

## ***Leptichnus tortus* isp. nov., a new cheilostome etching and comments on other bryozoan-produced trace fossils**

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**SUMMARY** - *Leptichnus tortus* isp. nov., a new cheilostome etching and comments on other bryozoan-produced trace fossils - A new etching trace *Leptichnus tortus* isp. nov. is described for small groupings of relatively widely spaced pits spirally arranged around a central, larger pit. The inclusion of this new ichnospecies within *Leptichnus* forces the generic diagnosis to be amended to take into account the latter character. Smaller isolated pits can be locally present, mostly near the central pit. The new ichnotaxon is presently reported from Upper Pleistocene sediments from the Ionian Sea and incipient formation of comparable traces has been commonly observed in thanatocoenoses from the Eastern Sicilian shelf. The producers are setoselliniform bryozoans belonging to *Setosella vulnerata* and *Setosellina capriensis* whose traces show no differences. Pit size and shape vary according to the development of basal lacunae and of local dissolution affecting the underlying substratum, and to substratum morphology, its mineralogical composition and above all its structure. The placement of *Leptichnus* within ichnotaxonomy (Fixichnia and Domichnia) is discussed. Confusion and ambiguity in treating boring bryozoans within zoological and ichnological taxonomies are discussed.

**RIASSUNTO** - *Leptichnus tortus* isp. nov., una nuova traccia di cheilostomi e commenti su altre tracce fossili prodotte da briozoi - Viene descritta una nuova traccia *Leptichnus tortus* isp. nov. per incisioni ovali poco profonde e ampiamente spaziate l'una dall'altra, presenti in piccoli gruppi e con un andamento spirale a partire da una depressione centrale più rotondeggiante e più grande rispetto alle altre. L'inclusione di questa nuova icnospecie all'interno del genere *Leptichnus* ha determinato un emendamento nella diagnosi per includere la presenza nella regione centrale di una depressione di dimensioni maggiori delle altre mentre le due specie precedenti, con diversa disposizione delle incisioni, si originavano sempre da depressioni centrali di dimensioni minori delle successive. Come nelle specie precedentemente conosciute, depressioni più piccole ellittiche e isolate possono essere presenti soprattutto associate alla depressione centrale. Il nuovo icnotaxon è attualmente riportato da sedimenti sommersi del Pleistocene superiore dell'area dello Ionio. Esemplari incipienti sono comuni in tanatocenosi della piattaforma continentale siciliana. I produttori della nuova traccia sono briozoi setoselliniformi delle specie *Setosella vulnerata* e *Setosellina capriensis* le cui incisioni non mostrano evidenti differenze. La taglia e la morfologia delle depressioni sembra variare in relazione allo sviluppo di lacune nella calcificazione della parete basale e alla parziale dissoluzione del substrato sottostante, e in funzione della morfologia del substrato stesso, della sua composizione mineralogica e, soprattutto, della sua struttura. Viene discussa l'attribuzione di *Leptichnus* alla classe etologica dei Fixichnia e/o dei Domichnia. Infine, si sottolinea l'ambiguità attualmente presente nel trattamento dei cosiddetti briozoi perforanti sia all'interno della tassonomia zoologica che di quella icnologica e la necessità di decisioni per evitare l'incremento di nomi non chiaramente definiti all'interno dei due sistemi, spesso includenti sinonimie incrociate.

**Key words:** trace fossils, new ichnotaxon, bryozoans, Pleistocene, Mediterranean area

**Parole chiave:** tracce fossili, nuovo icnotaxon, briozoi, Pleistocene, area mediterranea

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### 1. INTRODUCTION

Ctenostome Bryozoans have been known as trace-producers for a long time (d'Orbigny 1847; Ulrich 1879, *vide* Pohowsky 1978; Seguenza 1880), mostly boring within calcareous substrates, including invertebrate skeletons. In addition, some cheilostome species are able to produce shallow etching traces, whose activity was recognised and first treated ichnologically by Taylor *et al.* (1999). The ichnogenus *Leptichnus* Taylor, Wilson & Bromley, 1999 was proposed to accommodate groups, usually less than 10mm in diameter, of closely spaced pits etched in calcareous substrata, each pit

(0.1-0.9 mm wide) being excavated perpendicularly, ovoidal to pyriform in shape and shallower than wide. Smaller pits are usually present in the centre and interspersed elsewhere in some specimens. Taylor *et al.* (1999) described two new species of *Leptichnus*: *L. peristromata*, for groupings of pits entirely or predominantly multiseriably arranged with the pit long axes radially aligned from the centre; and *L. dromeus*, for pits arranged in uniserial, often branching rows, with their long axes congruent with the linear series, sometimes including thin grooves between the pits but never connecting them. This paper aims to describe a third ichnospecies which can be placed in *Leptichnus* following the examination of fossil and

dead material from the Ionian Sea. Problems relating to bryozoan-produced trace fossils are also discussed.

## 2. MATERIALS AND METHODS

Specimens described in this paper originate from two distinct areas in the Ionian Sea. A first set of specimens was recovered in samples from deep-water (400 to 1200 m) sediments collected in the coral-mound area off Santa Maria di Leuca during the APLABES (AP), CORAL (COR) and CORSARO (CR) cruises, during the study of benthic communities, thanatocoenoses and taphocoenoses (Mastrototaro *et al.* in press; Rosso *et al.* in press; Malinverno *et al.* in press). Bryozoan etching traces were present in only a few samples and were extremely rare. None specimens preserved any portion of their producers. A second set of samples, including large numbers of colonies of the expected etcher, was examined in order to discover etching-etcher couples and thus identify the producer. These samples, again from the Ionian Sea, came from the Gulf of Noto (PS/81 and Noto 96 cruises) and the Gulf of Catania (Cicopi 2000 cruise) including middle-to-outer shelf bottom sediments, respectively from 80-130 m and 53-102 m deep, for which additional information can be found in Rosso (1996, in press). Specimens were picked from > 500 micron fractions.

Low magnification photos were taken with a Zeiss Stereodiscovery V8 system equipped with AxioCam MRc and Axiovision acquisition system. Some untreated specimens were examined under low vacuum conditions in a Tescan Vega 2 LMU SEM.

