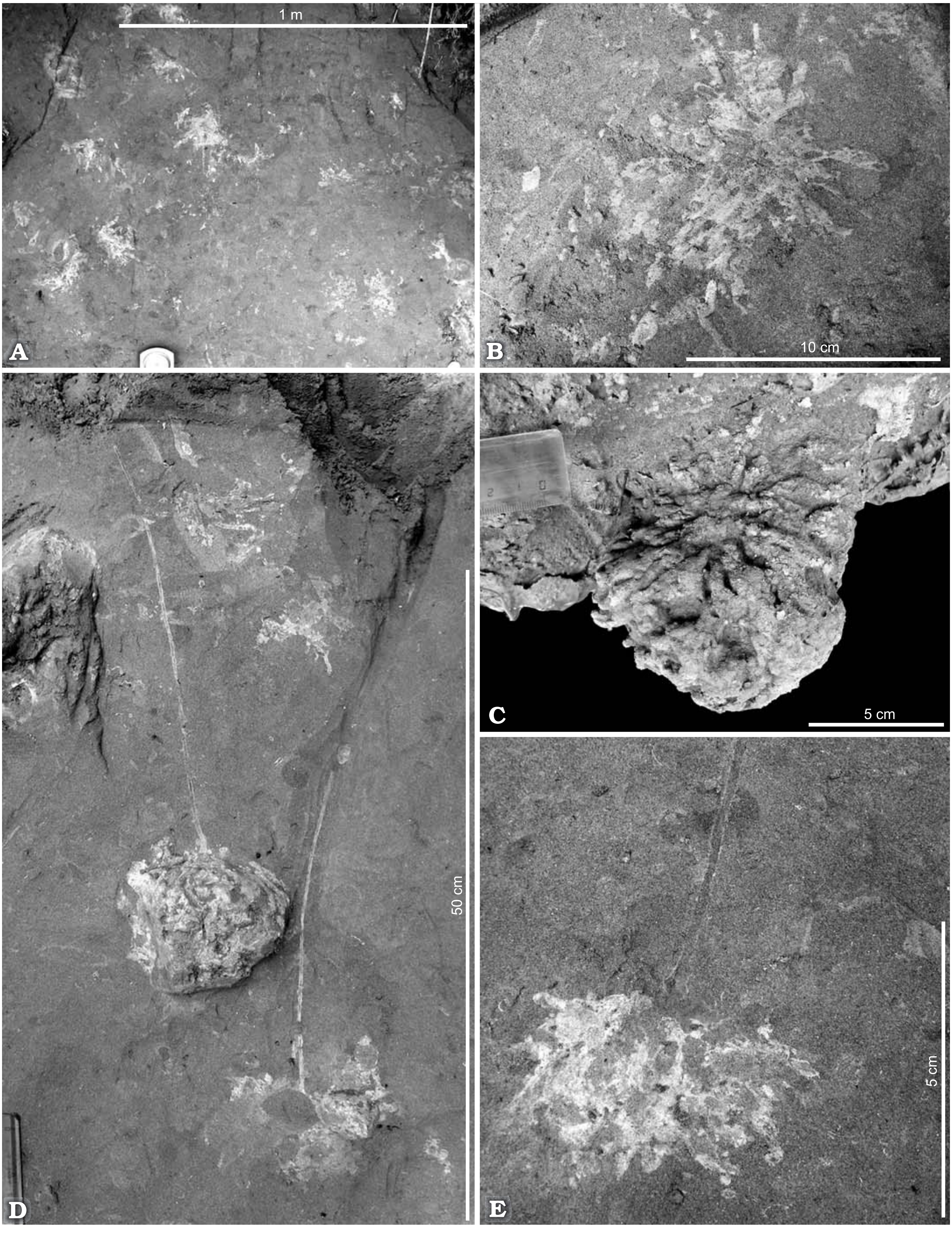


Fig. 3. Discontinuity surface. *Dactyloidites peniculus* (D) connected to the sequence boundary by steep shafts. *Ophiomorpha* (Oph) and *Dactyloidites* mutually cross-cut each other, whereas *Thalassinoides* (*Thalassinoides* boxwork) cross-cuts *Dactyloidites*. Field photograph (**A**) and its interpretation (**B**).

of them interpenetrate (Fig. 6A). Commonly more than 100 radial elements are present in one specimen.

