

Taphonomic and ethologic aspects of the ichnology of the Maastrichtian of the type area (Upper Cretaceous, The Netherlands and Belgium)

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Abstract

Three rare ichnotaxa from the type area of the Maastrichtian Stage (Upper Cretaceous) are described, and their morphology and palaeoecological significance discussed; a fourth ichnotaxon shows an unusual mode of preservation. The infill of an articulated lithophagid bivalve (Meerssen Member, Maastricht Formation) preserves the distinctive firmground burrow *Arachnostega gastrochaenae* BERTLING, 1992. This is the first report of this trace fossil, probably generated by polychaetes, from the Cretaceous of northern Europe. The producer may have been grazing the inside of the bivalve shell while burrowing through its sediment infill. An indeterminate patellid limpet exhibits an additional example. Tubercles are recognised for the first time within the pits of *Oichnus excavatus* DONOVAN & JAGT, 2002b (Meerssen Member, Maastricht Formation), indicating they were probably the result of embedment rather than boring. The producing organism may have obtained a firmer attachment to the test by having abundant spines of the host echinoid embedded in its soft tissues. The boring *Talpina* cf. *ramosa* VON HAGENOW, 1840, commonly preserved as natural casts in decalcified shells, occurs as holes in the oyster *Agerostrea unguolata* (VON SCHLOTHEIM, 1813). *Trypanites* cf. *solitarius* MÄGDEFRAU, 1937, shows an unusually flattened morphology, in which the boring form has been determined in part by the distribution of organic layers within the shell of the oyster *Rastellum macropterum* sensu STENZEL, 1971 (Nekum Member, Maastricht Formation).

Key words: Burrows, borings, embedments, Maastrichtian, The Netherlands, Belgium.

Résumé

Trois ichnotaxa rares provenant de la région type de l'étage Maastrichtien (Crétacé Supérieur) sont décrits; leur morphologie et leur signification paléoécologique sont discutées. Un quatrième ichnotaxon montre un mode de préservation inhabituel. Le remplissage d'un bivalve lithophage articulé (Membre de Meerssen, Formation de Maastricht) a conservé le terrier semi-consolidé caractéristique *Arachnostega gastrochaenae* BERTLING, 1992. C'est la première fois que cette trace fossile laissée probablement par les polychaetes, est signalée dans le Crétacé de l'Europe du Nord. L'animal à l'origine de ce terrier peut avoir raclé l'intérieur de la coquille du bivalve pendant qu'il creusait dans le sédiment de remplissage. Une patelle appartenant à un patellidé indéterminable en montre un autre exemple. Des tubercules ont été observés pour la première fois dans les cavités d'*Oichnus excavatus* DONOVAN & JAGT, 2002b (Membre de Meerssen, Formation de Maastricht) indiquant qu'elles résultent probablement d'un "enfouissement" plutôt que d'un creusement. L'organisme responsable peut avoir été plus fermement fixé

au test en ayant d'abondantes épines de l'échinide hôte enfouies dans ses tissus mous. L'organisme foreur *Talpina* cf. *ramosa* VON HAGENOW, 1840 généralement conservé sous forme de moulages naturels dans des coquilles décalcifiées, se présente sous forme de cavités dans l'huître *Agerostrea unguolata* (VON SCHLOTHEIM, 1813).

Trypanites cf. *solitarius* MÄGDEFRAU, 1937 présente une morphologie inhabituellement aplatie dans laquelle la forme du forage a été en partie déterminée par la distribution des niveaux organiques dans la coquille de l'huître *Rastellum macropterum* sensu STENZEL, 1971 (Membre de Nekum, Formation de Maastricht).

Mots-clefs: Terriers, forages, "enfouissement", Maastrichtien, Pays-Bas, Belgique.

Introduction

Trace fossils are an understudied, yet diverse and significant element of the biota of the Maastrichtian (Upper Cretaceous) in its type area in Liège-Limburg (Belgium) and southern Limburg (The Netherlands) (DORTANGS, 1998; DONOVAN & JAGT, 2002a; JAGT, 2003) (Fig. 1). The present authors are attempting to correct this omission by describing previously unreported but significant trace fossils from the various members included in the Maastricht Formation. Herein, we describe three unusual and/or rare and morphologically distinct ichnofossils from this unit, each of which shows unusual features related to preservation, plus add further observations to the original description of an ichnotaxon that suggests a most peculiar behaviour.