Studied material is housed at the Palaeontological Museum of the Catania University.

## 3. SYSTEMATICS

*Leptichnus tortus* isp. nov.  
(Figs 1A-C)

*Derivatio nominis.* From Latin *tortus* referring to the spiral arrangement of the pits.

**Holotype.** PMC I 1a. 18.4.2006, the only recovered specimen (Figs 1A-B), on a tube fragment of the serpulid *Ditrupa arietina* (O.F. Müller, 1776) from Pleistocene post Würmian submerged deep-water deposits, off Santa Maria di Leuca (N Ionian Sea) APLABES cruise, station AP30 bottom, 747 metres, 39° 28.09' N, 18° 24.42' E. **Paratypes.** PMC I 1b. 18.4.2006, two specimens from Upper Pleistocene submerged sediments from AP20, 647 m, 39° 26.79' N, 18° 30.48' E (Fig. 1C), and COR2-100, 447.5 m, 39° 37.17' N, 18° 23.38' E stations, off Santa Maria di Leuca (N Ionian Sea).

**Other material:** Several specimens from Holocene

shelf sediments collected in the Gulf of Noto and the Gulf of Catania. A few specimens from Holocene submerged sediments from some stations off Santa Maria di Leuca (N Ionian Sea). Rosso Collection PMC.R.I.H.I-1.

### 3.1. Description

Small-sized *Leptichnus*, usually not exceeding two millimetres in diameter, formed by a group of one to two dozen closely spaced, shallow pits of elliptical to pyriform shape, often irregularly lobate at one or both end(s); lateral walls are abruptly vertical or slightly inclined toward the flat floor. Pits roughly 150-210 µm long by 100-120 µm wide. A larger, more circular pit measuring 280-320 µm by 210-230 µm, is present at the centre of the group. It is surrounded by the other pits, roughly arranged in spirals, marked by the alignment of pits and their slightly inclined long axes, occasionally disrupted by the insertion of isolated pits and new pit rows. Significantly smaller, usually round transverse elliptical pits are rarely interspersed between the larger pits, one or two often placed near the central pit.

### 3.2. Remarks

The new taxon *Leptichnus tortus* isp. nov. differs from both previously established species, *L. peristromata* Taylor, Wilson & Bromley, 1999 and *L. dromeus* Taylor, Wilson & Bromley, 1999, but is most similar to *L. peristromata*.

*L. tortus* isp. nov. differs significantly from *L. dromeus*, which consists of uniserial branching rows of pits whose long axes are congruent with the linear direction of the series. In contrast, features shared with *L. peristromata* include the contiguous pits grouped to form patches. Nevertheless, *L. tortus* isp. nov. shows spirally arranged pits from a central area, pit long axes being roughly congruent with the spirals, whereas *L. peristromata* specimens have pit long axes radially aligned from the centre. The different arrangement of pits appears significant enough to support the erection of the new species, in agreement with the statement by Taylor *et al.* (1999) that the disposition of pits could be regarded as a unique basic criterion for erecting species within the genus.

Furthermore, it is worth noting that, although a few centrally placed smaller-sized pits can be present in *L. tortus* isp. nov., in agreement with the genus definition by Taylor *et al.* (1999: p. 596), a single, usually roundish pit significantly larger than the subsequent ones marks the origin of the group (see above). Although this feature alone appears insufficient for creating a new genus, it is here proposed to amend the generic diagnosis of *Leptichnus* to include the possible presence of a larger pit in the centre of the grouping. Finally, it has been observed that both entire specimens and single pits of *L. tortus* isp. nov. are smaller in size than those of *L. peristromata*, 200 µm in

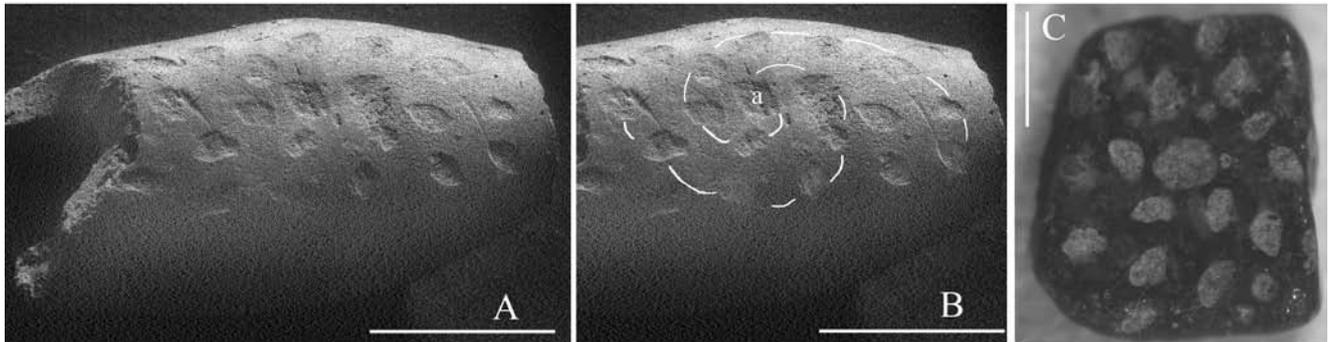


Fig. 1 - *Leptichnus tortus* isp. nov. A. Holotype on *Ditrupa arietina* and B. the same with the two rows of spirally arranged pits marked by lines. Upper Pleistocene. Ionian Sea, Station AP30. Scale bars: 1 mm. C. Paratype on unidentified bioclast. Upper Pleistocene. Ionian Sea. Station COR 2-100. C: Scale bar: 500 µm.

Fig. 1 - *Leptichnus tortus* isp. nov. A. Olotipo su *Ditrupa arietina* e B. lo stesso con l'indicazione della doppia spirale formata dalle corrosioni prodotte dagli zooidi. Pleistocene superiore. Mar Ionio, Stazione AP30. Scale: 1 mm. C. Paratipo su bioclasto non identificato. Pleistocene superiore. Mar Ionio, Stazione COR 2-100. Scala: 500 µm.

length being the approximate boundary between pit zone in the two species.