The radial tubes are built of and lined with light-coloured siltstone material contrasting in grain size with the surrounding very fine-grained sand. They are coated and partly filled with the same material. The coating and the fill material displays a pelleted structure. Only some tubes are filled with fine-grained sand. Locally, the pelletal structure is not seen

Fig. 4. Field photographs of *Dactyloidites peniculus* in the range of 49 to 51 m of the Stirone section. **A**. Oblique view of a sub vertical section shows the distribution and frequency of this trace fossil. **B**. Horizontal section of a single *Dactyloidites peniculus* shows star like diverging tiny tubes. **C**. Oblique view of weathered *Dactyloidites peniculus* preserved *in situ*. **D**. Two examples of *Dactyloidites peniculus* with connected long, subvertical tubular shafts. **E**. Vertical section of *Dactyloidites peniculus* with connected shaft meeting the oblate ellipsoid at its highest central point. The thin, bright linings of the shaft contrast with the darker filling, and the surrounding sediment. →


1 m
A
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10 cm
C
5 cm
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E
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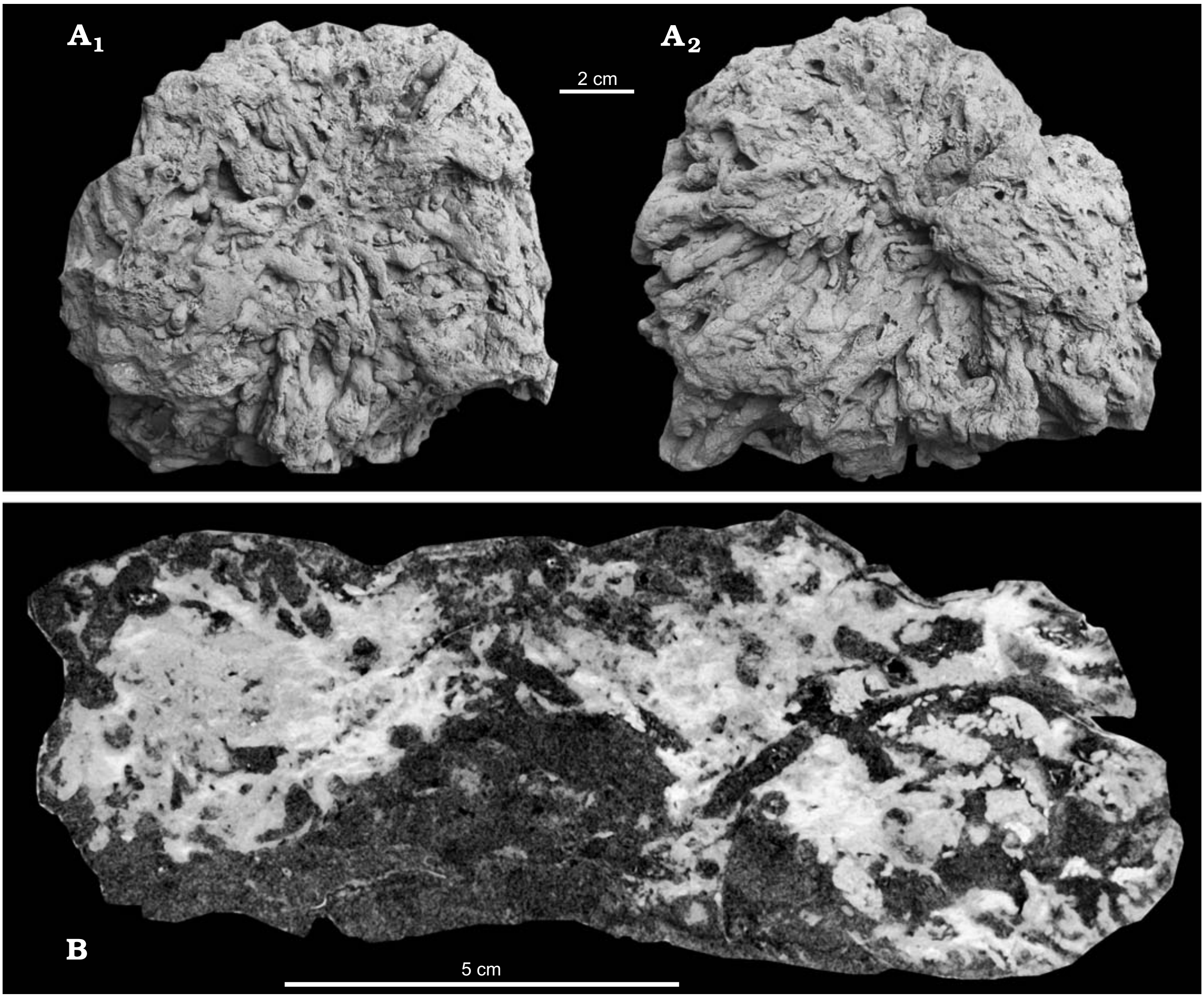

