COMPARATIVE ANALYSIS OF FOSSIL AND RECENT ECHINOID BIOEROSION

by R. G. BROMLEY

ABSTRACT. One of the most abundant forms of bioerosion sculpture on Mesozoic and Cainozoic shells and other hard substrates has a pentaradiate symmetry based on a regular, stellate module consisting of five radiating grooves. Regular echinoids today, browsing on encrusting and boring organisms on hard substrates, produce identical sculpture to the trace fossil, and a common origin is suggested. The tooth scratches lose their pentaradiate orientation and become subparallel where the echinoid gnaws along edges of shells and flat pebbles; a corresponding sculpture is also encountered in the trace fossil. The pentaradiate trace fossil is designated as *Gnathichnus pentax*, ichnogen. et ichnosp. nov.

A TYPE of hard substrate trace fossil that, despite its abundance, has received scant attention from geologists, is the sculpture produced by browsing and foraging animals. Such sculpture, commonly termed 'bioerosion' (Neumann 1966), occurs on substrate surfaces that have been exposed at the sea floor for a period of time. Indeed, in some post-Palaeozoic sediments of shallow marine origin it is difficult to find fossils unaffected by superficial bioerosion.

One of the most common types of bioerosion sculpture has a basic pentaradiate symmetry and comparison with the traces produced by the teeth of living regular echinoids strongly suggests a common origin.

DESCRIPTION OF FOSSIL MATERIAL

The surface sculpture of bioeroded shells and other substrates may consist of random or grouped scratches of various depths and sizes. Examples have been described by Abel (1935), Boekschoten (1966, 1967), Riegraf (1973), Bishop (1975), and many others. Among these different types of scratches there is a single group that can be treated separately owing to its distinctive pentaradiate organization and regular morphology. The aspect presented by this type depends on (1) the spacing between the scratches, (2) the curvature of the substrate, and (3) the presence of borings in the substrate.

More or less flat surfaces

In its simplest form the trace fossil consists of a regular stellate arrangement of five radiating grooves making an angle of approximately 72° with each other. Such a 'star' is rarely seen in isolation but may be regarded as the 'modular unit' (Heinberg 1973) of the ultimate bioerosion sculpture. The 'rays' of this stellate module have a uniform length and depth. The diameter of the module rarely exceeds 5 mm and in most cases is less than 2 mm.

Considerably more common than single stars are compound traces built up of a series of overlapping identical stars in which equivalent rays are repeated parallel

to one another (Pl. 85, fig. 1). In those cases where repeated rays lie closer together than they do to other rays of the same star, the closely spaced group of parallel grooves representing the repetition of a single ray may be erroneously interpreted as the module (as e.g. McKerrow *et al.* 1969, pl. 12, fig. 3) rather than the pentaradiate star itself.

Compound stellate bioerosion sculptures may become increasingly complex by repetition of overlapping stars until the individual stars can no longer be distinguished and the substrate surface is completely covered with grooves of similar depth and length (Pl. 86, figs. 4–5). Nevertheless, plotting of the orientation of the grooves over selected areas of the surface reveals the underlying stellate module. Indeed, the pentaradiate distribution of the grooves is so pronounced in most cases that it can be discerned with the naked eye, and accentuated by oblique illumination.

Sharply curved and irregular surfaces

The full development of the trace fossil as described above is seen only on flat substrates (e.g. smooth mollusc shells). Where the surface is irregular, the stellate module is commonly reduced to fewer rays, but the 72° angle between rays remains constant (Pl. 85, fig. 3; Pl. 89, fig. 1). In cases where the substrate describes a sudden and extensive convex curve, as at the edge of a flat pebble, the basic module changes so that the grooves become densely packed and more or less parallel (Pl. 86, fig. 2). Where perforations occur in the substrate which exceed the diameter of the basic module, these are commonly surrounded by a series of closely packed grooves in this case aligned more or less perpendicular or normal to the edge of the hole. The dimensions of the individual grooves are precisely similar to those of the pentaradiate sculptures on related flat surfaces.