#### 4. DISCUSSION

##### 4.1. Trace producer

*Leptichnus* traces are typically produced by encrusting cheilostome bryozoans etching the surfaces of their carbonate substrata (Figs 2A-F; 3A-Q). Taylor *et al.* (1999) indicated uniserial running colonies as the producers of *L. dromeus*, with typical representatives belonging to the genus *Hippothoa* Lamouroux, 1821 (to which *Aetea* Lamouroux, 1812 could probably be added: see Pohowsky 1978, although traces of both genera were first misinterpreted and synonymised with bryozoan boring genera (e.g. Waters 1879). In contrast, *L. peristromata* is formed by species growing as multiserial sheets. Species belonging to several genera, namely *Jellyella* Taylor & Monks 1996, *Electra* Lamouroux, 1816, *Conopeum* Gray, 1848, *Figularia* Jullien, 1886, *Celleporella* Gray, 1848, *Chorizopora* Hincks, 1880, *Tecatia* Morris, 1980, *Microporella* Hincks, 1877, *Chiastossella* Canù & Bassler, 1934, *Escharella* Gray, 1848, have been quoted as producers of *L. peristromata* (see Taylor *et al.* 1999). Furthermore, a few colonies belonging to *Escharina vulgaris* (Moll, 1803) and *Herentia hyndmani* (Johnston, 1847) leave etchings on large mollusc bivalves from several Sicilian Pleistocene fossil assemblages (Rosso & Sanfilippo 2005; Rosso pers. obs.).

Nevertheless, *L. tortus* isp. nov. could not be referred to the activity of any of the above reported genera as none of their species is known to develop small-sized colonies with spiral arrangements of zooids. In contrast, setoselliniforms are known to develop small-sized colonies with spirally arranged zooids on sandy-to-fine gravely

clasts (Lagaaij & Gautier 1965, Rosso in press). In samples containing *L. tortus* isp. nov. specimens, species developing setoselliniform growth morphology were recovered, namely *Setosella vulnerata* (Busk, 1860) and *Setosellina capriensis* (Waters, 1918). Furthermore, study of material from Santa Maria di Leuca, as well as of thanatocoenoses from samples collected along the eastern Sicily shelf, led to the discovery of a remarkable number of setoselliniform colonies partially detached from their substrata, thus revealing etchings produced by individual zooids underneath. The species involved were primarily *S. vulnerata* (Fig. 2B-F; 3I, J, O) and very occasionally *S. capriensis* (Fig. 3K), which thus appear as the two taxa responsible for *L. tortus* isp. nov. Nevertheless, etchings were not always present where broken colonies partly revealed the surfaces of encrusted substrata and, consequently, they do not always form. Other setoselliniform species are known from the Pleistocene and Recent Mediterranean area besides *S. vulnerata* and *S. capriensis*, belonging to the same genera, namely *Setosella cavernicola* Harmelin, 1977 and *Setosellina roulei* Calvet, 1906, to which *Heliodoma angusta* Rosso, 1998 can also be added (Rosso 1998; Rosso & Di Geronimo 1998; Rosso 2005), but no direct evidence of etching activity has been yet reported or observed in these species.

The recognition of etching activity in both *S. vulnerata* and *S. capriensis* allows the bryozoan families Setosellidae and Heliodomidae to be added to the list of *Leptichnus* producers, together with the Family Escharinidae and possibly Aeteidae (see above), reported by Taylor *et al.* (1999), namely Membraniporidae, Electridae, Cribriliidae, Hippothoidae, Pasytheidae (to which *Tecatia* is now referred), Microporellidae, Hippoporinidae? and Romancheinidae. The addition of further families neither closely related to each other nor with those previously known to produce *Leptichnus*, corroborates the idea of Taylor *et al.*

