Concepts in ichnotaxonomy illustrated by small round holes in shells

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SUMMARY

Trace fossil classification requires a double system of nomenclature. The trace fossil name (ichnotaxon) is based on the morphology of the structure whereas the biological taxon represents the interpreted phylogenetic position of the causative organism. The two nomenclatural systems are in no way interchangeable, and both are required for the complete classification of the trace fossil. Many trace fossils have not yet been designated a descriptive ichnotaxon, but since trace fossils require names if they are to be treated systematically, an interpretative biotaxon is commonly offered in such cases in place of the lacking ichnotaxon. This procedure tends to deflect attention from the true nature of the trace fossil and implies a spurious accuracy in phylogenetic determination, which leads to unreliable palaeobiological conclusions.

Small, round drill-holes in shells illustrate these points well. They are abundant trace fossils and, having no ichnotaxon, tend to be referred to as the work of shell-drilling muricid and naticid gastropods. However, several other groups of gastropods, as well as the octopodid cephalopods, turbellarians, nematodes and articulate brachiopods also produce round holes, although their work is little understood. Prior to embarking on such speculation as to causative organisms, an ichnotaxon is required in order to draw attention to these trace fossils and increase the rigour of their treatment. When their morphology and distribution are more fully understood we shall be in a better position to discuss their phylogenetic attributions.

RESUMEN

La clasificación de las pistas fósiles requiere un doble sistema de nomenclatura. El nombre de la pista fósil (ichnotaxón) está basado en la morfología de la estructura, mientras que el taxón biológico representa la posición filogenética que se interpreta del organismo causante. Los dos sistemas de nomenclatura no se pueden intercambiar, y ambos son necesarios para la completa clasificación de la pista. A muchas de estas pistas no les ha sido aún atribuido un ichnotaxón descriptivo, pero ya que las pistas fósiles requieren nombres si han de ser tratadas sistemáticamente, se ofrece comunmente en tales casos un biotaxón interpretativo en lugar del ichnotaxón que no se ha descrito todavía. Este procedimiento tiende a desviar la atención de la verdadera naturaleza de la pista fósil e implica una falsa exactitud en la determinación filogenética, lo cual conduce a conclusiones paleobiológicas poco seguras.

Estos puntos quedan bien ilustrados por el ejemplo de unas perforaciones pequeñas y redondas sobre conchas. Son pistas fósiles abundantes y, no teniendo ichnotaxón, tienden a ser relacionadas con la acción perforante de los gasterópodos —naticidos y murícidos— sobre conchas. Sin embargo, varios grupos más de gasterópodos producen perforaciones redondas, al igual que los cefalópodos octópodos, turbelarios, nemátodos y braquiópodos articulados, pero su acción es poco conocida. Antes de embarcarse en tales especulaciones, como son los organismos causantes, es necesario un ichnotaxón para atraer la atención hacia estas pistas fósiles y aumentar el rigor de su tratamiento. Sólo cuando su morfología y distribución sean mejor conocidas estaremos en una posición mejor para discutir sus atribuciones filogenéticas.

RESUM

La clasificació de les pistes fòssils requereix un doble sistema de nomenclatura. El nom de la pista fòssil (icnotaxó) està basat en la morfologia de l'estructura,

mentre que el taxó biològic representa la posició filogenètica que s'interpreta de l'organisme causant. Ambdós sistemes de nomenclatura no es poden intercanviar, i ambdós són necessaris per a la completa classificació de la pista fòssil. A moltes d'aquestes pistes encara no els ha estat atribuït un icnotaxó descriptiu, però, donat que les pistes fòssils requereixen noms si han d'ésser tractades sistemàticament, normalment s'ofereix en aquests casos un biotaxó interpretatiu en comptes de l'icnotaxó que ens manca. Aquest procediment tendeix a desviar l'atenció de la vertadera naturalesa de la pista fòssil i implica una falsa exactitud en la determinació filogenètica, la qual cosa porta a conclusions paleobiològiques poc segures.

Aquests punts queden ben il·lustrats per unes perforacions petites i rodones sobre closques. Són pistes fòssils abundants i, en no tenir icnotaxó, tendeixen a ésser relacionades amb l'acció perforant dels gasteròpodes (muricids i naticids) sobre closques. Tanmateix, altres grups de gasteròpodes produeixen perforacions rodones, així com els cefalòpodes octòpodes, turbelaris, nemàtodes i braquiòpodes articulats, però llur acció és poc coneguda. Abans d'embarcar-nos en tals especulacions, com són els organismes causants, cal un icnotaxó per tal d'atraure l'atenció cap aquestes pistes fòssils i augmentar-ne el rigor de llur tractament. Només quan la morfologia i distribució d'aquestes pistes siguin més conegudes, estarem en una posició millor per discutir llurs atribucions filogenètiques.