Presence of sessile organisms within and upon the substrate

Concentration of the grooves also occurs around borings and encrusting skeletons that are smaller than the diameter of the module. In contrast to the subparallel orientation of the grooves around large-scale perforations in the substrate, the grooves around smaller sites exhibit the characteristic regular pentaradiate arrangement. This relationship is particularly noticeable in the case of borings of organisms in the substrate, where the grooves are generally deep and associated with breakage of the rim of the boring. Well-developed stars are seen around acrothoracic barnacle

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EXPLANATION OF PLATE 85

Fig. 1. *Gnathichnus pentax* on a belemnite from Reutlingen, near Tübingen, West Germany. Upper Lias delta. Printed from a peel. ×9.

Fig. 2. Bite traces of a Recent echinoid on gastropod shell, *Charonia tritonis*. Locality unknown. MMH 13387, Mineralogisk Museum, Copenhagen. ×7.

Fig. 3. *Gnathichnus pentax* (holotype) on an oyster shell from lowermost Pleistocene at Kritika, Rhodes. MMH 13386. ×8.

Fig. 4. Bite traces of *Sphaerechinus granularis* on a flat, algal-coated limestone pebble. The traces were made in an aquarium at the Institut Rudjer Bošković-Zagreb, Centre for Marine Research at Rovinj, Yugoslavia. The specimen is housed in the North Adriatic Collection of the Geologisch-Paläontologisches Institut, Göttingen University. ×9.
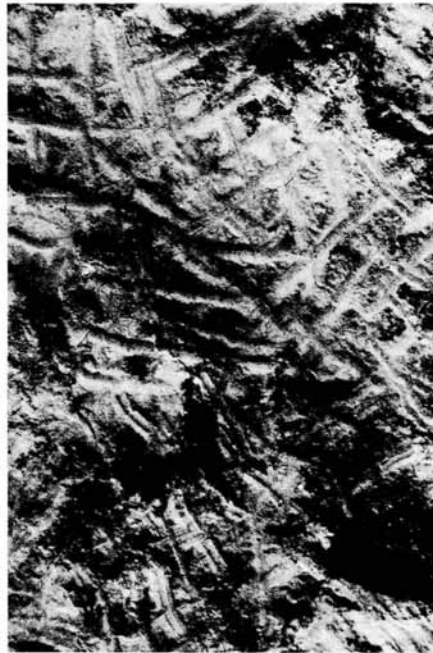
PLATE 85

BROMLEY, echinoid bite traces

borings (Pl. 88, figs. 1–3), borings of small worms (Pl. 86, fig. 3; Pl. 87, fig. 6), and the papillar orifices to clionid sponge borings. A particularly close association is found in the last case, and commonly a large proportion of the papillar orifices are surrounded by multiple stellate modules (Pl. 87, figs. 1–5). Other comparable inhomogeneities of the substrate can also be surrounded by stellate groove patterns, such as the ambulacral pores of echinoids (Pl. 88, figs. 4–5).

GNAWING TRACES PRODUCED BY PRESENT-DAY MARINE ANIMALS

Several groups of animals cause bioerosion through their eating activities. In many of these groups the process is chiefly one of 'biting' and 'crushing' and is caused by biramous tools, i.e. a pair of opposable jaws or claws, as in, for example, parrot fish and grapsid crabs. These animals work over hard substrates, breaking up the surface, especially around borings, in search of epilithic and endolithic organisms or eroding living substrate such as coral (Bakus 1964, 1966). The result of such foraging is generally a series of highly irregular scratches, pits, and broken protuberances that in no way resembles the uniform, pentaradiate traces discussed here (Pl. 89, fig. 3) (Abel 1935, p. 325). In certain circumstances, however, fish can produce groups of subparallel scratches at breakage cavities (Kier and Grant 1965, p. 55).

A more homogeneous form of bioerosion is produced by the methodical grazing of gastropods and polyplacophores. Boekschoten (1966, fig. 11) illustrated typical chiton rasping traces, while those of grazing gastropods have received more attention (see particularly Abel 1935, fig. 338; Ankel 1929, 1936, 1937). In these cases, extensive areas of substrate are eroded, but the rather even scratches have a subparallel distribution within arcuate groups that reflect the swinging movement of the head as the gastropod progresses slowly over the substrate, and scratches of the individual teeth of the radula may be preserved (Ankel 1936, fig. 8, 1937, figs. 2 and 11). Predatory boring gastropods may scratch the shell surface of their prey with their radula before boring, but these scratches have random orientation and very local distribution (Carriker 1969, figs. 11–15). This radular erosion does not produce a sculpture of pentaradiate module.