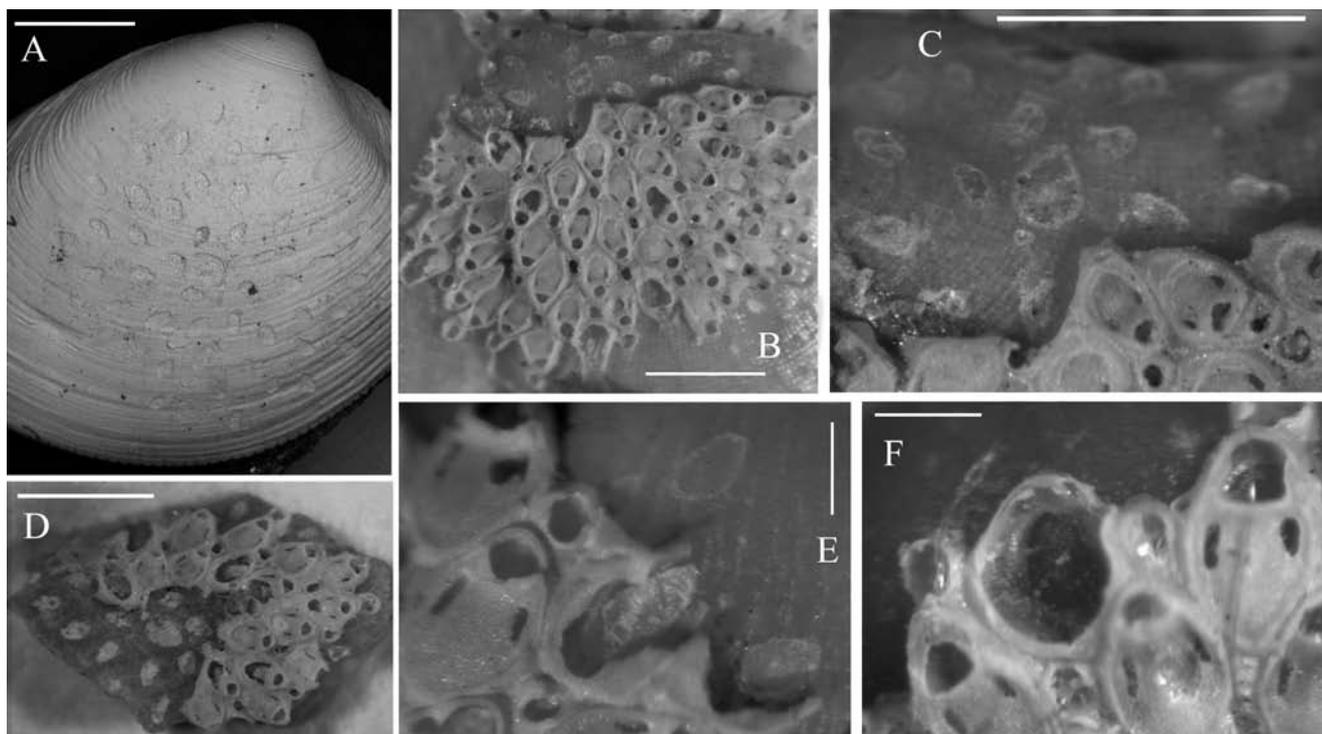


Fig. 2 - Incipient *Leptichnus tortus* isp. nov. beneath colonies of the setoselliform bryozoan *Setosella vulnerata* (Busk, 1860), whose colonies are partly detached from their substrata. Recent thanatocoenoses, eastern Sicily continental shelf. A. Outer surface of a right valve of *Nucula sulcata* Bronn, 1831 exposing scars produced by a completely detached colony. Note larger pit at the centre and the spiral arrangement. Ciclopi 2000, Station 10G. Scale bar: 1 mm. B-C. One specimen and a detail of its central part on a pectinid valve outer surface. Ciclopi 2000, Station 8F. Scale bar: 1 mm. D. A further example on a bioclast. Ciclopi 2000, Station 8F. Scale bar: 1 mm. E. Detail of partly broken zoecia and their individual basal scars. Ciclopi 2000, Station 12F. Scale bar: 200  $\mu$ m. F. Growing edge of a recently dead colony with a zoecium showing its only partly mineralised basal wall leaving a large basal lacuna. PS/81, Station 4C1. Scale bar: 200  $\mu$ m.

Fig. 2 - Formazione incipiente di *Leptichnus tortus* isp. nov. sotto esemplari del briozoo setoselliniforme *Setosella vulnerata* (Busk, 1860), le cui colonie sono parzialmente staccate dal substrato. Tanatocenosi attuali della piattaforma continentale della Sicilia orientale. A. Superficie esterna della valva destra del bivalve *Nucula sulcata* Bronn, 1831 mostrante le corrosioni prodotte da una colonia interamente staccata. Si noti la traccia centrale piú larga e la disposizione a spirale. Ciclopi 2000, Stazione 10G. Scala: 1 mm. B-C. Esempio e dettaglio della sua parte centrale sulla superficie esterna della valva di un pettinide. Ciclopi 2000, Stazione 8F. Scala: 1 mm. D. Un ulteriore esempio su un bioclasto. Ciclopi 2000, Stazione 8F. Scala: 1 mm. E. Dettaglio di zooidi parzialmente rotti e delle loro tracce di corrosione basale. Ciclopi 2000, Stazione 12F. Scala: 200  $\mu$ m. F. Bordo di crescita di una colonia appena morta con uno zoecio mostrante la sua parete basale solo parzialmente mineralizzata e con un'ampia lacuna centrale. PS/81, Stazione 4C1. Scala: 200  $\mu$ m.

(1999) that etching ability evolved polyphyletically in cheilostomes.

#### 4.2. Pit "host-granules"

Despite the large number of carbonate clasts in the examined samples, traces of *L. tortus* isp. nov. were found only on unidentified bioclasts (Fig. 1C) and fragments of the serpulid tube *D. arietina* (Figs 1A-B) in Pleistocene samples. In modern thanatocoenoses comparable etchings were present on the same substrata (Figs 3B-E), but also on bivalves (Figs. 2A-C, E-F; 3A, I-Q), which represent nearly the 70% of the etched clasts. Gastropods, decapod (Fig. 3F-G) and cirriped crustacean fragments and plates, calcareous algae, carbonate granules of unknown origin were also etched. Bryozoan substrata did not bear *Leptichnus* pits except for a single phidolopodid fragment etched on its dorsal side (Fig. 3H).

Furthermore, traces appeared largely restricted to small-sized grains, normally 1-3 mm wide, overlapping with the grain-size of clasts selected for colonization by Mediterranean setoselliniforms (Rosso in press).

Finally, unlike other ichnospecies of *Leptichnus* which are nearly always found on the inside surfaces of bivalve shells, thus pointing to a cryptic habit of the trace-producing cheilostome species (Taylor *et al.* 1999), *L. tortus* is almost invariably present on convex surfaces, often on the outer side of small cup-shaped bivalves (Figs 2A; 3J-K).

#### 4.3. Pit shape-size variability

Close inspection of *L. tortus* isp. nov. specimens concealed beneath partly preserved colonies of *S. vulnerata* and *S. capriensis* (see Fig. 3I and 3K, for instance) shows no obvious difference between etchings produced by the two

species. Furthermore, although both *S. vulnerata* and *S. capriensis* possess small heterozoids (vibraculoid avicularia) located distally to each autozoid, corresponding pits are rarely observed.

The size and shape of pits left by autozoids vary among and within colonies in patterns which appear not to be strictly linked to the location of the pits within colonies.

Pit size is presumably due to the development of the calcification of the zooidal basal wall and, consequently, to the extent of the basal wall lacuna through which zooidal soft tissues are directly in contact with the substratum surface. This surface could be probably affected by a biologically mediated local dissolution comparable with the extension of the resorption process suggested by Pinter Morris (1975) and Taylor *et al.* (1999) for *Celleporella* and other cheilostomes. This surface roughly corresponds to the distal half to two-thirds of each zoid (Figs. 2C-E). As a consequence, *L. tortus* isp. nov. pits are widely spaced (Figs. 2A, C-D; 3I). The near absence of heterozoid pits could be caused by their inability or reduced ability to open basal windows and etch carbonates from their substratum. In contrast, pits left by ancestrulae, which are usually slightly wider than periancistrular and even autozoids (Rosso pers. obs.), are two to three times wider than the subsequent pits in *L. tortus* isp. nov. traces.