INTRODUCTION

There are two major groupings of fossils. (1) Body fossils are the preserved bodily remains of the organisms themselves. (2) Trace fossils, by contrast, are structures produced by the activity of organisms in unconsolidated sediment or in hard substrates.

The relationship between body and trace fossils varies greatly in different groups of organisms. For instance, an articulate brachiopod produces two calcite valves and a spiculate lophophore —and mantle-skeleton, all of which constitutes an incipient body fossil; its pedicle, meanwhile, if attached to a carbonate substrate, may etch a characteristic scar which will become a trace fossil. By contrast, an arthropod, say a burrowing trilobite, produces by ecdysis a large number of skeletons or incipient body fossils, while its burrowing activities may produce a variety of sedimentary structures preservable as trace fossils.

As parts of organims, body fossils are treated nomenclaturally as an extension of biological nomenclature and, although there are problems concerning incomplete preservation and parataxa, it is clear that the biological nomenclatural systems (zoological and botanical) are the right places for palaeontological taxa. Trace fossils, on the other hand, have an entirely different significance from body fossils. Represen-

ting an interaction between organisms and their substrates, trace fossils generally reveal more information on the trace-maker's behaviour and the substrate's consistency than on the trace-maker's systematic position.

Thus, brachiopods of widely different phylogeny may produce identical anchorage scars where they are attached to similar substrates under similar conditions; in contrast, individuals of the same species of brachiopod produce very different traces where attached, on the one hand, to a massive carbonate substrate or, on the other, to loose carbonate sand (Bromley & Surlyk, 1973). Again, a single individual trilobite will produce a number of distinctive sediment structures varying in form according to different behavioural activities within the sea floor (e.g., Seilacher, 1970); its behaviour may also change with ontogeny (Crimes, 1970).

Trace fossils require names in order that they may be studied systematically. Osgood's (1970, p. 295) epigram is now celebrated: «Trace fossils must be named to survive». But it should be clear from the above that names based on trace fossils (ichnotaxa) can have nothing to do with biological taxa. The two types of taxa can never be interchangeable because they are based on completely different principles and data (Seilacher, 1956, p. 158; Osgood, 1970, p. 296-7; Häntzschel, 1975, p. 25).

DUAL NOMENCLATURE

The dual nature of the fossil record requires that there be a dual nomenclature for its classification (Bromley and Für-sich, 1980). This may be demonstrated by a hypothetical example. If the remains of the burrowing shrimp *Callianassa biformis* were to be found in a Pleistocene mud-lined burrow, the structure could be described equally accurately as (1) *Ophiomorpha nodosa* or (2) the burrow of *C. biformis*. The first is an ichnotaxon, the second an interpretation of the trace-maker. The two taxa are in no sense equivalents; they have a relationship only in individual cases where the trace and body fossils are found in genetic association. The shrimp *C. biformis* ceases to construct incipient *O. nodosa* in clayey substrates, and produces instead a boxwork corresponding to *Thalassinoides suevicus* (see Hertweck, 1972). Likewise, *C. biformis* is not the only animal that constructs *O. nodosa*. Other species of *Callianassa* and, indeed, other arthropods only distantly related to *Callianassa*, when constructing branched burrow systems in unstable sand, line their walls with mud and produce *Ophiomorpha* systems (Bromley and Frey, 1974; Frey et al. 1978). The ichnogenus *Ophiomorpha* dates back to the start of the Mesozoic, whereas the genus *Callianassa* appears only shortly before its close.