Fig. 5. The radial part of *Dactyloidites peniculus* after preparation. **A**. Specimen INGUJ 200P1 after sand jet preparation, in top (A_1) and bottom (A_2) views. **B**. Specimen INGUJ 200P4, extra large vertical thin section.

and a gradual transition from pelleted to massive fill structure or coating can be observed. Some pellets can be seen in thin sections (Fig. 5B), on polished surfaces (Fig. 6A, C) and on the surface after sand jet preparation (Fig. 6B). The pellets are 1.5–1.7 mm long and 0.5–0.7 mm wide, cylindrical in shape, with hemispherical terminations. The coatings can coalesce and form irregular clumps, which are up to 35 mm thick and 45 mm wide. The pellets are concentrically arranged around some tubes (Fig. 6A). Locally, the contact between pellets in the tubes is angular (Fig. 6C). The filling of tubes is locally meniscate (Fig. 6A).

Margins of the radial structure are commonly uneven and seem to be disturbed by burrowing animals other than the trace maker (Fig. 4A, B). The degree of destruction is variable. In the extreme situation only "ghosts" of the structure are visible. Some of the radial elements protrude beyond the structure. The marginal parts of the radiating elements have a tendency to be curved up. Some specimens are slightly concave in the central lower part and convex in the central top part. This part of the trace fossil is commonly preferentially cemented and it sticks out from a weathered rock as a ball (Fig. 4C).

A vertical or subvertical, straight to slightly curved shaft runs up from the central top part (Fig. 4D, E). The shaft was traced up for a distance of 410 mm but it is probably much longer. The shaft is 2 to 4 mm wide (outer dimension). It is thinly lined with silty material, similar to that found along the radial elements. The thickness of the lining ranges from 0.5 to 1.2 mm. Locally, the outer margin of the shaft is finely lobate in longitudinal section, what suggests its external surface could be pelleted.

Remarks.—The original diagnosis is as follows "A *Dactyloidites* having numerous, regular, symmetrically, radiating branches, themselves apparently unbranched and containing a limited retrusive spreite" (after D'Alessandro and Bromley