Terminology of the morphology of trace fossils follows HÄNTZSCHEL (1975). The philosophy of open nomenclature follows BENGTON (1988). Annotations within synonymy lists follow MATTHEWS (1973). All specimens are deposited in the Natuurhistorisch Museum Maastricht, The Netherlands (NHMM); JJ = J.W.M. Jagt collection, LN = L. Nelissen collection, MK = W.M. Felder collection.

Systematic ichnology

Ichnogenus *Arachnostega* BERTLING, 1992

TYPE ICHNOSPECIES

Arachnostega gastrochaenae BERTLING, 1992, p. 179, by original designation. The only nominal ichnospecies.

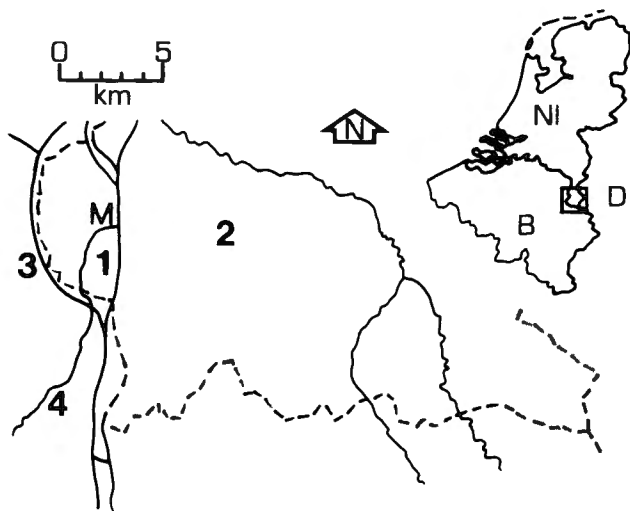


Fig. 1 — Outline map of study area (redrawn and simplified after JAGT, 1999, fig. 1), showing political boundaries (dashed lines), rivers and canals (solid lines) and the city of Maastricht (M). Key to localities: 1 = ENCI-Maastricht BV quarry; 2 = Ankerpoort-'t Rooth quarry; 3 = temporary sections in Albertkanaal; 4 = CBR-Romontbos quarry. The inset map of the Netherlands (NI), Belgium (B) and Germany (D) shows the approximate position of the main map (box).

DIAGNOSIS

(From BERTLING, 1992, p. 179.) "Irregular elongate and net-like burrows in sediment fills of shells. Visible on the surface of internal moulds. The size of the meshwork may vary from microns to centimetres, depending on the shell-bearing and the burrow biota involved."

REMARKS

Archnostega is a distinctive network of channels that is superficially reminiscent of structures such as the clionid sponge boring *Entobia* BRONN, 1838, although lacking swollen chambers and not penetrating a calcareous shell or limestone substrate. That *Archnostega* itself is not a boring was only determined by the astuteness of BERTLING (1992, pp. 182-183), who recognised that morphologically identical burrows occurred in unusual firm-ground settings within sediment-filled shells of the infaunal bivalve *Mya* sp. within the North Sea Basin, generated by more than one taxon of polychaete annelid (REINECK, 1980). However, *Archnostega* has only been formally recorded hitherto from the fossil record of the Jurassic of northern Europe (BERTLING, 1992; FÜRSICH *et al.*, 1994) and the Cretaceous of the Middle East (WILSON & TAYLOR, 2001).

***Archnostega gastrochaenae* BERTLING, 1992**
(Pl. 1, Figs. 1-3)

* 1992 *Archnostega gastrochaenae* BERTLING, pp. 177, 179-185, figs. 2, 3.

1993 *Archnostega* – TODD, p. 417.

1994 *Archnostega gastrochaenae* BERTLING – FÜRSICH *et al.*, pp. 146, 161, pl. 3, figs. 1, 2, 4.

? 2001 *Archnostega* – WILSON & TAYLOR, p. 26, pl. 2, fig. 1.

MATERIAL

Two specimens. An incomplete internal mould of an indeterminate lithophagid bivalve, NHMM JJ 12354, with *A. gastrochaenae* apparent within the moulds of both valves (Pl. 1, Figs. 1, 2). The internal mould of the bivalve, preserved in a medium- to coarse-grained biocalcarenite, is broken both anteriorly and posteriorly, preserving little detail of the internal surface of the mollusc shell except for some coarse growth lines.

The second specimen, NHMM MK 367, is an internal mould of an indeterminate patellid limpet of the type described by KAUNHOWEN (1898, p. 15, pl. 1, figs. 3-4), with *A. gastrochaenae* weakly developed (Pl. 1, Fig. 3).