NATURE OF ICHNOTAXA

Names based on the work of organisms have been erected, in fact, on the basis of very different principles. These differences reflect the considerable spectrum of attitudes and backgrounds of workers using trace fossils, from the sedimentologist using them as tools in elucidating palaeoenvironments, to the zoologist examining a group of endolithic animals and treating their fossil borings nomenclaturally as body fossils. There is also a historical aspect to the problem: many of the older trace fossil names were designated in the belief that the structures were body fossils, particularly algae (see Häntzschel, 1975, p. 24).
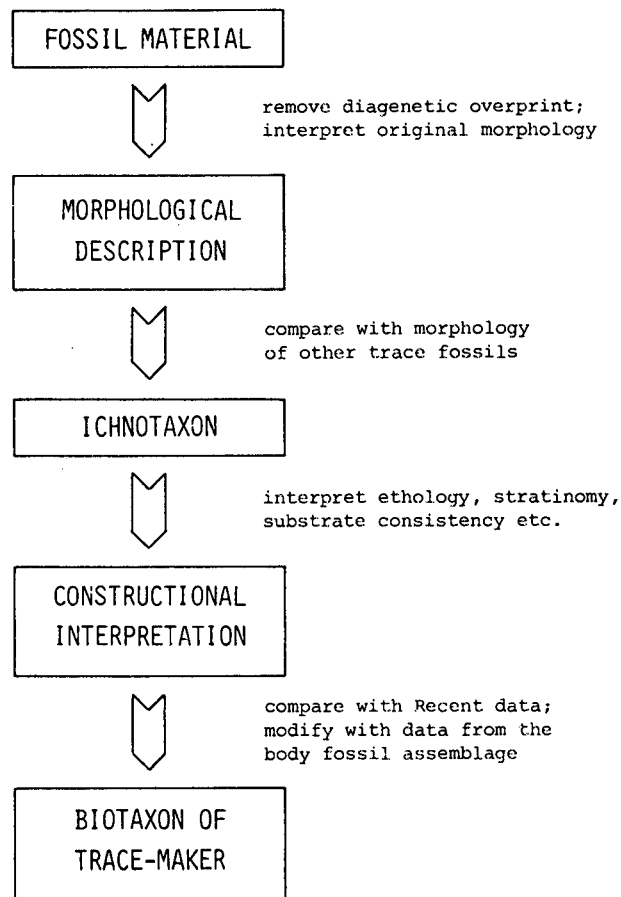
Text-fig. 1. Analysis of trace fossil material generally follows a series of steps such as these, each step involving increasing subjectivity. The scheme shows ichnotaxon and biotaxon to be clearly separate concepts.

The majority of ichnologists today, however, treat ichnotaxonomy as a morphological classification. Ichnospecies are defined and erected on the basis of form, and in this way the name epitomizes the morphological description of the trace fossil.

Only after analysis of the morphology of the trace fossil should the next, interpretative step be taken towards a phylogenetic evaluation (text-fig. 1). Where the trace fossil lacks an ichnotaxon, however, the stages of analysis lose clarity. Some sort of name is necessary, and in this case a biotaxon is commonly used in place of the lacking ichnotaxon, carrying with it a spurious sense of accuracy of interpretation. This in turn tends to remove the incentive to analyse the trace fossil further, and can lead to unwarranted palaeobiological conclusions.

Let us take a particularly abundant, but as yet unnamed, trace fossil to illustrate these points: small, round holes in carbonate skeletons.

FOSSIL ROUND HOLES IN SHELLS

In most fossil shell assemblages, a proportion of the shells contain small round holes. Abundance varies; round holes are relatively uncommon in the Palaeozoic, enormously abundant in the Cenozoic. They are also abundant today and have attracted much attention from biologists. Unfortunately, the emphasis of biological investigation has been influenced by economic factors, and our knowledge of the production of round holes in shells today is heavily biassed towards the depredations of predatory snails on mussels. Of these gastropods, the boring Muricacea and Naticidae have received by far the most attention.

In fossil material the round hole is never preserved with its maker in situ. Its origin is therefore a matter for speculation, and this normally centres around comparison with biological findings today. Consequently, the usual conclusion drawn is that the hole was drilled by a predatory gastropod. In Tertiary deposits this interpretation may be justifiable, and the conclusions drawn from it reasonable. Even here, however, the possibility of the holes not being of predatory gastropod origin is not usually entertained. In Mesozoic and Palaeozoic occurrences, glib attribution to drilling snails can be quite unwarrantable and lead to untenable conclusions (Pl. 2, fig. 5).

For example, Müller (1969) assumed a naticid origin for numerous round-bottomed pits in the apex of a holasteroid echinoid from the Upper Cretaceous chalk of Germany (see Pl. 1, figs. 1, 2). None of the pits penetrated the test completely, implying that the snail had made about 760 abortive attempts representing several months work. A more reasonable interpretation of the origin of such pits (Pl. 1, fig. 3) might be the work of a parasite, perhaps indeed a gastropod: species of the prosobranch genus *Pelseneeria* today insert their enlarged proboscis into echinoderm tissues (Köhler and Vaney, 1908; Köhler, 1924).

Ordovician brachiopods containing round holes have received considerable attention, and have chiefly been interpreted as evidence of gastropod predation. Cameron (1967), for example, entitled his paper «Oldest carnivorous gastropod borings...». Carriker and Yochelson (1968), however, gave a detailed analysis of our knowledge of modern gastropod borings and the geological history of the boring snails. They concluded that the Ordovician borings require another explanation and suggested attachment scars of sedentary soft-bodied organisms. They furthermore concluded, in agreement with Fischer (1962), that only selected borings from the late Mesozoic onwards could be attributed reasonably to gastropod predation. Sohl (1969) searched the literature and museum collections and claimed that, whereas the Naticidae and Muricacea appeared in the Jurassic and Cretaceous respectively, trace fossils attributable to them do not appear until the Cenomanian and Campanian respectively.