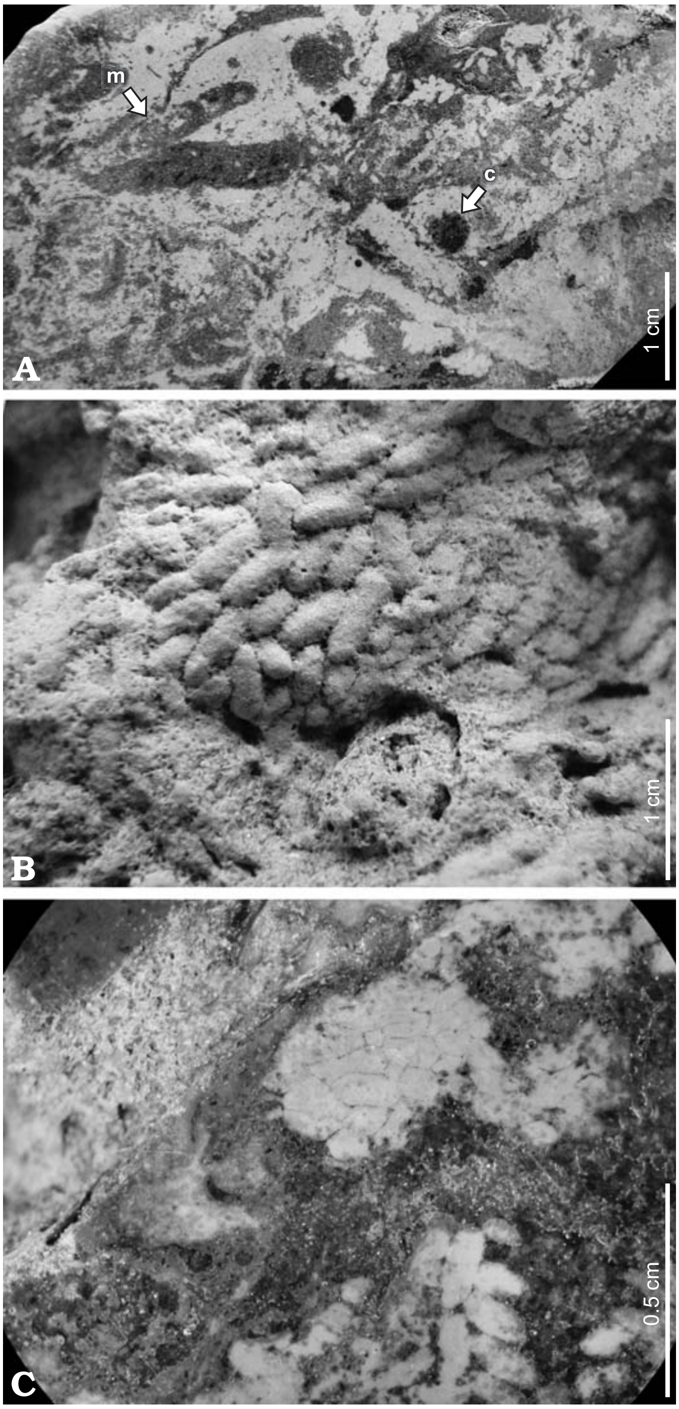

Fig. 6. Morphological details of *Dactyloidites peniculus*. **A**. Specimen INGUJ 200P2, vertical cross section of the radial structure showing light pelletal masses, tubes and dark sandy sediment; distinct coatings containing the pellets (c) are seen around some tubes. Some tubes display a meniscate fill structure (m). **B**. Specimen INGUJ 200P1, a clump of pellets on the surface of the radiating structure. **C**. Specimen INGUJ 200P3, compressed pellets in a tube showing angular contacts.

1986). In the amended diagnosis, the reference to *Dactyloidites*, taking in account problems of its type ichnospecies, is avoided. Moreover, a relation to the shaft and the presence of pellets is underlined.

Occurrence in the section and associated trace fossils

Approximately 500 *Dactyloidites peniculus* specimens can be observed in one cubic metre of sediment (compare Fig. 4A). The radial elements of *D. peniculus* occur in an about 120 cm-thick interval of the section. The topmost occurrence is just above a partially cemented *Thalassinoides* boxwork and below an uneven discontinuity surface, which probably marks a sequence boundary (Figs. 2, 3).