LOCALITY AND HORIZON

NHMM JJ 12354 is from ENCI-Maastricht BV quarry, south of Maastricht, southern Limburg (The Netherlands), base of subunit IVf-4, Meerssen Member, Maastricht Formation. Upper Cretaceous; uppermost Maastrichtian (for simple lithostratigraphic section, see JAGT *et al.*, 1998, figs. 1, 2). The label of NHMM MK 367 states "Nekami, Bemelen [now known as Ankerpoort-'t Rooth quarry], ?Nekum Member," Maastricht Formation. Upper Cretaceous; upper Maastrichtian (Fig. 1).

DIAGNOSIS

(After BERTLING, 1992, p. 180). "Ramified burrows on the surface of internal moulds with an oval cross-section, which increases slowly in diameter by a factor of 5 to 10, approximately. At ramifications, the bent main burrow is not reduced in size. Lateral burrows mostly have a smaller diameter. Polygonal areas on the surface of internal moulds may be produced by the unification of ramified burrows."

DESCRIPTION

Based mainly on NHMM JJ 12354. Burrows more intensely developed adjacent to the right(?) valve (Pl. 1, Figs. 1, 2) than left(?). Burrows best seen on surface of moulds, preserved in a surface layer that has, in part, peeled away on NHMM JJ 12354 (Pl. 1, Fig. 2), revealing less common burrows below. Burrows of incomplete circular or elliptical section, preserved as grooves with overhanging edges and not infilled, individual burrows varying from c. 0.1 to 0.6 mm in maximum diameter; broader sections of burrows(?) may be a taphonomic artifact. Larger diameter burrows forming reticulate pattern at surface of mould.

REMARKS

This is the first reported occurrence of this distinctive, but cryptic, ichnotaxon from the Maastrichtian of the type area. WILSON & TAYLOR (2001, p. 26) recorded it from approximately coeval sedimentary rocks of the Qahlah Formation in Oman, uniquely preserved in mudstones infilling *Gastrochaenolites* isp. borings. However, the unusual mode of occurrence of *A. gastrochaenae* within in-

filled shells and borings prevents its identification except within mouldic material, so it is probably more widespread in the Mesozoic and Cainozoic than has been reported hitherto (see also comments in FÜRSICH *et al.*, 1994).

Although present internally, the best development of burrows is undoubtedly on the surface of the internal mould, where movement would have been constrained by the molluscan shell. This may indicate that the producing polychaetes(?) were in some way grazing the interior of the shell. They may have been feeding on non-photosynthetic microbes that had been living on the inside of the shell.

Ichnogenus *Oichnus* BROMLEY, 1981

TYPE ICHNOSPECIES

Oichnus simplex BROMLEY, 1981, p. 60, by original designation.

OTHER ICHNOSPECIES

Oichnus asperus NIELSEN & NIELSEN, 2001; *O. coronatus* NIELSEN & NIELSEN, 2001; *O. excavatus* DONOVAN & JAGT, 2002b; *O. gradatus* NIELSEN & NIELSEN, 2001; *O. ovalis* BROMLEY, 1993; *O. paraboloides* BROMLEY, 1981.

DIAGNOSIS

(After DONOVAN & PICKERILL, 2002, p. 87). "Small, circular, subcircular, oval or rhomboidal holes or pits of biogenic origin in hard substrates, commonly perpendicular to subperpendicular to substrate surface. Excavation may pass directly through substrate as a penetration, most commonly where the substrate is a thin shell, or may end within the substrate as a shallow to moderately deep depression or short, subcylindrical pit, commonly with a depth:width ratio of ≤ 1 , with or without a central boss."

REMARKS

Following the recent paper by TODD & PALMER (2002), further examination of the type series of *Oichnus excavatus* DONOVAN & JAGT, 2002b, by the authors has revealed new and significant morphological features of the substrate that clarify the mode of formation.

Oichnus excavatus DONOVAN & JAGT, 2002b (Pl. 1, Figs. 4, 6, 7)

- 1993 [unnamed boring in *Hemipneustes striatoradiatus* (LESKE, 1778)]; DEFOUR *et al.*, fig. 3c.
 2000 [unnamed boring in *Hemipneustes striatoradiatus* (LESKE, 1778)]; JAGT, pl. 24, figs. 4-5.
 v* 2002b *Oichnus excavatus* DONOVAN & JAGT, pp. 69-73, figs. 2a, c, 3a, b, 4c, 5.
 2002 *Oichnus excavatus* Donovan & Jagt – DONOVAN & PICKERILL, p. 86.
 ?2003 *Oichnus excavatus* Donovan & Jagt – BLISSETT & PICKERILL, pp. 221-223, fig. 2.