Since then, Thomas (1976, p. 489) has illustrated the «earliest recorded gastropod boring» in a glycymerid shell from the Albian Blackdown Sand of England. The morphology suggested the work of a muricacean. Taylor et al. (1980, p. 397) called these Blackdown Sand borings «unequivocal» predation holes, attributed them to both naticids and muricids on the basis of their morphology, and recorded the presence of body fossils of several naticid species and two or three muricids in the same sediment.

Certainly the presence of body fossils of gastropods from families possessing the boring habit today, in the same sediment as the bored shells, greatly increases the likelihood that the body and trace fossils are genetically associated (Pl. 1, fig. 4; Pl. 2, fig. 1). However, the interpretation of the holes cannot be considered «uneqivocal». We know little about boring groups other than muricaceans and naticids today, and next to nothing about those of the Albian. Let us briefly review the present state of knowledge of modern shell-drilling organisms.

RECENT ROUND HOLES IN SHELLS

Organisms that drill more or less round holes in shells today are taxonomically diverse and bore for a variety of reasons. The following list is presumably not complete, but it will serve to demonstrate the unequal coverage the different groups of organisms have received, and thereby reveal some of the pitfalls that await interpretations of fossil material. The first six groups belong to the Gastropoda.

(1) Naticidae (Mesogastropoda, Prosobranchia). The naticids are probably the most renowned of predatory snails, and their habits are well-known (e.g., Ziegelmeier, 1954; Fretter and Graham, 1962). Although some species hunt on the sea floor, all naticids prey on infaunal molluscs, and feed infaunally. In prey that cannot be entered otherwise, a boring of very characteristic form is drilled by combined chemical and physical means. The hole is wide externally, narrow internally, and has paraboloid walls (see Carriker and Yochelson, 1968, pl. 2, figs. 6-25) (Pl. 1, figs. 4, 5). In thick shells the paraboloid form is exceeded, and the shape approaches a spheroid, the external opening having a smaller diameter than the maximum width of the boring. The degree of completion of the inner opening varies, and the shape and size of that opening is therefore highly variable. The boring is usually strategically placed, avoiding the thickest part of the shell. Incomplete borings usually have a slight central boss. There are few temperate and subtropical shorelines today that are not strewn with shells bearing the characteristic drill-holes of naticids. Body fossils of naticids make their appearance in the Jurassic.

(2) Muricacea (Neogastropoda, Prosobranchia). Predation by muricaceans is also well-known owing to the abundance of these carnivores in shallow seas, where they prey on epifaunal forms such as barnacles, limpets and oysters. We have a detailed knowledge of the feeding habits of several species, owing largely to the work of M. R. Carriker. An excellent summary was given by Carriker and Yochelsen (1968). The shape of the boring varies somewhat, but is generally slightly conical, approaching cylindrical, perpendicular to the shell surface (cf. Pl. 2, figs. 2, 3). As in naticids, the means of boring involves a combination of chemical and physical methods. Again, the drill-hole is normally strategically placed for efficiently entering and feeding on the prey. Incomplete borings have a rounded to flat-rounded termination. Variation in morphology is well illustrated by Carriker and Yochelson (1968, pl. 1). Body fossils of muricaceans appear in the top of the Lower Cretaceous (Sohl, 1969, fig. 1).

(3) Tonnacea (Mesogastropoda, Prosobranchia). The three main families comprising the Tonnacea are all known to drill prey (Day, 1969), but very little is known of their feeding habits or of the holes they produce. The habits of the Cassidae are best known. Hughes and Hughes (1971) described how *Cassis tuberosa* cuts a disc from the test of regular echinoids in order to feed on them. The resulting hole is approximately circular and has a rough edge. A large proportion of dead
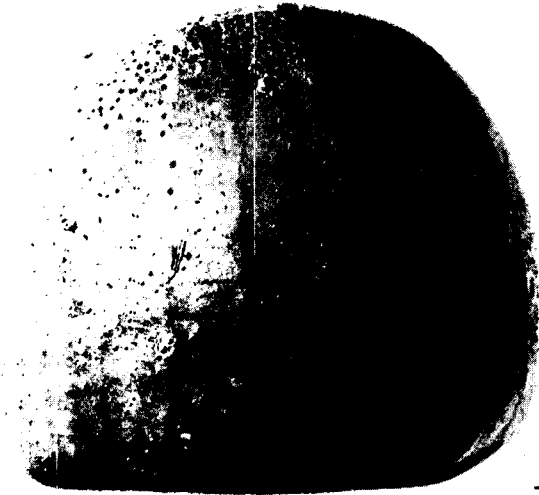
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Echinometra lucunter tests on Caribbean beaches contain such holes, but it is not known to what extent other cassids may produce similar holes.