The surrounding sediment is totally reworked and commonly the radial structures are partially destroyed by the bioturbation. There are only three ichnogenera that co-occur in the same horizon with *D. peniculus*: *Thalassinoides* isp. boxworks and mazes of different size (from 7 to 45 mm in diameter), differently oriented, unbranched *Ophiomorpha nodosa* Lundgren, 1891 (inner diameter 12–21 mm; outer diameter 16–37 mm) and rare *Tursia* isp. (for this rare trace fossil see D'Alessandro and Fürsich 2005). Variable spatial relationships are observed among these trace fossils (Fig. 7). *Thalassinoides* and *Ophiomorpha* usually crosscut *D. peniculus*, although some *D. peniculus* cut *Ophiomorpha* and occupy part of the *Ophiomorpha* wall, i.e., they were formed after *Ophiomorpha*. *Tursia* isp. crosscuts *D. peniculus. D. peniculus* penetrates some large, tubular, poorly outlined trace fossils. There are no evidences that *D. peniculus* cuts through *Thalassinoides*.

Discussion

Palaeobiological aspects.—The central shaft in *Dactyloidites* is so far poorly documented in the literature except for the lowermost remnants, mostly in *D. ottoi* (Fürsich and Bromley 1985; Pickerill et al. 1993; Gibert et al. 1995). D'Alessandro and Bromley (1986) mentioned a short shaft in the *D. peniculus*, but their photograph (pl. 13: 3) shows only the lowermost part of the shaft. The examined Pliocene *D. peniculus* displays an at least 41 cm long shaft (Fig. 4D), which classify it as a deep-tier trace fossil. This is confirmed also by the fact that *D. peniculus* crosscuts deep-tier *Ophiomorpha nodosa* shafts. Thus, the radial part of *D. peniculus* was formed at a depth of at least about half a metre. Its occurrence in an about 120 cm thick layer suggests that have been several colonization surfaces. The crosscutting relationships with *Ophiomorpha* show that the trace makers of both trace fossils worked simultaneously.

The disturbances of *D. peniculus* by bioturbation suggest sediment reworking at a depth of at least about half a metre without discrete trace fossil record, except for *Ophiomorpha* and *Tursia*. Also these trace fossils have been disturbed by later bioturbation. Such a deep, intense bioturbation is expected in a low-energy shelf, what fits well to the protected palaeo-Adriatic Sea in the Po Plain area.

The presence of pellets is a new fact for *Dactyloidites*. The fine-grained (silt) material composing the pellets differs from the fine-grained surrounding sand and indicates a selective feeding of the animal. The large amounts of pellets actively placed at the walls of the radial elements and in their coatings is a very important element of *D. peniculus*. The angular contacts between pellets in some segments of the radial tubes are evidences of compression caused by the trace maker. Deposition of pellets deeply in the sediment is energetically costly and thus, it must have some biological significance. It is not excluded that the pellets were a compost for gardening of microbes deeply in the sediment below the redox boundary. The trace maker had contact with oxygenated water by the long shaft. Gardening could have been an additional food source to deposit feeding. Such behaviour is not unique among burrowers. It is supposed that the *Zoophycos* trace maker deposits its faecal pellets deeply in the sediment for further feeding (Bromley 1991; Bromley and Hanken 2003). Some polychaete worms, such as *Scolecolepis squamata* and *Pygospio elegans* (see Reise 1981) or *Polycirrus eximius* and *Tharyx acutus* (see Myers 1977) deposit their pellets deeply in the sediment. Also the deep-sea bivalve *Abra longicallus* (Scacchi) deposits faecal pellets in sediment around tunnels for a possible gardening (Allen 1983; Bromley 1996).

Palaeoenvironmental significance.—The restricted occurrence of *D. peniculus* within the section (Fig. 2) suggests a restricted environmental range for this trace fossil. The host sediment is very fine sand and almost totally bioturbated. The horizontal parts of the trace fossil *Thalassinoides* and vertical parts of *Ophiomorpha* and *Tursia* occur here. *Scolicia* and *Macaronichnus* are present in the 2 m thick interval of the underlying strata. Down the section, *Thalassinoides*, *Scolicia*, *Bichordites*, *Schaubcylindrichnus*, *Macaronichnus*, *Planolites*, *Palaeophycus*, and *Chondrites* occur. The entire trace fossil assemblage is typical of the *Cruziana* ichnofacies, what together with the ichnofabric features points to a lower or middle shoreface setting of the horizon with *D. peniculus* (see Pemberton et al. 2001).