EXPLANATION OF PLATE 86

Fig. 1. Gnawing traces of *Sphaerechinus granularis* on the rounded edge of an algal-coated limestone pebble. Details as for Plate 85, fig. 4. ×3.

Fig. 2. Gnawing traces on the edge of a shell fragment (*Inoceramus* sp.) from Lower Maastrichtian white chalk, Dronningestolen, Møns Klint, Denmark. MMH 13388. ×6.

Fig. 3. *Gnathichnus pentax* along a worm boring, the roof of which has been largely broken away. Upper Campanian, Bluffport Marl Member, Demopolis chalk, north of Parker, Alabama, U.S.A. MMH 13389. ×6. See also Plate 87, fig. 6.

Fig. 4. Surface of an oyster (*Arctostrea diluviana*) entirely sculptured with *Gnathichnus pentax*. Uppermost Lower Campanian calcarenite, Ivö Klack, Ivö, Scania, Sweden. MMH 13390. ×6.

Fig. 5. Enlargement of part of fig. 4. ×20.

PLATE 86

BROMLEY, echinoid bite traces

Echinoid-gnawing traces

The work of one particular group of organisms, however, is highly distinctive and provides an excellent model for the pentaradiate trace fossils, namely the browsing traces of regular echinoids. A considerable part of the body of these animals is taken up by the jaw apparatus, the so-called 'Aristotle's Lantern', the five teeth of which can be brought to bear on the substrate with considerable power through the muscula-ture of the lantern and the concerted effort of the numerous tube feet. Regular echinoids are highly efficient bioeroders and cause considerable rock destruction in their quest for food. Umbgrove (1939) described intertidal notch erosion in coral rock chiefly by *Echinometra mathaei* in the East Indies (text-fig. 1) and Neumann (1966) attributed extensive notch erosion in limestone immediately below spring low tide in Bermuda chiefly to the work of *Lytechinus variegatus*. Neumann (1965) also emphasized the production of quantities of fine rock powder by the bioerosive

TEXT-FIG. 1. A 'toadstool island' from the north coast of Batoe Daka, Togian Islands, Celebes, sketched after Umb-grove (1939, fig. 21). The intertidal notch is chiefly eroded by *Echinometra mathaei*.
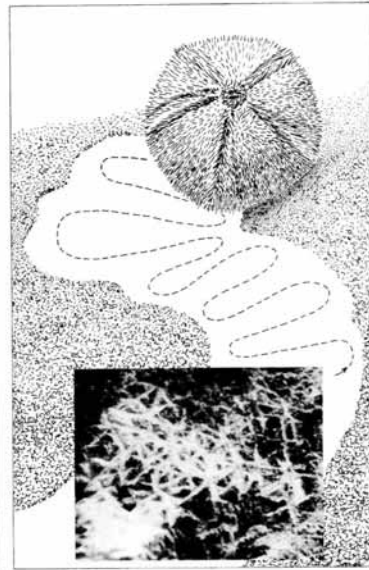
TEXT-FIG. 2. *Echinus esculentus* clears a browsing path about as wide as its own test by meandering over the substrate. Sketched from a photograph of an animal in the natural environment on the sea floor at Heligoland, West Germany. Inset photograph of gnawing traces of this species in an aquarium. Both from W. E. Krumbein, pers. comm. Meandering line from Krumbein and Van der Pers (1974, fig. 6a).

activities of *Lytechinus variegatus*. In many rocky shores echinoids use their teeth to bore deep protective cavities, commonly with narrow entrances, in granite, limestone, and artificial substrates (Märkel and Maier 1967; references in Bromley 1970).

The prime function of the great jaw apparatus is for the exploitation of organisms encrusting and boring into hard substrates. A study of the feeding habits of regular echinoids reveals many features that render these animals likely candidates for the originators of the pentaradiate trace fossils.

The mode of employment of the echinoid tooth involves a powerful scraping action, producing a single groove that has, on an even substrate, a characteristic and uniform width and depth. The simultaneous action of all five teeth produces a stellate pattern of grooves identical in form to the module of the trace fossil (Pl. 85, fig. 2). This trace has been described by many workers.