The other families, Cymatiidae and Tonnidae, also include facultative borers (e.g., Morton & Miller, 1968, p. 466), but our knowledge of their work is negligible. The superfamily appears in the Mesozoic and expands in the Tertiary.

(4) Capulidae (Mesogastropoda, Prosobranchia). The capulids tend towards a parasitic mode of life, and some species attach to pectinoid bivalves and steal food from their gills (Orr, 1962). In some such cases the shell margin of the host is notched, to allow easier access to the snail's proboscis; in others, a hole is produced through the shell of the host (Pl. 2, fig. 6). Matsukuma (1978) has recently added significantly to our understanding of capulid boring and has summed up previous literature. The few borings that have been studied are oval or tear-shaped. They lie either centrally on the host, or beside one of the ears. The life-long site of attachment of the parasite may produce recognizable scars of abrasion on the host shell and there may be slight growth deformation of the host shell in reaction to the presence of the parasite. Matsukuma (1978) consequently has been able to identify probable fossil examples of capulid borings (Pl. 2, fig. 7). The Capulidae emerge in the Mesozoic and are important faunal elements by the Late Cretaceous.

(5) Nudibranchs (Opisthobranchia). A dorid nudibranch, *Okadaia elegans,* was reported by Young (1969) to bore smooth, round, bevelled holes in the calcareous tubes of polychaetes on which it fed. The holes were not illustrated, but were said to be «similar in shape to the boreholes produced by naticid gastropods» (Young, 1969, p. 904-5). No other instances of nudibranchs boring have yet been recorded. The present case would seem to constitute a serious threat to the identification of naticid borings in the fossil record. Opisthobranchs appeared in the Carboniferous, but the nudibranchs themselves have left a negligible body fossil record.

(6) Pulmonata. Several records exist of holes being bored by pulmonate gastropods. Oleacinids rasp ragged holes in other shells, possibly in part to obtain calcium and in part to eat the prey within (*fide* Carriker and Yochelson, 1968, p. 3). Certain zonitid species have also been observed to rasp irregular holes in other land snail shells in order to consume the part of the prey that cannot be reached through the aperture of the shell (Mordan, 1977).

(7) Octopodidae (Cephalopoda). It has long been known that, under certain circumstances, octopi drill holes in shells of prey molluscs, but only recently have details of the borings been studied. In contrast to the carnivorous gastropods, the octopus does not drill a hole to eat through. It merely injects venom through the boring, and then waits for the prey to weaken (Pilson and Taylor, 1961; Wodinsky, 1969). Consequently, octopus borings are relatively small, and the inner opening is commonly minute. The external opening is generally larger than the inner and the boring may have an oval outline (Pl. 3, fig. 7). The holes have variable shapes, however, even those drilled by the same individual (Arnold and Arnold, 1969; Nixon, 1979a). Furthermore, recent research has indicated that the morphology of the boring also varies according to differences in substrate. Thus, holes bored by *Octopus vulgaris* in *Mytilus edulis* tend to be minute, oval and conical (Pl. 3, fig. 7) whereas in *Murex trunculus* they are rounder and more cylindrical (Pl. 3, fig. 4) (Nixon, 1979a).

Octopus drills holes by means of the thorny salivary papilla, not the radula, and apparently does not use chemical methods (Nixon, 1979b, 1980; Nixon et al., 1980). Boring is accomplished rapidly, and sometimes more than one hole is bored in the prey shell. In gastropod prey, the octopus commonly chooses a position in the spire (Arnold and Arnold, 1969), in contrast to naticids, which generally bore the last whorl (Pl. 2, fig. 1); and in bivalves, the octopus commonly drills accurately into or beside one or both adductor muscles (pers. observation).

The fact that some species of *Octopus* bore holes today opens the possibility that other cephalopod groups now extinct may also have done so. Octopodids themselves may have a long history, possibly back to the Palaeozoic (cf. Saunders and Richardson, 1979). The reduction of skeleton in some groups of cephalopods has left us in ignorance of their history and diversity in the geological past.

(8) Turbellaria. The flatworm *Pseudostylachus ostreophagus* is known to drill minute key-hole-shaped to oval holes in juvenile oysters (Yonge, 1964, p. 108). Details of the form of the holes are not well documented.