MATERIAL

All pits preserved in tests or test fragments of the holasteroid *Hemipneustes striatoradiatus* (LESKE, 1778). Spe-

cimens considered herein include the holotype pit in NHMM MK 4689 (Pl. 1, Fig. 6, arrowed), and selected paratypes, including 17 other pits in NHMM MK 4689 (Pl. 1, Figs. 4, 6, 7) and all pits in NHMM JJ 699 (at least 61 individual pits).

LOCALITY AND HORIZON

Upper 5-10 m of the Meerssen Member, Maastricht Formation, formerly exposed along the Albertkanaal at Vroenhoven-Riemst, Limburg (Belgium) (DONOVAN & JAGT, 2002b, fig. 1). Upper Cretaceous; uppermost Maastrichtian (Fig. 1).

DIAGNOSIS

(Slightly revised after DONOVAN & JAGT, 2002b, p. 69.) Circular to elliptical, non-penetrative *Oichnus*, almost invariably with a broad, high, raised central boss. Aperture of pit overhanging and walls concave.

DESCRIPTION

(Further to features described in DONOVAN & JAGT, 2002b.) All surfaces of pits bearing sculpture of irregularly distributed to well-ordered tubercles, commonly very small (granular), although may be present in two sizes (Pl. 1, figs 4, 6, 7). In at least one shallow pit, small tubercles are arrayed around larger tubercles in a circle. Large tubercles are perforate and crenulate.

REMARKS

The structures described above did not become readily apparent until the pits were first painted with black food colouring and then whitened with ammonium chloride. Although these structures are absent in parts of at least some specimens, this may be a preservational artifact.

The functional significance of these structures, both to the host echinoid and the boring organism, is uncertain, but they are too close in morphology to the spine-bearing tubercles of the holasteroid test for this to be mere coincidence. This interpretation is strongly reinforced by the example in which a larger primary(?) tubercle is surrounded by a circlet of smaller secondary(?) tubercles in an arrangement typical of *Hemipneustes striatoradiatus*. If the interpretation of these structures is correct, it would suggest that *Oichnus excavatus* is not a boring as originally interpreted (DONOVAN & JAGT, 2002b), but more probably an embedment structure that left the ectoderm of the echinoderm intact. Although debatable, it is most probable that these tubercles did bear spines. This determination may seem improbable, as these spines would be numerous and would presumably penetrate the soft tissues of the trace-forming organism. Counter-intuitively, this may have been advantageous to the producing organism in giving it further anchorage to the test, additional to that provided by the concave walls and large central boss (discussed by DONOVAN & JAGT, 2002b). Indeed, the function of the large central boss is easier to explain if it supported spines that were embedded in the soft tissues of the trace producer. Whatever their origin, these tubercles add a unique element to the function of these distinc-

tive pits, although the tubercles themselves must be considered a morphological feature of the host echinoid rather than the trace fossil *per se*.

PICKERILL & DONOVAN (1998) synonymised *Tremichnus* BRETT, 1985, with *Oichnus* BROMLEY based on their identical morphology. Subsequently, this ichnotaxonomic decision has been supported by some authors and criticised by others (NIELSEN & NIELSEN, 2001, 2002; DONOVAN & PICKERILL, 2002; TODD & PALMER, 2002; NIELSEN *et al.*, in press).

The diagnosis of *Oichnus excavatus* was recently emended by BLISSETT & PICKERILL (2003) to include more conical specimens in a Miocene *Conus* sp. from Jamaica. The ichnospecific diagnosis given herein defines the type species and does not embrace the range of morphologies shown by the Jamaican specimens. The latter may be deserving of description as a new ichnospecies.

Ichnogenus *Talpina* VON HAGENOW, 1840

TYPE ICHNOSPECIES

Talpina ramosa VON HAGENOW, 1840, p. 671, by the subsequent designation of HÄNTZSCHEL (1962, p. W231).

OTHER ICHNOSPECIES

Talpina annulata VOIGT, 1975; *T. eduliformis* QUENSTEDT, 1858; *T. hirsuta* VOIGT, 1975; *T. gruberi* MAYER, 1952; *T. scalariformis* GHARE, 1982.

DIAGNOSIS

(Slightly modified after HÄNTZSCHEL, 1975, p. W133.) "Straight to curved tunnel systems in shelly substrates, commonly branched, diameter *ca.* 0.2 mm; numerous oval or circular openings towards exterior."