The morphology of basal lacunae also contributes to pit shape, which seems otherwise strongly affected by the surface features (sculptured *versus* smooth: Figs. 3A-B), the mineralogy and, above all, the structure of the etched substrata. Interestingly, pit outlines appear more regular, continuous and better defined on calcite skeletons exhibiting outer layers characterised by structures of densely packed crystallites. The depth of such pits gradually increases through gently sloping sides, as observed for etchings produced in the *Ditrupa* tubes (Fig. 3C), whose outer surface is characterised by needle-like crystallites arranged in lamellae (Sanfilippo 1999), in some pectinids such as *Similipecten similis* (Laskey, 1811) (Fig. 3L), in the unique phidoloporid bryozoan (Fig. 3H) and in crab carapace fragments even when surfaces are strongly sculptured (Figs. 3F-G). In contrast, pits etched on aragonite skeletons show well marked, more irregular outlines and abruptly deepen towards their flat floor which sometimes represent the basal surface of the outermost shell layer. This feature was observed for several bivalves, such as the arcoid *Bathyarca pectunculoides* (Scacchi, 1835) (Figs. 3K, N), the veneroid *Kelliella abyssicola* (Forbes, 1844) (Figs. 3J, M) and the nuculoid *Nucula sulcata* Bronn, 1831 (Figs. 2A; 3Q), usually showing a thin outer shell layer of horizontal-to-reclined lamellar fibrous prisms (Carter 1990). Comparable or even more irregularly outlined pits can be observed also on the calcite left valves of some pectinids exhibiting an outer layer with foliated structure (Carter 1990; Waller 2006). This is the case for the pterioid *Palliolium incomparabile* (Risso, 1826) on whose left valves the umbo-ventral alignment of crystals and their arrangement slightly inclined to the shell surface strongly influences pit construction (Figs. 3O-P).

The presumed mechanism through which cheilostomes and nearly all ctenostome bryozoans leave their traces is by chemical etching (see Taylor *et al.* 1999). Nevertheless, inspection of pit etch surfaces in comparison with natural fractures from the same host skeleton show, besides clear etching effects (Fig. 3P), a certain fragmentation and disarrangement of crystals (Figs. 3L, Q and mostly 3D-E). This feature could point to a partly mechanical action of soft tissues in disaggregating and rearranging weak crystals, which in recently dead colonies appear bounded by organic matter, as testified by local high Carbon content.

#### 4.4. Distribution

*L. tortus* isp. nov. has been only recovered in Upper Pleistocene sediments from a single area in the northern Ionian Sea. The holotype specimen derives from the subsurface layers of sample AP30 which includes large branches of the scleractinian coral *Lophelia pertusa* Linnaeus, 1758 dated using U/Th as  $13.96 \pm 0.18$  ky (Malinverno *et al.* in press). In contrast, the trace has not been detected in other Pleistocene samples including those in which rare setoselliniform specimens were present, such as the bathyal muds from Furnari (Di Geronimo *et al.* 2005).

Comparable etchings are more widespread in Holocene thanatocoenoses from shelf environments, mostly from the Ionian Sea.

The stratigraphic distribution of *L. tortus* isp. nov. is restricted when compared with the known range for both *L. peristromata* and, particularly, *L. dromeus*, respectively going back to the Eocene and the Late Cretaceous. This could be partly linked to the relatively recent appearance of a true setoselliniform growth habit, including adhesion to substratum grains which not become incorporated in the colony. This feature seems not to be exhibited by the oldest *Setosellina* representatives, as demonstrated by *Setosellina gregoryi* Cheetham, 1966 whose zooids are arranged in spiral series from the centre, but whose colonies were seemingly free living to judge by their lunulitiform-like basal surfaces (Cheetham 1966).

Setoselliniform cheilostomes are usually rare and have special ecological requirements (see Rosso in press) and their traces can be easily overlooked as a consequence of the small size of etched substrata together with the inconspicuousness of the pits.

#### 4.5. Placement in ethological systematics

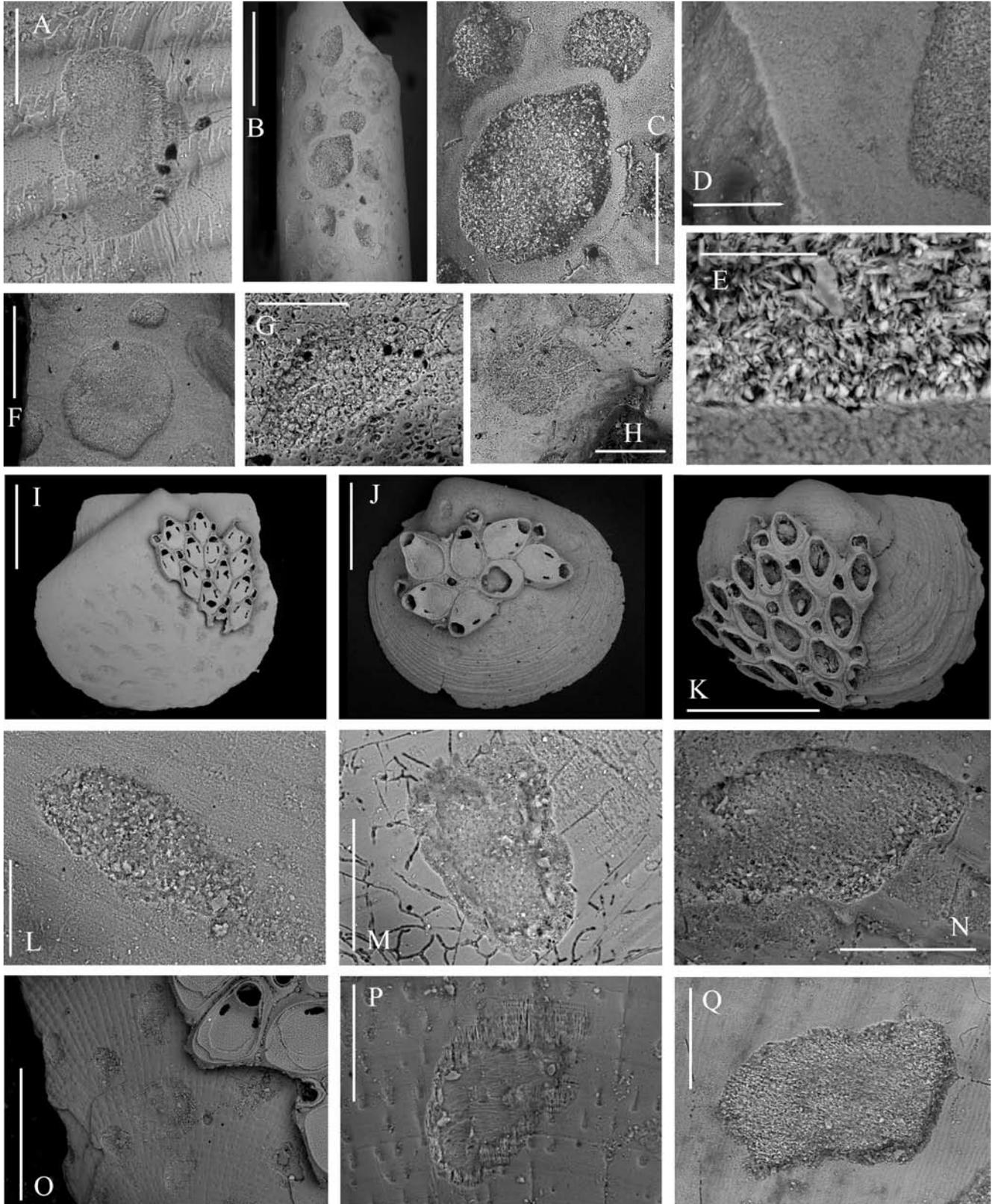
The producers of *L. tortus* isp. nov. can be considered as epibionts on small clasts or, following Taylor & Wilson (2003), they could be distinguished into epilithobionts and episkeletobionts, able to colonize both lithic grains and bioclasts respectively.