Krumbach (1914) stated that the scratch produced by *Sphaerechinus granularis* on limestone in the Adriatic Sea was up to 0·5 mm deep (Pl. 85, fig. 4; see also Abel 1935, fig. 310). Krumbach observed that each bite in this species took 30–35 seconds at a temperature of 10 °C—a little faster at higher temperatures—and comparable speeds have been recorded for other species (e.g. Milligan 1916). Between individual bites, i.e. during the time required to reopen the jaws, the echinoid will have travelled a certain distance over the substrate, so that at the next bite the five teeth cut fresh substrate adjacent to the first bite. In this way successive stars are scratched side by side. Krumbein and Van der Pers (1974) observed that as the browsing echinoid progresses over the substrate it follows a regularly meandering course and covers a strip of substrate approximately the same width as the animal's test (text-fig. 2). Owing to the non-cephalization of regular echinoids, the orientation of the body and its tooth apparatus remains more or less unaltered as the animal wanders, and the stellate grooves of the browsed area consequently show a corresponding constant alignment. This constancy of orientation is also characteristic of the trace fossil (Pl. 85, figs. 3 and 4).

There has been much speculation over the food preferences of regular echinoids and conflicting evidence has been recorded in the literature. Most species, however, appear to take advantage of a variety of types of organic matter. Shallow-water species feed predominantly on algal films on hard substrates, and some appear to be exclusively algal browsers. Encrusting animals, particularly bryozoans, are also scraped off shell and rock surfaces. Milligan (1916) recorded *Psammechinus miliaris* from British waters eating empty mollusc shell and serpulid tubes, and also the periostracum of the shells of living molluscs. Jensen (1969) regarded bryozoans as of vital importance as food for *P. miliaris* in Danish and Norwegian waters, whereas Krumbein and Van der Pers (1974) recorded a preference for the boring worm *Polydora ciliata* in this species and *Echinus esculentus* at Heligoland.

Ormond and Campbell (1971) emphasized the browsing efficiency of *Diadema setosum* and *Echinothrix diadema* in the Red Sea off Sudan. These echinoids emerged from their borings and crevices at night to browse freely on the surrounding coral rock surfaces, which were kept largely clean from encrusting organisms. Only locally, where both echinoids were absent, were rich developments of encrusting algae to be found.

The methodical exploitation of encrusting organisms for food invariably causes

scratching of the underlying substrate. The resulting stellate pattern of overlapping superimposed grooves (Krumbach 1914, fig. 1; Abel 1935, fig. 310; Neumann 1966, fig. 7; Krumbein and Van der Pers 1974, fig. 11; Pl. 85, figs. 2 and 4) precisely duplicates the trace fossil.

Furthermore, when an echinoid, browsing over a flat, algal-coated pebble, arrives at a sharply curved edge of the pebble, the mode of employment of the teeth changes to accommodate the different topography. The hitherto stellate orientation of the grooves is replaced around this edge by a subparallel orientation perpendicular to the boundary of the pebble (Pl. 86, fig. 1), since on the curved surface only two or three teeth can operate at a time. The pattern again duplicates the trace fossil (Pl. 86, fig. 2).

The occurrence of the trace fossil finds a parallel in the feeding predelection of present-day regular echinoids for boring animals in general and clionid sponges in particular. Hancock (1957) reported that *Psammechinus miliaris* kept under experimental conditions attacked only those oyster shells (dead or alive) that were infested by the sponge *Cliona celata* or the polychaete worm *Polydora ciliata*, and that these boring organisms were the sole reason for the attack. The echinoid caused severe erosion of the shell in order to expose and eat the enclosed worms and sponges. In the natural environment of the North Sea, Krumbein and Van der Pers (1974) also recorded active erosion of limestone by *Echinus esculentus* feeding on *Polydora ciliata*.

EXPLANATION OF PLATE 87

Fig. 1. *Gnathichnus pentax* around a pore of a sponge-boring (*Entobia megastoma* (Fischer)) in a belemnite (*Belemnitella mucronata*) from Upper Campanian white chalk, Keswick, Norfolk, England. 85.964(4), Norwich Castle Museum. ×20.