(9) Nematoda. Sliter (1971) recorded that living adult specimens of the benthic foraminifera *Rosalina globularis* d'Orbigny occasionally contain a single living predaceous nematode. Examination of these same foraminifera revealed one to three minute borings penetrating the dorsal wall of the chamber or chambers containing the nematode, and it was assumed that the nematode was responsible for these borings. The borings were 5.3 - 14.3 μm in diameter, round to oval at external and internal openings, and approximately cylindri-

PLATE 1.

Fig. 1. Lateral view of *Echinocorys scutata.* The upper surface of this specimen contains numerous small pits, see fig. 2. Santonian, Upper Cretaceous chalk; White Ness, Kent, England. Institute of Geological Sciences, London: PH 55. Slightly enlarged.

Fig. 2. Close view near apical area of the echinoid shown in fig. 1. Note variation in the size of the pits, from 0.4 to 1.0 mm in diameter, and the tendency for adjacent pits to fuse.

Fig. 3. Similar, but isolated pits to those in figs 1 and 2, 0.5 mm in diameter, in the ahermatypic coral *Lophelia* sp. Many such pits occur chiefly in areas of the coral skeleton that show no other bioerosion, and thereby seem to have been constructed in the living parts of the colony that were still covered by the coenosarc. Vasfi Formation, Pleistocene; near Vasfi, Rhodes, Greece.

Fig. 4. *Natica millepunctata* bearing a single *Oichnus paraboloides* (holotype) in the final whorl. The morphology, location on the shell, and faunal association all suggest *N. millepunctata* as the trace maker. Inset: natural size.

Fig. 5. Holotype of *Oichnus paraboloides,* external view; see fig. 4. X 12.5.

cal. The outer opening was roughly bevelled in some cases, the inner generally irregular and rough, though the cylinder itself was smooth. Closely similar borings (Sliter, 1971, type 1) were found in fossil foraminifera of Holocene and Cretaceous age and a nematode origin was suggested for these also.

A somewhat similar but rather larger boring is also common in some foraminifera communities (Sliter, 1971, type 2). It occurs either in haphazard groupings or regularly, one into each chamber of the outer whorl of the test (Pl. 3, figs. 1, 2). The outer opening may be bevelled. They have been recorded from the Quaternary (e.g., Henbest, 1942), Tertiary (e.g., Livan, 1937), Cretaceous (Sliter, 1971) and Jurassic (Livan, 1937). A predatory gastropod origin for these holes has been suggested in most cases, but Sliter (1971) showed that evidence for this was incomplete, and assumed that soft-bodied predators, perhaps nematodes or polychaetes, may have been responsible.

(10) Brachiopoda. The attachment base of the pedicle of several articulate brachiopods has been shown to have the ability to etch the surface of carbonate substrates (Ekman, 1896; Bromley and Surlyk, 1973). In certain forms, e.g., *Terebratulina* spp., the pedicle may split into a bundle of many strands, somewhat resembling the byssus of bivalves. Each strand has the ability of penetrating and passing through carbonate grains with which it comes into contact. A groove or round hole is produced in the substrate surface, having random orientation and a diameter of up to about 100 μm (Pl. 3, figs. 5, 6).

Articulate brachiopods were far more diverse in the Palaeozoic than they are today. Members of both Rhynchonellida and Terebratulida possess substrate-etching pedicles today and it might therefore be assumed that these and other groups did so in the past. Schumann (1969) even showed that certain genera in both Strophomenida and Spiriferida divided their pedicle before these emerged from the shell and that the separate strands passed through small, circular «borings» in the shell. It would seem highly likely in that case that these same strands, on attachment to a carbonate substrate, would be capable of dissolving similar perforations there.

Although as yet no perforations from the Palaeozoic have been attributed to brachiopods, it would seem to be a promising field for exploration.

SYSTEMATICS

It is hoped that the above will suggest that there is a much wider range of possible producers of round penetrations in carbonate skeletons than is generally implied in the interpretation of fossil material. An ichnogenus is therefore offered here to cover such borings in the hope that this will encourage examination of their morphology and distribution, and stimulate research into the modes of origin of particular examples.

Both total penetrations and pits («incomplete» penetrations) are covered together in the following ichnotaxonomy, as every intermediate stage occurs.

Ichnogenus *Oichnus*, nov.
Diagnosis: Circular to subcircular holes of biogenic origin bored into hard substrates. The hole may pass right through the substrate as a penetration, where the substrate is a thin shell; or end within the substrate as a shallow to deep depression or short, subcylindrical pit.
Derivation of name: Letter O, the shape of the trace; iknhos, Greek, track.
Type species: *Oichnus simplex*, ichnosp. nov.
Remarks: Examples that do not penetrate right through the substrate are generally extremely short, at most three or four times their diameter. The shortest *Trypanites* spp. are considerably longer than this and there sould be no confusion between these two ichnogenera of cylindrical borings.