When erected, the genus *Leptichmus* was included in the ethologic class of Domichnia by Taylor *et al.* (1999). Subsequently, Gibert *et al.* (2004) introduced the Class Fi-

xichnia for shallow etchings representing anchoring or fixation traces produced by epibiont organisms attaching themselves to a substratum by means of soft or skeletal body parts. Consequently, Gibert *et al.* (2004) included *Leptichnus* within the new class. This placement also takes in-

to account the suggestion by Taylor *et al.* (1999) that *Leptichnus* scar production was functional to improve adherence to the substratum.

Nevertheless, it could be remarked that *Leptichnus* is not strictly analogous to all other traces included within the



class Fixichnia, namely *Centrichnus* Bromley & Martinell, 1991, *Podichnus* Bromley & Surlyk, 1973, *Renichnus* Mayoral, 1987 and *Stellichnus* Mayoral, 1987. *Podichnus*, produced by the attachment of brachiopod pedicle fibres, represents the pure record of a fixation activity. Within *Centrichnus*, *C. eccentricus* Bromley & Martinell, 1991, produced by anomiid bivalves leaving byssus scars, could be strictly considered as a simple attachment documentation. In contrast, the attribution of *C. concentricus* Bromley & Martinell, 1991, produced by verruciid barnacles, *Renichnus*, left by vermetid gastropods, *Stellichnus*, left by the presumed ctenostome bryozoan *Paravinella* Mayoral, 1987, which presumably also possesses a tubular mineralised skeleton (see Mayoral 1987), and *Leptichnus* to Fixichnia is equivocal. All these traces record anchoring activity (see also Bromley & Heinberg 2006), but their formation involves excavation, even shallow, of the substratum produced through a process of dissolution. It follows that the surface of the excavated substratum actually constitutes part of the inner skeletal surface, and the usable volumes of pits and etchings increase the

skeletal cavity in which the producer can live. Consequently, this second group of Fixichnia traces, although basically recording fixation to a substratum, also represent contribution to dwelling cavities.

#### 4.6. Other bryozoan traces

Domichnia strictly include traces left by boring bryozoans which are soft-bodied ctenostomes able to evert lophophores externally, but living deep inside carbonate substrata (Taylor *et al.* 1999; Bromley & Heinberg 2006). Borings of single zooid are usually widely spaced and connected by a network of stolons. At least 13 boring bryozoan genera are known (Tab. 1), erected on detailed descriptions of the morphology of borings they produce and colony development, but treated as animals and included in conventional zoological taxonomy (see Pohowsky 1978, for instance). It is worth noting that some of them, namely *Orbignyopora* Pohowsky, 1978, *Haimeina* Terquem & Piette, 1865, *Cookobryozoon* Pohowsky, 1978, *Marcusopora* Pohowsky,

← Fig. 3 - Examples of incipient *Leptichnus tortus* isp. nov. and details of individual pits showing morphological and size variation relating to features of the substratum. A. Lobate outline of individual pit caused by the costulate sculpture of the cardiid bivalve substrate. PS/81, Station 11E. Scale bar: 100  $\mu$ m. B. Specimen on a *Dirupa arietina* (O.F. Müller, 1776) tube and detail (C) of the central pit corresponding to the ancestrula and small-sized pits. Ciclopi 2000, Station 10G. B. Scale bar: 500  $\mu$ m. C. Scale bar: 200  $\mu$ m. D. Pit near a natural fracture of the same *D. arietina* tube showing disturbance in crystal orientation at pit level. Scale bar: 50  $\mu$ m. E. Detail of a pit edge from the same specimen. Scale bar: 20  $\mu$ m. F. Roundish central pit with an associated pit etched by a heterozoooid on the outer surface of a crustacean carapace. Ciclopi 2000, Station 12F. Scale bar: 200  $\mu$ m. G. Pit on a weathered crab fragment. Noto 96, Station WP 132. Scale bar: 100  $\mu$ m. H. Very shallow, weakly defined pit on the dorsal surface of a phydoloporid bryozoan. PS/81, Station 4C1. Scale bar: 200  $\mu$ m. I., L. Incipient *L. tortus* isp. nov. produced by *Setosella vulnerata* (Busk, 1860) on the right valve of the pterioid *Similipecten similis* (Laskey, 1811), and detail of a single pit. Ciclopi 2000, Station 8F. Scale bars: 1 mm and 100  $\mu$ m, respectively. J., M. Incipient *L. tortus* isp. nov. produced by *Setosella vulnerata* (Busk, 1860) on the left valve of the veneroid *Kelliella abyssicola* (Forbes, 1844) and detail of a single pit. PS/81, Station 4C. Scale bars: 500  $\mu$ m and 100  $\mu$ m, respectively. K., N. Incipient *L. tortus* isp. nov. produced by *Setosellina capriensis* (Waters, 1918) on the left valve of the arcoid *Bathyarca pectunculoides* (Scacchi, 1835) and detail of a single pit. PS/81, Station 6D. Scale bars: 1 mm and 100  $\mu$ m, respectively. O., P. Portion of an incipient *L. tortus* isp. nov. produced by *Setosella vulnerata* (Busk, 1860) on the left valve of the pterioid *Palliolium incomparabile* (Risso, 1826), and detail of a single pit. Ciclopi 2000, Station 8F. Scale bars: 500  $\mu$ m and 100  $\mu$ m, respectively. Q. Single pit on the outer surface of the right valve of *Nucula sulcata* Bronn, 1831, depicted in Fig. 2A. Ciclopi 2000. Station 10G. Scale bar: 100  $\mu$ m.