Dactyloidites peniculus occurs below a discontinuity surface, which occurs 20–30 cm above the topmost occurrence of a 1.8 metres thick *Thalassinoides* boxwork capped by fine-grained sands and shell debris layers (Fig. 3). Horizons with *Chlamys* and transported but well-preserved *Glycymeris* shells mark an erosion surface probably representing a sequence boundary. The distinct decrease in grain size (silt) marks the marine flooding of a new sequence. It seems that *D. peniculus* occurs at the top of a high-stand system tract (Fig. 7) and it was produced together with *Ophiomorpha* and *Tursia* in soft sand. The sediment was slightly eroded sub-aquatically during the following lowering of sea level and an uneven discontinuity surface interpreted as a sequence boundary was formed (Fig. 7). There are no evidences of emersion, such as root traces, soils, soil concretions or continental deposits. The radial part of *Dactyloi-*

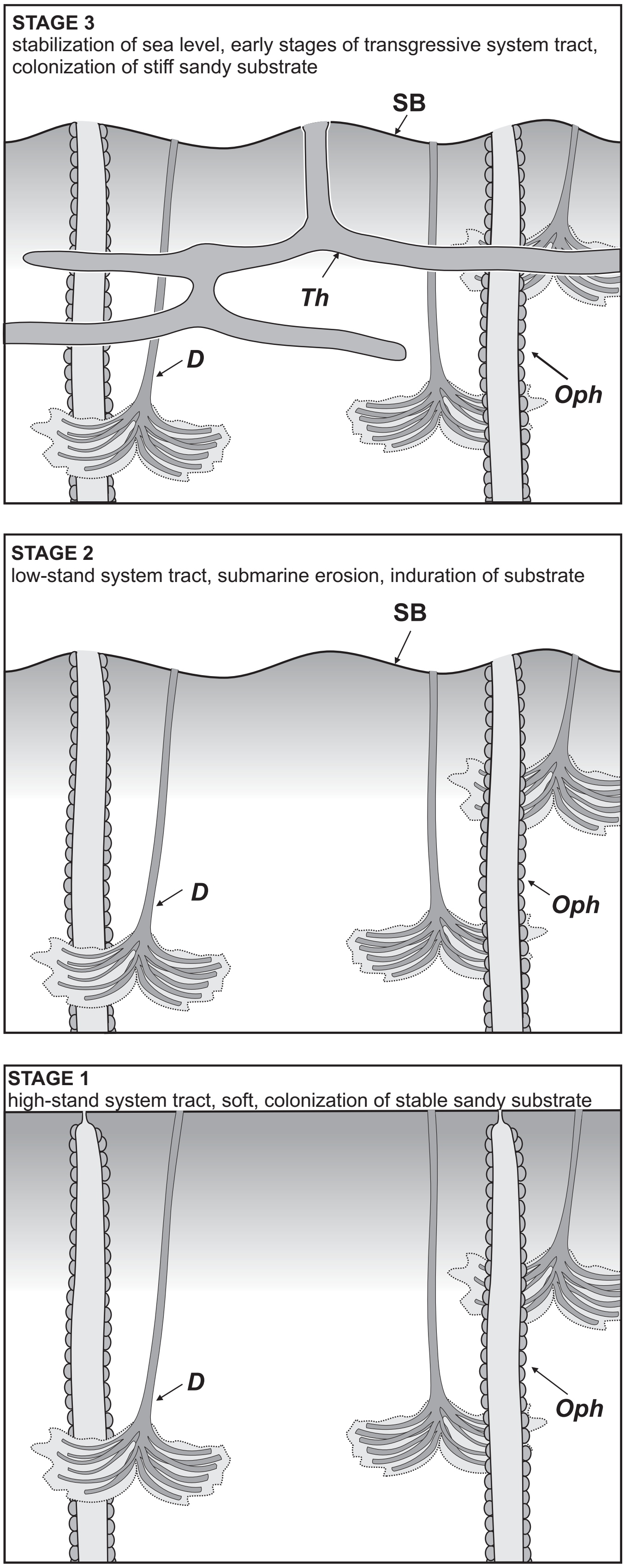

Fig. 7. Two dimensional schemes showing the development of the spatial relations among *Dactyloidites*, *Ophiomorpha*, and *Thalassinoides*. *D*, *Dactyloidites*; *Oph*, *Ophiomorpha*; *Th*, *Thalassinoides*; SB, sequence boundary.