Fig. 2. *Gnathichnus pentax* around a pore of *Entobia megastoma* in *Belemnitella mucronata* from Upper Campanian white chalk, Norwich, England. 2127(1), Norwich Castle Museum. ×20.

Fig. 3. *Gnathichnus pentax* around pores of *Entobia cretacea* Portlock (sponge-boring) in *Inoceramus digitatus* J. de C. Sowerby (non Schlüter). Probably Coniacian, white chalk, south-east England, locality unknown. Paratype. GSM 115027. ×5.

Fig. 4. *Gnathichnus pentax* around broken open boring of a sponge in *Belemnitella* aff. *lanceolata*. Degree of destruction of the substrate lies between those in figs. 2 and 8. Lower Maastrichtian white chalk, Kongsted, Denmark. MMH 13391. ×6.

Fig. 5. An unusually clearly pentaradiate *Gnathichnus pentax* around a clionid sponge papillar boring in *Belemnitella* sp. Lower Maastrichtian, Zeltberg/Lüneburg, West Germany. Collection of Niedersächsischen Landesamtes für Bodenforschung, Hannover, catalogue kma 12. Photo E. Voigt. ×12.

Fig. 6. As Plate 86, fig. 3. ×4.

Fig. 7. Typical location of *Gnathichnus pentax*, around the muscle attachment area of oysters. Loss of the aragonite myostracum leaves only that part of the trace that extended on to the surrounding calcite shell surface. Lower Campanian Burditt Marl Member, Austin chalk from Little Walnut Creek, east of Austin, Texas, U.S.A. MMH 13392. ×3·5.

Fig. 8. 'Wreck' of a *Belemnitella* sp. broken open by foraging animals eating the boring sponges that produced the internal cavities. Scratches around the holes indicate the work of regular echinoids. Uppermost Campanian white chalk, 1 m below horizon 595, Saturn Quarry, Kronsmoor, West Germany. MMH 13393. ×3.

PLATE 87
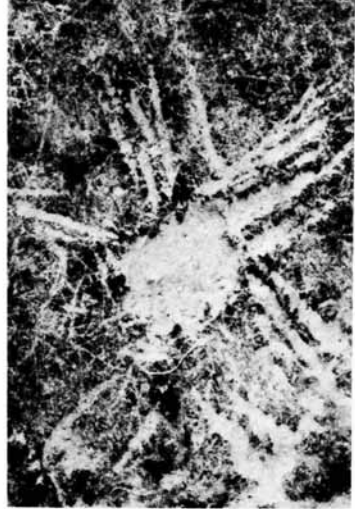

BROMLEY, echinoid bioerosion

DISCUSSION

The close similarity of the fossil material with the work of many species of browsing and foraging regular echinoids renders it probable beyond reasonable doubt that the trace fossil is also the work of echinoids. The geological occurrence lends further support to this interpretation. The bioerosion sculpture has so far been found only in deposits that appear to have been laid down in fully marine conditions. The trace fossil is particularly abundant in sediments representing shallow-water well-oxygenated environments.

So far the pentaradiate trace fossil, common in Jurassic and younger strata, has not been found in Triassic or Palaeozoic rocks. This may be correlated with evolutionary changes in the structural development of the jaw apparatus in regular echinoids. The first perignathic girdles appeared in the Permian and progressive evolutionary changes of both the girdle and the lantern occurred during the Mesozoic. Kier (1974, pp. 53–56 and 62) interpreted these changes in terms of promoting the biting power and mobility of the lantern. The appearance of the strengthened tooth with T-shaped cross-section in the stirodont lantern, and change over from apophyses to auricles in the girdle occurred in late Triassic to early Jurassic times. It is significant, therefore, that the earliest pentaradiate bite known is of early Jurassic age (Pl. 85, fig. 1). The fully developed camarodont lantern appeared in the Maastrichtian, having extremely large muscles capable of moving the pyramids and their teeth with great force against the bottom (Kier 1974, p. 55). It may therefore also be significant that the earliest known occurrences of extensive areas browsed uniformly by five teeth date from only shortly before the Maastrichtian (Pl. 86, figs. 4–5; Pl. 88, fig. 7).