Fig. 3 - Esempi di *Leptichnus tortus* isp. nov. in incipiente formazione e dettagli di singoli pit per mostrare le variazioni morfologiche e di taglia in rapporto al tipo di substrato. A. Incisione a contorno lobato risultante dalla costolatura della valva di cardide che funge da substrato. PS/81, Stazione 11E. Scala: 100  $\mu$ m. B. Esempio su tubo di *Dirupa arietina* (O.F. Müller, 1776) e dettaglio (C) della sua parte centrale con una grande incisione corrispondente all'ancestrula e incisioni di piccola taglia. Ciclopi 2000, Stazione 10G. B. Scala: 500  $\mu$ m. C. Scala: 200  $\mu$ m. D. Dettaglio di un'incisione vicina ad una frattura naturale del tubo di *D. arietina* che mostra lo sconvolgimento della struttura cristallina alla superficie della depressione. Scala: 50  $\mu$ m. E. Dettaglio del bordo di un'incisione, sempre dallo stesso esemplare in B. Scala: 20  $\mu$ m. F. Incisione centrale rotondeggiante e piccola incisione ovoidale lasciata da un eteromorfo sulla superficie del carapace di un crostaceo. Ciclopi 2000, Stazione 12F. Scala: 200  $\mu$ m. G. Incisione su un frammento alterato di un granchio. Noto 96, Stazione WP 132. Scala: 100  $\mu$ m. H. Incisione lieve e poco definita sulla superficie dorsale di un briozoo phydoloporide. PS/81, Stazione 4C1. Scala: 200  $\mu$ m. I., L. Incipiente formazione di *L. tortus* isp. nov. prodotto da *Setosella vulnerata* (Busk, 1860) sulla valva destra dello pterioide *Similipecten similis* (Laskey, 1811), e dettaglio di una singola incisione. Ciclopi 2000, Stazione 8F. Scala: 1 mm e 100  $\mu$ m, rispettivamente. J., M. Incipiente *L. tortus* isp. nov. prodotto da *Setosella vulnerata* (Busk, 1860) sulla valva sinistra del veneroide *Kelliella abyssicola* (Forbes, 1844) e dettaglio di una singola incisione. PS/81, Stazione 4C. Scala: 500  $\mu$ m e 100  $\mu$ m, rispettivamente. K., N. Incipiente *L. tortus* isp. nov. prodotto da *Setosellina capriensis* (Waters, 1918) sulla valva sinistra dell'arcoide *Bathyarca pectunculoides* (Scacchi, 1835) e dettaglio di una singola incisione. PS/81, Stazione 6D. Scala: 1 mm e 100  $\mu$ m, rispettivamente. O., P. Porzione di un incipiente *L. tortus* isp. nov. prodotto da *Setosella vulnerata* (Busk, 1860) sulla valva sinistra dello pterioide *Palliolium incomparabile* (Risso, 1826), e dettaglio di una singola incisione. Ciclopi 2000, Stazione 8F. Scala: 500  $\mu$ m e 100  $\mu$ m, rispettivamente. Q. Singola incisione sulla superficie della valva destra di *Nucula sulcata* Bronn, 1831, illustrata in Fig. 2A. Ciclopi 2000. Stazione 10G. Scala: 100  $\mu$ m.

Tab. 1 - List of boring bryozoan genera and bryozoan-produced ichnogenera erected using morphological characters of borings left in hard substrata. Their interpretation as body fossils or trace fossils and their inclusion in the zoological or ichnological taxonomy are reported (see text for further information). Data uniquely from Pohowsky (1978) and <http://bryozoa.net>, edited by Phyl Bock when no specific reference is reported. Stars indicate genera for which soft parts are known, at least for a single species.

*Tab. 1 - Lista dei generi dei briozoi perforanti e degli icnogeneri prodotti da briozoi descritti utilizzando i caratteri morfologici delle perforazioni lasciate nei substrati duri. Per ciascun genere o icnogenero vengono riportati l'interpretazione come corpo fossile o traccia fossile e la sua conseguente inclusione nella tassonomia animale o in quella delle tracce fossili secondo alcuni Autori recenti (ulteriori informazioni nel testo). Quando nessun riferimento bibliografico è specificatamente riportato, i dati provengono principalmente da Pohowsky (1978) e dal sito <http://bryozoa.net>, curato da Phyl Bock. Gli asterischi indicano quei generi per i quali si conoscono le parti molli di almeno una specie.*