Oichnus simplex ichnosp. nov.
Diagnosis: *Oichnus* having a simple cylindrical or subcylindrical form, axis more or less perpendicular to the substrate surface. Where the substrate is not penetrated right through, the distal end is flattened hemispherical.
Holotype: Perforation in the shell of an oyster, *Arctostrea diluviana* (Linnaeus), Pl. 3 fig. 3. External diameter 1.8 mm, internal diameter 1.4 mm. Housed in the Geological Museum, University of Copenhagen, Denmark, no. MGUH 15351.
Type locality and horizon: Ivö Klack, Scania, Sweden. Uppermost Lower Campanian (Cretaceous). (See Christensen, 1975, p. 12.).
Remarks: The cylindrical walls may be smooth, but commonly show an etched relief reflecting the ultrastructure

PLATE 2.

Fig. 1. Three *Natica millepunctata*, each containing an *Oichnus paraboloides* in the final whorl. Morphology, location on the shells, and faunal association all suggest that these are cases of cannibalism by *N. millepunctata*. Volterra, Italy; Pliocene. J. Martinell coll. X 2.

Figs. 2 & 3. External and internal views of a plate of a large balanid barnacle containing three *Oichnus simplex*. The morphology of the borings, the substrate species and the associated body fossils all suggest predation by *Nucella lapillus*. However, the unfinished boring has caused growth deformation in the barnacle, producing a swelling internally (fig. 3). If predation were the cause of the holes, then the abortive middle hole must predate the others of the group by a period of time sufficient for the barnacle to partially repair its skeleton. Diameter of holes 1.5 - 2.0 mm. See also fig. 4.

Fig. 4. A further problematicum from the same locality as figs. 2 & 3. A *Buccinum undatum* contains at least 39 examples of *Oichnus simplex*, 13 of which are visible in the figure. Diameters of the holes vary from 0.1 to 1.5 mm. Saxicava Sand (10 000 BP), Uddevalla, Sweden. V. Nordmann coll.

Fig. 5. A palaeonuculid bivalve from the Cymodoce Zone, Lower Kimmeridgian, Upper Jurassic; Blue Circle Cement Co. clay pit, Westbury, Wiltshire, England. C. K. Clausen coll. The original aragonite is well preserved, and one shell contains a single *Oichnus simplex*. The morphology and location on the shell suggest predation, and the fact that the two valves have remained together may indicate that this occurred infaunally. Shell length 11 mm; X 6.

Fig. 6. An individual of *Pecten albicans* which has been bored by *Capulus dilatatus*. The parasitey has produced a tear-shaped hole near the centre of the valve, to the right of which a circular, pale area can be seen where the shell of the parasite has slightly abraded that of the host. Pacific coast of southwest Japan; National Science Museum, Tokyo. X 13.

Fig. 7. Valve of *Cryptopecten vesiculosus* containing a tear-shaped hole in the ear around which, eccentrically, is a distinct, subcircular abrasion scar. Comparison with fig. 6 strongly suggests this to represent a case of capulid parasitism (Matsukuma, 1978). Pleistocene; Moeshima Shell Bed, Shinjima, Kagoshima Prefecture, Japan. National Science Museum, Tokyo: GK-M 10001. X 4.6.

of the substrate. This ornament may be enhanced to an unknown degree by diagenesis. These substrate-imposed features («Fremdskulptur» of Voigt, 1971) should not affect the diagnosis.

Range: No age restriction.

Oichnus paraboloides ichnosp. nov.

Diagnosis: *Oichnus* having a spherical paraboloid form, truncated in those cases where the boring penetrates right through the substrate. Where it does not so penetrate, the paraboloid may be deformed by a slightly raised central boss.

Holotype: Perforation in the shell of *Natica millepunctata* Lamarck. External diameter 3.8-4.1 mm, internal diameter 1.8-2.2 mm. MGUH 15352. Pl. 1, figs. 4, 5.

Type locality and horizon: Monte Smith, Rhodos town, Rhodes, Greece. Near base of the Rhodos Formation, Pleistocene.

Remarks: In many cases the outer opening is enlarged by local or complete bevelling. The wall of the boring is commonly ornamented by etching patterns reflecting the ultrastructure of the substrate.

Range: No age restriction. A possible example has been recorded by Matthews and Missarzhevsky (1975) from the basal Cambrian; Fenton and Fenton (1931) figured apparent *O. paraboloides* from the Devonian. Incipient *O. paraboloides* is produced by naticid gastropods today.

CONCLUSIONS

Some of the problems presented by ichnological taxonomy are illustrated by small, round perforations drilled by organisms in skeletons.