REMARKS

The diagnosis of HÄNTZSCHEL (1975, p. W133) considered that this ichnotaxon was only found "... in the rostra of belemnoids ..." As demonstrated herein, other robust, shelly substrates were also utilised by these borings (FÜRSICH *et al.*, 1994). As noted by HÄNTZSCHEL (1975), *Talpina* was originally interpreted as a bryozoan boring, but it is now considered to be a product of the activities of phoronids (VOIGT, 1973, 1975, 1978), the lophophorate horseshoe worms (EMIG & DE MITTELWIHR, 1999).

Talpina cf. ramosa VON HAGENOW, 1840 (Pl. 1, Fig. 5)

MATERIAL

A single specimen, NHMM MK 160, preserving a complex pattern of borings in the surface of a valve of the oyster *Agerostrea ungulata* (VON SCHLOTHEIM, 1813). Trace fossil not infilled.

LOCALITY AND HORIZON

From Ankerpoort-'t Rooth quarry, Meerssen(?) Member, Maastricht Formation. Upper Cretaceous; uppermost Maastrichtian (Fig. 1).

DESCRIPTION

Slender, elongate, straight to arcuate, heterotomously branched grooved borings of semicircular to more completely rounded section, preserved in the central third of the surface of the oyster *Agerostrea ungulata*. Infestation moderately densely packed. Branches diverge between about 45-90°. Borings appear discontinuous in some areas. Associated with circular pits of small diameter which are particularly common on the sloping, ribbed sides of the shell (poorly seen in Pl. 1, Fig. 5).

REMARKS

The main interest of this specimen is in its preservation, which differs from other reported examples of this ichnotaxon from these deposits. Further, it is a fine example of preservation of the borings in the shell. *Talpina* in the type area of the Maastrichtian is otherwise preserved as a cast within a natural mould of the host shell (VOIGT, 1978).

Subsequent to the diagnosis by HÄNTZSCHEL (1975, p. W133), a variety of shelly substrates have been recorded as infested with fossil *Talpina* ispp. and Recent phoronid borings, such as scleractinians, scaphopods, bivalves and crinoids (VOIGT, 1975, 1978). This is not unexpected, for the systematic position of the substrate should not be considered a valid ichnotaxobasis for a boring (PICKERILL, 1994; BROMLEY, 1996; PICKERILL & DONOVAN, 1998; DONOVAN & PICKERILL, 2002).

Ichnogenus *Trypanites* MÄGDEFRAU, 1937 (emend. BROMLEY, 1972)

TYPE ICHNOSPECIES

Trypanites weisei MÄGDEFRAU, 1937, by monotypy.

OTHER ICHNOSPECIES

Trypanites fimbriatus (STEPHENSON, 1952); *T. fosteryeo-mani* COLE & PALMER, 1999; *T. solitarius* (VON HAGENOW, 1840).

DIAGNOSIS

(Slightly modified after BROMLEY & D'ALESSANDRO, 1987, p. 403.) Single-entrance, cylindrical or subcylindrical, unbranched borings in lithic substrates, having circular to subcircular cross-section throughout length. The axes of borings may be straight, curved or irregular.

REMARKS

BROMLEY & D'ALESSANDRO (1987, p. 403) considered *Trypanites* to have a circular cross-section. Specimens such as that considered below, with an oval cross-section, fit the revised diagnosis above, yet are morphologically distinct from other pouch-shaped borings (compare with discussions in BROMLEY, 1972; BROMLEY & D'ALESSANDRO, 1987). BROMLEY & D'ALESSANDRO (1987, p. 404) considered straightness versus limited sinuosity of *Trypanites* ispp. to be unsuitable ichnotaxobases, because "Deviations of a boring from a straight course can be caused by many factors ..." Similarly, too rigid a defini-

tion of boring cross-section would eliminate ichnotaxa that vary from the diagnosis due to factors controlled in part by the nature of the substrate, such as thickness (e.g., thin versus thick shell) and substrate inhomogeneity (as below).

Trypanites cf. solitarius MÄGDEFRAU, 1937
(Fig. 2)

MATERIAL

A single specimen, NHMM LN 7384, within an internal mould of a valve of the oyster *Rastellum macropterum sensu* STENZEL, 1971, in which the boring is preserved as a cast.

LOCALITY AND HORIZON

Upper third of the Nekum Member, Maastricht Formation, CBR-Romontbos quarry, Eben Emael, Bassenge, Liège (Belgium) (for lithostratigraphic section, see JAGT, 1995). Upper Cretaceous; upper Maastrichtian (Fig. 1).