From Upper Cretaceous rocks there is some evidence that the sculpture may prove a useful palaeoenvironmental indicator. Substrates from localities representing shallow-water environments have been extensively browsed (Pl. 86, fig. 4) while in deeper-water deposits of comparable age the trace fossil is concentrated locally around borings (Pl. 87, figs. 1–4). This difference may be a reflection of the presence and absence, respectively, of algal films in these environments.

In most of the rocks in which these trace fossils have been found, one or more

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EXPLANATION OF PLATE 88

Figs. 1–3. *Gnathichnus pentax* around acrothoracic borings (*Rogerella mathieui* Saint-Seine) in *Echinocorys* sp., showing different stages in the destruction of the borings. ×6. 1, Santonian or Coniacian, white chalk from Guston near Dover, England. Institute of Geological Sciences, London, CJW 806. 2, Campanian white chalk from West Harnham, SW. of Salisbury, England. I.G.S., London, Zn 1903. 3, Lower Maastrichtian white chalk of Gråryg, Møns Klint, Denmark. MMH 13394.

Fig. 4. *Gnathichnus pentax* around the aperture of a small boring in *Echinocorys* sp. Bed S, Lower Maastrichtian white chalk at Sidestrand, England. ×10.

Fig. 5. *Gnathichnus pentax* at site of attack of four tubefeet of *Echinocorys* sp. Santonian white chalk of the coast between Kingsgate and Foreness, Thanet, Kent, England. I.G.S., London, GSM 88258. ×6.

Fig. 6. *Gnathichnus pentax* around a broken open boring in *Inoceramus digitatus*. Same specimen as Plate 87, fig. 3. ×6.

Fig. 7. Paratype of *Gnathichnus pentax*. Extensive but light bioerosion of the external surface of an *Inoceramus* sp. of '*cuvieri*' group. Turonian? White chalk of SE. England, locality unknown. GSM 115029. ×1·5.

PLATE 88
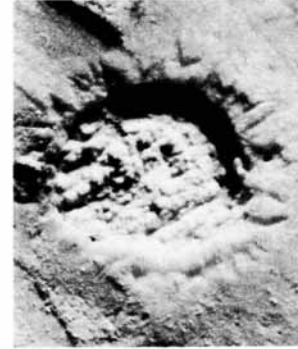

BROMLEY, *Gnathichnus pentax*

regular echinoids are preserved that may represent the trace maker(s) (e.g. Voigt 1972, p. 119). In the Lower Campanian chalk (*Gonioteuthis quadrata* Zone) of Hampshire, England, the trace fossil occurs with *Stereocidaris* sp., *Salenia granulosa*, and *Phymosoma* sp. In the Upper Campanian chalk of England they are accompanied by *Stereocidaris* 'serrifera', *Salenia heberti*, and *Phymosoma regularis*, while in the Maastrichtian chalk of England, Germany, and Denmark the sculpture is accompanied by *Salenia pygmaea*, *Stereocidaris* spp., *Phymosoma* sp., and (Denmark only) *Tylocidaris baltica* (C. J. Wood, pers. comm. 1975). On the other hand, the extensive but otherwise rather similar grooves on shells in the Campanian littoral deposits of Sweden are again accompanied by species of *Salenia*, *Tylocidaris*, and *Stereocidaris* but the species are different from those of the correlative deeper-water chalk facies.

In those cases where several regular echinoid species accompany the trace fossil it is doubtful whether the traces produced by the different species can be distinguished. The large *Echinus esculentus* and the small *Psammechinus miliaris*, feeding together in aquaria, each produce large or small traces according to local changes of feeding habits (W. Krumbein, pers. comm. 1974). Stars of a particular echinoid individual also tend to be smaller on hard substrates than on softer rocks (Krumbein and Van der Pers 1974, p. 12). Krumbach (1914), however, noted that *Sphaerechinus granularis* consistently produced more widely separated stars than *Strongylocentrotus lividus* in the same environment. The scratches of *S. lividus* were so close together that they overlapped so that the entire substrate surface was eroded clean of algae, but the grazing was restricted to limited territories. *Arbacia pustulosa* also fed in the same environment, but this species restricted its activities to narrow clefts in the substrate and to the underside of stones and overhangs, so that its feeding traces were readily separable from those of the other two species.