Such holes illustrate admirably the general need in ichnology for a dual nomenclature: an ichnotaxon based on physical facts presented by the trace fossil, and a biotaxon based on the phylogeny of the borer. Thus, an individual boring may be classified either as *Oichnus paraboloides* or, if the evidence justifies it, as the presumed boring of a naticid gastropod.

Trace fossils have extremely varied modes of origin. The more simple the morphology of the trace fossil, the wider the scope of possible interpretations. For example, production rate for a muricacean gastropod may be more than one incipient *O. simplex* per week throughout its life. On the other hand, only a single incipient *Oichnus* sp. may be produced in the life-time of a capulid gastropod parasitizing a bivalve host. This difference in production and significance of trace fossils also serves to emphasize the fundamental difference between ichnotaxa and biotaxa, and the concurrent need for both.

Round holes in shells are among the most common trace fossils, yet their morphological simplicity renders their biological interpretation hazardous. We know a great deal about two groups of predatory snails and their borings today, but have only a glimpse of our ignorance of the habits of other boring snails, octopi and turbellarians.

If some octopi drill shells today, maybe many species will be found to do so. We must then expect that they have done so for some time in the geological past. There is also a possibility that the major extinct groups of cephalopods of the Mesozoic and Palaeozoic also included shell-drilling forms. Also, the knowledge that there is a nudibranch today that drills holes that resemble those drilled by naticids is disturbing. We must learn to distinguish octopodid and nudibranch drill-holes from muricid and naticid drill-holes before we can use the fossil borings in palaeobiological studies. The classification of these holes as trace fossils, however, should help to increase the rigour of their treatment and protect them from premature phylogenetic interpretation.

ACKNOWLEDGEMENTS

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PLATE 3.

Fig. 1. A robertinacean foraminiferan, *Ceratobulimina contraria* (Reuss, 1851), containing many circular borings 15 to 30μm in diameter. Oligocene; Hvorslev, Denmark. SEM.

Fig. 2. Details of a single boring 30μm in diameter, see fig. 1. The aragonite test of the foraminiferan may have undergone some diagenetic alteration and the walls of the boring may have been slightly modified; a lath is seen in the act of falling away. SEM.

Fig. 3. *Oichnus simplex*, external view; holotype. X 19.

Figs. 4 & 7. SEM pictures of Recent borings of *Octopus vulgaris*, external views. Fig. 4 in *Murex trunculus*; the circular outer opening is 0.5 mm in diameter and slightly bevelled. Fig. 7 in *Mytilus edulis*; the oval pit is 0.5 mm wide and is surrounded by a more or less circular area of bevelling; the inner, oval opening is very small. Specimens by courtesy of M. Nixon.

Figs. 5 & 6. SEM pictures of Recent borings in a serpulid polychaete tube produced by the divided pedicle of the brachiopod *Terebratulina retusa*. Fig. 5: X 37. Fig. 6: X 500, diameter of the hole 90μm. Geological Museum, University of Copenhagen: MGUH 12807.
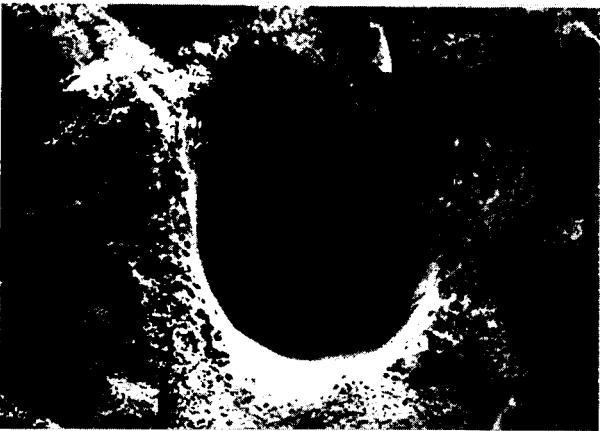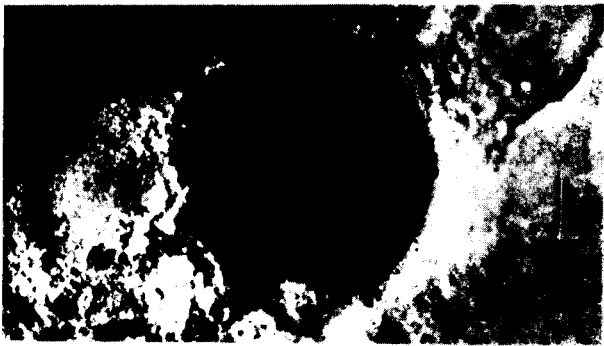
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