DESCRIPTION

Boring preserved in internal mould of oyster valve as a cast in flint. Boring elliptical in section, with smooth, unsculptured surface. Aperture conical, round, but asymmetrical, opening on inner surface of oyster valve. Boring showing strong geniculation close to the aperture. Close

to aperture boring skewed slightly sideways, subperpendicular to oyster valve internal surface, showing three infoldings of wall that give it a rope-like appearance. Distal to the geniculation the shaft of boring (about 8 mm in length) shows no such infoldings, and is broad and flattened parallel to the inner surface of the oyster. Main shaft has a constricted and round termination adjacent to the muscle scar of the oyster, which it did not penetrate. This main shaft supports a lozenge-like structure close to the end, separated from the shaft by a further infolding and situated on the side away from the inner surface of the valve. Total length c. 11 mm.

REMARKS

The Mesozoic and Cainozoic fossil record of oysters includes numerous examples in which their commonly large, thick shells have been encrusted and penetrated by a diversity of organisms or have in turn overgrown a variety of organic substrates (TODD, 1993). Thus, the boring in NHMM LN 7384 is not an unusual phenomenon *per se*, but, rather, it is of interest because of its unusual morphology, which is particularly apparent due to the mode of preservation.

The boring entered the valve on its internal surface, indicating that the host was a dead oyster shell and most probably already disarticulated. The infoldings of the in-