Genus	described as	considered as	species	stratigraphic range	
<i>Casteropora</i> Pohowsky, 1978	ctenostome zootaxon	currently ctenostome	1	Devonian	Europe, N America
<i>Cookobryozoon</i> Pohowsky, 1978	ctenostome zootaxon	currently ctenostome	2	Cretaceous-Pliocene	Oceania
<i>Fiskerella</i> Pohowsky, 1978	ctenostome zootaxon	currently ctenostome	1	Carboniferous	N America
<i>Foraripora</i> Voigt & Soule, 1973	ctenostome zootaxon	currently ctenostome	1	Cretaceous	Europe
<i>Haimeina</i> Terquem & Piette, 1865	ctenostome zootaxon	currently ctenostome	1	Trias-Jurassic	Europe
<i>Ichnogutta</i> Botquelen & Mayoral, 2005	ichnotaxon for <i>Casteropora</i> produced borings		1	Devonian	Europe
<i>Immergentia</i> Silen, 1946 *	ctenostome zootaxon	currently ctenostome; ichnotaxon: Barrier & D'Alessandro (1985)	13	Cretaceous-Recent	Worldwide
<i>Iramena</i> Boeckschoten, 1970	ichnotaxon for <i>Immergentia</i> -like borings fide Mayoral, 1988	currently ctenostome; ichnotaxon: Barrier & D'Alessandro (1985); Mayoral (1988)	2	Paleocene	Europe
<i>Marcusopora</i> Pohowsky, 1978	ctenostome zootaxon	currently ctenostome	1	Cretaceous	N America
<i>Orbignyopora</i> Pohowsky, 1978	ctenostome zootaxon	currently ctenostome; ichnotaxon: Vogel <i>et al.</i> (1987); Mayoral <i>et al.</i> (1994)	5	Silurian-Pliocene	Europe, N America
<i>Penetrantia</i> Silen, 1946 *	ctenostome zootaxon	currently ctenostome; cheilostome, at least some species: Smyth (1988)	10	Cretaceous-Recent	Worldwide
<i>Pennatichnus</i> Mayoral, 1988	ichnotaxon for <i>Spathipora</i> -like borings		1	Pliocene	Europe
<i>Pinaceocladichnus</i> Mayoral, 1988	ichnotaxon for <i>Terebripora</i> -like borings	<i>Terebripora</i> and <i>Orbignyopora</i> -like traces: Mayoral (1991); Mayoral <i>et al.</i> (1994)	4	Ordovician-Pliocene	Europe

(Tab. 1 - continued)  
(Tab. 1 - continua)

Genus	described as	considered as	species	stratigraphic range	
<i>Ropalonaria</i> Ulrich, 1879	ichnotaxon	ctenostome: Pohowsky (1978); ichnotaxon: Mayoral (1988); Mayoral <i>et al.</i> (1994); Wilson & Lazzuri (2000); Taylor & Wilson (2003)	6	Ordovician-Cretaceous	Eurasia, N America
<i>Spathipora</i> Fischer, 1866 *	ctenostome zootaxon	currently ctenostome; ichnotaxon: Beuck & Freiwald (2005)	11	Jurassic-Recent	Eurasia, America
<i>Terebripora</i> d'Orbigny, 1847 *	ctenostome zootaxon	currently ctenostome; ichnotaxon: Barrier & D'Alessandro (1985)	8	Eocene-Recent	Europe and worldwide
<i>Voigtella</i> Pohowsky, 1978	ctenostome zootaxon	seemingly not a bryozoan	3	Permian-Cretaceous	Eurasia, N America

1978, *Foraripora* Voigt & Soule, 1973, *Fischerella* Pohowsky, 1978, *Casteropora* Pohowsky, 1978 and *Voigtella* Pohowsky 1978 (doubtfully regarded as a bryozoan) are known only from the morphology of their borings.

Further genera, such as *Spathipora* Fischer, 1866, *Terebripora* d'Orbigny, 1847, *Immergentia* Silen, 1946 and *Penetrantia* Silen, 1946, were all first described taking into account the morphology of their borings, but soft-tissues organisation is now known for at least some of their species (Soule & Soule 1969, Pohowsky 1978 and references therein). Except for *Penetrantia*, often regarded as a cheilostome (e.g. Smyth 1988), they are unanimously considered as ctenostomes (see Pohowsky 1978 for a review). Despite their erection as zootaxa, some Authors among which Barrier & D'Alessandro (1985) and Beuck & Freiwald (2005) treated them as ichnotaxa.

In contrast, *Ropalonaria* Ulrich, 1879, often treated as a ctenostome bryozoan (Pohowsky 1978), was actually first described as "impressions" (although they were attributed to *Hippothoa* and erroneously assigned to crisiid cyclostomes thus causing further mistakes) and, consequently, considered as an ichnogenus by Wilson & Lazzuri (2000) and Taylor & Wilson (2003). It was almost a century before the introduction of the first genus treated ichnologically, *Iramena* Boekschoten, 1970. Nevertheless, *Iramena* was subsequently included within ctenostomes by Pohowsky (1978), but also treated as an ichnogenus by Barrier & D'Alessandro (1985) and by Mayoral (1988).

Great confusion has arisen from the failure to make

clear-cut distinctions between trace fossils and body fossils. Consequently, at the same or in subsequent times, the same "object" has been treated as a trace fossil or as a body fossil and included within one or the other taxonomical framework. The debate goes back to the opposing views of Boekschoten (1970) and Bromley (1970) who considered genera such as *Terebripora* and *Spathipora* as trace fossils, and those of Pohowsky (1974: 561) who asserted that the same genera could be treated as body fossils owing to the fidelity of their borings in recording all of the external morphological characters useful for genus and species identification. An idea drawn on more recently by Golubic (1990) and subsequently by Tavenier *et al.* (1992) asserting that "boring traces that conform closely to the body shapes of their makers reveal specific details of the organisms external morphology representing at the same time the works of the organisms and their moulds". Furthermore, the highest inconsistency has been occurred with the erection of further new ichnogenera, namely *Pennatichnus* Mayoral, 1988, *Pinaceocladichnus* Mayoral, 1988 and *Ichnogutta* Botquelen & Mayoral, 2005. Each of the former two is believed to be produced by more than a single maker belonging to the "ctenostome" genera *Spathipora*, *Terebripora*, *Orbignyopora* and *Immergentia* (Mayoral 1988, 1991; Mayoral *et al.* 1994), whereas the last one seems to result from the bioerosional activity only of *Casteropora* (Botquelen & Mayoral 2005). It follows that the producers of these trace fossils are organisms whose names were included in the zoological nomenclature and taxonomy, but whose description was first directly and

exclusively made on the borings left in carbonate substrata (i.e. trace fossils) fully agreeing with the definition given by Bertling *et al.* (2006: 266). An effort is thus needed to reorganise the existing taxa giving the valid names in both zoological and ichnological nomenclature.

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