NAMING THE TRACE FOSSIL

For future reference it is necessary to name the distinctive groove pattern as a trace fossil. The name is applied to the basic stellate unit, multiplication of which produces the characteristic bioerosion sculpture. This is analogous to soft sediment trace fossils in which the isolated burrow bears the name, but its repetition produces a

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EXPLANATION OF PLATE 89

Fig. 1. Phosphatic pebble from Cenomanian greensand at Mülheim/Ruhr, near Essen, West Germany. Grooves scattered over the entire surface resemble the work of browsing regular echinoids. Private collection of H. Klaumann. ×4.

Fig. 2. External surface of a shell of *Arctica islandica* (L.) bioeroded by browsing organisms (Bromley and Tendal 1973, pl. 1d). A remnant island of original shell surface at left, carrying a patch of black periostracum, shows the surface to have been lowered generally by about 1 mm. The double ridge is a ghost of an encrusting serpulid tube that originally protected the shell surface. Four orifices of a sponge-boring (papillae of *Cliona celata* are visible within) are surrounded by radiating grooves typical of the work of browsing echinoids (probably *Psammechinus miliaris*). The remainder of the surface bears fine striae from the radulae of gastropods. Dredged in southern Kattegat, Denmark. Housed in the Zoological Museum, Copenhagen. ×13.
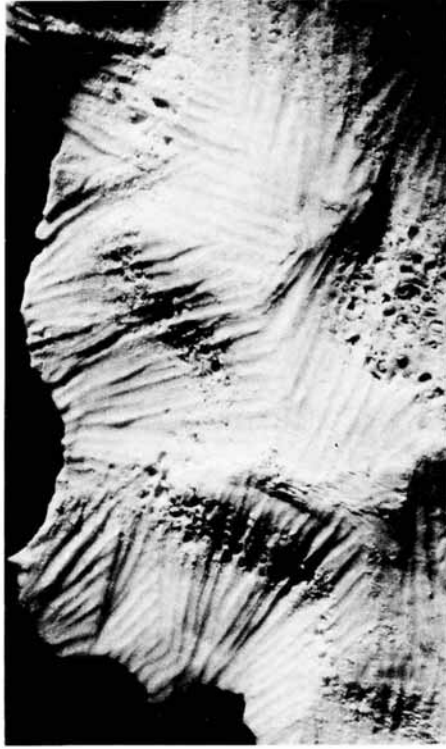
Fig. 3. Rodent gnawing traces on terrapin bone (plastron). Nacogdoches, Texas, U.S.A. ×3.

PLATE 89

BROMLEY, echinoid bioerosion

bioturbation fabric. The definition of the name is based on morphological characters alone, with the understanding that the structures have a biogenic origin. The generic name is available for trace fossils of other types produced by rasping, biting, and gnawing animals.

Ichnogenus GNATHICHNUS nov.

Type ichnospecies. Gnathichnus pentax nov.

Diagnosis. Biogenic sculpture consisting of grooves, pits, and scratches on hard substrates.

Ichnospecies *Gnathichnus pentax* nov.

Plate 85, figs. 1–3; Plate 86, figs. 3–5; Plate 87, figs. 1–7; Plate 88, figs. 1–7.

Type material. The variable aspects of the trace fossil cannot be represented by a single specimen. The holotype is an example showing particularly good preservation of the grooves. The paratypes illustrate two other typical modes of occurrence.

Holotype. MMH 13386, housed in the Mineralogisk Museum, Copenhagen, Denmark (Pl. 85, fig. 3). Paratypes. GSM 115029 (Pl. 88, fig. 7) and GSM 115027 (Pl. 87, fig. 3; Pl. 88, fig. 6), housed in the Institute of Geological Sciences, London.

Locus typicus. Kritika, Rhodes, Greece.

Stratum typicum. Sgourou Formation, lowermost Pleistocene.

Diagnosis. Gnathichnus consisting of a regular stellate grouping of five similar grooves radiating at *c.* 72°.

Description. The trace fossil almost invariably occurs in multiples of several overlapping stars and can cover considerable areas of substrate with grooves of similar dimensions intersecting at more or less 72° (and 144°). Commonly concentrated around skeletons of encrusting organisms and apertures to borings.

Interpretation. Browsing and foraging traces attributed to dental erosion by regular echinoids.

Range. Lower Jurassic to Recent.

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