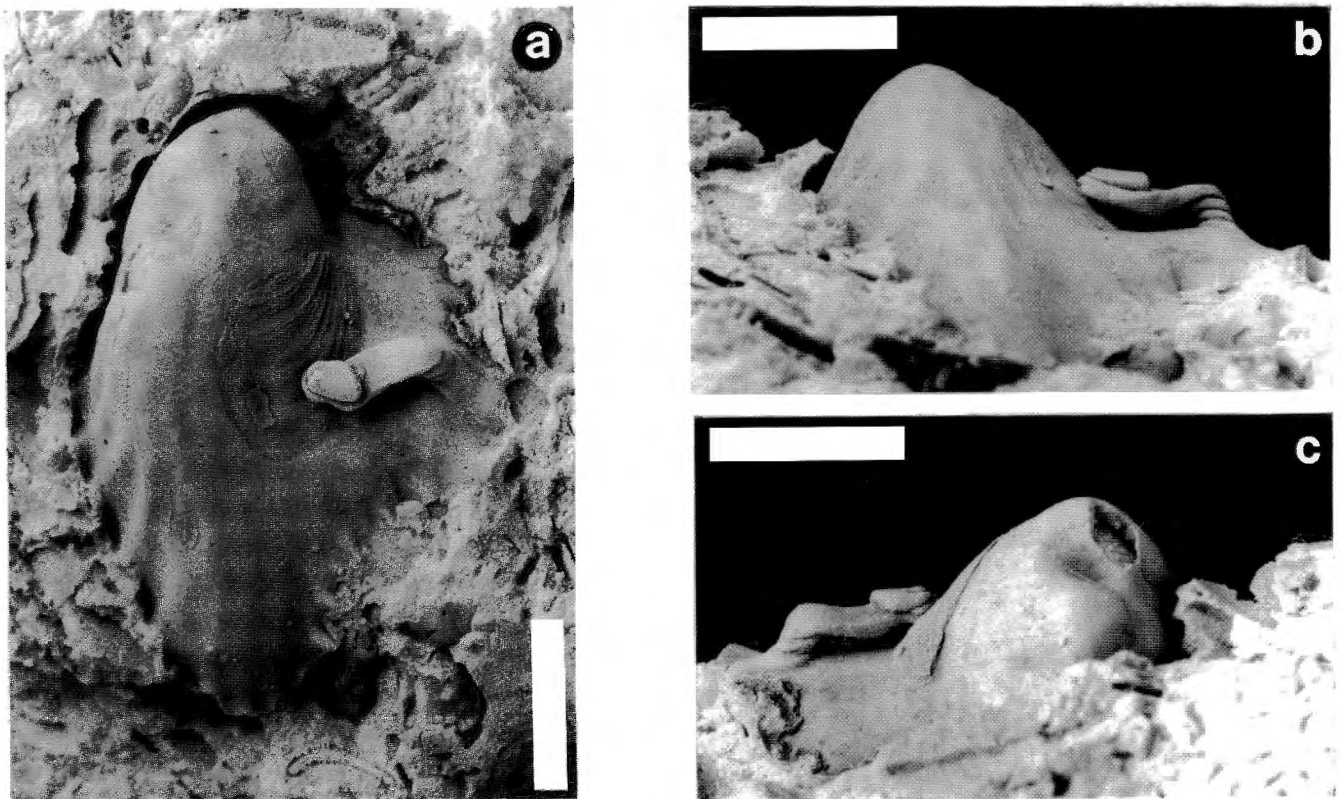


Fig. 2 — Cast of *Trypanites cf. solitarius* (VON HAGENOW, 1840), NHMM LN 7384, preserved in association with an internal mould of a valve of the oyster *Rastellum macropterum sensu* STENZEL. (a) Oyster in plan view, boring right of centre, with base adjacent to muscle scar of mollusc. (b) Ventral view of oyster, boring to right and shaped like a recumbent 'L.' (c) Dorsal view of oyster, boring to left. All scale bars represent 10 mm.

itial, short shaft perpendicular to the inner valve surface are interpreted as having been produced in reaction to zones within the shell structure that were particularly difficult to penetrate. The broad, conical aperture indicates that the shell calcite was perforated with relative ease and, using this observation as our guide, it appears that the producing organism penetrated in turn five calcareous layers, separated by four thin, non-calcareous layers. The latter were undoubtedly the thin organic layers of the shell that, in life, separated the thicker prismatic calcareous layers. That these layers were difficult for the producer to penetrate is indicated both by the constrictions of the shaft and also by the main shaft distal to the geniculation apparently being confined to one shell layer and, in consequence, being elliptical in section (compare with HARPER, 1994). Such a sculpture imposed by the substrate represents an unusual form of xenoglyph (BROMLEY *et al.*, 1984) (= Fremdschulptur of VOIGT, 1971).

Of the ichnospecies of *Trypanites*, the type *T. fimbriatus*, and *T. fosteryeomani* occur perpendicular to the host substrate. BROMLEY & D'ALESSANDRO (1987, pp. 406-

407) recognised three forms, A, B and C, of *T. solitarius*, of which the specimen described herein is closest in morphology to their form C. However, because of its unusual cross-section, NHMM LN 7384 is only included tentatively within this ichnospecies.

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References

- BENGTSON, P., 1988. Open nomenclature. *Palaeontology*, **31**: 223-227.
- BERTLING, M., 1992. *Arachnostega* n. ichnog. – burrowing traces in internal moulds of boring bivalves (Late Jurassic, Northern Germany). *Paläontologische Zeitschrift*, **66**: 177-185.
- BLISSETT, D.J. & PICKERILL, R.K., 2003. *Oichnus excavatus* Donovan & Jagt, 2002, from the Moneague Formation, White Limestone Group, Jamaica. *Caribbean Journal of Science*, **39**: 221-223.
- BRETT, C.E., 1985. *Tremichnus*: a new ichnogenus of circular-parabolic pits in fossil echinoderms. *Journal of Paleontology*, **59**: 625-635.
- BROMLEY, R.G., 1972. On some ichnotaxa in hard substrates, with a redefinition of *Trypanites* Mägdefrau. *Paläontologische Zeitschrift*, **46**: 93-98.
- BROMLEY, R.G., 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geológica Hispanica*, **16**: 55-64.
- BROMLEY, R.G., 1993. Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*. *Bulletin of the Geological Society of Denmark*, **40**: 167-173.
- BROMLEY, R.G. 1996. Trace Fossils: Biology, Taphonomy and Applications (2nd edition). Chapman and Hall, London, xvi + 361 pp.
- BROMLEY, R.G. & ALESSANDRO, A.D', 1987. Bioerosion of the Plio-Pleistocene transgression of southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, **93**: 379-442.
- BROMLEY, R.G., PEMBERTON, S.G. & RAHMANI, R.A., 1984. A Cretaceous woodground: the *Teredolites* ichnofacies. *Journal of Paleontology*, **58**: 488-498.
- BRONN, H.G., 1837-1838. *Lethaea Geognostica, oder Abbildungen und Beschreibungen der für die Gebirgs Formationen bezeichnendsten Versteinerungen*. E. Schweizerbart, Stuttgart, 1350 pp.
- COLE, A.R. & PALMER, T.J., 1999. Middle Jurassic worm borings, and a new giant ichnospecies of *Trypanites* from the Bajocian/Dinantian unconformity, southern England. *Proceedings of the Geologists' Association*, **110**: 203-209.
- DEFOUR, E., GEUSSENS, T., INDEHERBERGE, L. & STRIJBOS, V., 1993. Vormvariaties van *Hemipneustes striatoradiatus* en *Hemaster prunella* uit het Boven-Krijt van Limburg. *LIKONA (Limburgse Koepel voor Natuurstudie), Jaarboek 1993*: 7-14.
- DONOVAN, S.K. & JAGT, J.W.M., 2002a. Ichnology of the type area of the Maastrichtian Stage (Upper Cretaceous): burrowing and boring immediately prior to the K/T boundary event. *Palaeontological Association Newsletter*, #51: 91.
- DONOVAN, S.K. & JAGT, J.W.M., 2002b. *Oichnus* Bromley borings in the irregular echinoid *Hemipneustes* Agassiz from the type Maastrichtian (Upper Cretaceous, The Netherlands and Belgium). *Ichnos*, **9**: 67-74.
- DONOVAN, S.K. & PICKERILL, R.K., 2002. Pattern versus process or informative versus uninformative ichnotaxonomy: reply to Todd and Palmer. *Ichnos*, **9**: 85-87.
- DORTANGS, R.W., 1998. Sporenfossielen. In: JAGT, J.W.M., LELOUX, J. & DHONDT, A.V. (Editors), Fossielen van de St. Pietersberg. *Grondboor & Hamer*, **52** (4/5): 150-151.
- EMIG, C.C. & MITTELWIHR, C. DE, 1999. What is a phoronid? <www.com.univ-mrs.fr/DIMAR/Phoro/>.
- FÜRSICH, F.T., PALMER, T.J. & GOODYEAR, K.L., 1994. Growth and disintegration of bivalve-dominated patch reefs in the Upper Jurassic of southern England. *Palaeontology*, **37**: 131-171.
- GHARE, M.A., 1982. Borings on belemnoid rostra from the Utatur Group of Upper Cretaceous rocks of Trichinopoly district, Tamil Nadu. *Journal of the Geological Society of India*, **23**: 129-135.
- HAGENOW, F. VON, 1840. Monographie der Rügen'schen Kreide-Versteinerungen, II. Radiarien und Annulaten. *Neues*