dites peniculus occurs still about 10 cm below the discontinuity (Fig. 3). Taking into account the about half a metre long shaft of this trace fossil, at least the upper 40 cm of sediment were eroded. Nonetheless, the expected shallowing related to the sea-level fall was not dramatic because it was compensated by a subsidence resulted from crust loading by the overthrusting orogen (e.g., Doglioni and Prosser 1997). At the time of sea-level fall, the substrate became stiff *sensu* Wetzel and Uchman (1998) due to the erosional exhumation of buried sediments and early diagenetic processes. During the subsequent stabilization and rise of the sea level, non-deposition or very reduced deposition of fine-grained material at a very low rate is inferred. The fine-grained sediment above the discontinuity containing shell debris and shells of *Glycymeris* and the overlying silts belongs to this phase, which is interpreted as a transgressive system tract. In the stiff substrate, the *Thalassinoides* boxwork was formed (Fig. 7). It is filled with very fine-grained sand, which probably derived from above the discontinuity. Such a situation is common below discontinuities marking marine flooding at the top of parasequences (e.g., Ghibaudo et al. 1994; Gingras et al. 2002) or below regressive surfaces of erosion and sequence boundaries (e.g., Pemberton et al. 2004).

The geological situation is comparable to that of the occurrence of *Dactyloidites peniculus* in the Pleistocene of southern Italy (D'Alessandro and Bromley 1986), where it occurs together with *Ophiomorpha nodosa*, *Cylindrichnus concentricus* Toots in Howard, 1966, and *C. errans* D'Alessandro and Bromley, 1986 in a cross-bedded sandstone, just below silty sand, which is distinctly finer than the host rock. D'Alessandro and Bromley (1986: 75) concluded that *D. peniculus* "indicates a quiet, time-consuming, deposit-feeding activity". The first author observed *Dactyloidites* cf. *D. peniculus* in the Middle Miocene (Badenian) shoreface-foreshore sands at Gleboviti, Ukraine (Radwański and Wysocka 2006) below an intensively burrowed layer, which top marks probably some discontinuity. Comparison of those two situations from Italy shows that *D. peniculus* occurs in two energetically different regimes, i.e., totally bioturbated sands of Pliocene age and cross-bedded sands of Pleistocene age. In any event, it was formed under quiet conditions before deposition of sands finer than the host sediment in both cases. Such a situation is common during the latest stages of the high-stand system tract formation or shortly before and during marine flooding when sedimentation rate is low and the sea floor is stable. In both cases, however, a soft, sandy substrate is necessary. Thus, *D. peniculus* is a good candidate to mark of soft and latter stabilized sands. Their deposition can be related to relative sea-level changes in some cases. However, such an interpretation requires further testing. Other, relatively well-known ichnospecies of *Dactyloidites*, *D. ottoi* occurs in shallow-marine, high energy, mostly deltaic environments, but also mainly at the top of shallowing-up units (Agirrezabala and Gibert 2004).

Conclusions

The radial trace fossil *Dactyloidites peniculus* displays long, narrow shafts deviating from the centre of the radiating structure.

The radial structure of *D. peniculus* contains abundant faecal pellets deposited actively by the trace maker for probable gardening of microbes.

D. peniculus occurs exclusively in a narrow limited horizon at the top of a shallowing up section interpreted as a high-stand system tract and below a discontinuity surface interpreted as a sequence boundary. It was produced in soft sand in a stable environment and is a candidate for indication of similar environmental situations.

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