PLATE 1

- Figs. 1, 2 — *Arachnostega gastrochaenae* BERTLING, 1992, NHMM JJ 12354. 1: Detail of part of internal mould of right(?) valve of lithophagid bivalve. 2: Complete internal mould of same valve.
- Fig. 3 — *Arachnostega gastrochaenae* BERTLING, 1992, NHMM MK 367, detail of part of internal mould of patellid gastropod showing sparsely developed burrows.
- Figs. 4, 6, 7 — *Oichnus excavatus* DONOVAN & JAGT, 2002b, NHMM MK 4689, circular pits in a test of the holasteroid echinoid *Hemipneustes striatoradiatus* (LESKE). Paratypes unless stated otherwise. 4: Pit showing tubercles on wall and side of central boss. 6: Three pits (holotype arrowed); confluent pair show tubercles on central boss and floor of holotype. 7: Two strongly tuberculated pits. Right example has two sizes of tubercles on central boss and bevelled lip of pit.
- Fig. 5 — *Talpina* cf. *ramosa* VON HAGENOW, 1840, NHMM MK 160, borings in shell of oyster *Agerostrea ungulata* (VON SCHLOTHEIM), Nekami, Bemelen, southern Limburg, Meerssen(?) Member, Maastricht Formation.

All specimens painted with black food colouring and subsequently coated with ammonium chloride sublimate. All scale bars represent 10 mm.

Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, **1840**: 631-672.

HÄNTZSCHEL, W., 1962. Trace fossils and problematica. In: MOORE, R.C. (Editor), *Treatise on Invertebrate Paleontology, Part W, Miscellanea*. Geological Society of America and University of Kansas Press, New York and Lawrence, pp. W177-W245.

HÄNTZSCHEL, W., 1975. Trace fossils and problematica. Second edition (revised and enlarged). In: TEICHERT, C. (Editor), *Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement 1*. Geological Society of America and University of Kansas Press, Boulder and Lawrence, xxi + 269 pp.

HARPER, E.M., 1994. Are conchiolin sheets in corbulid bivalves primarily defensive? *Palaeontology*, **37**: 551-578.

JAGT, J.W.M. 1995. A Late Maastrichtian ammonite faunule in flint preservation from northeastern Belgium. *Mededelingen van de Rijks Geologische Dienst*, **53**: 21-47.

JAGT, J.W.M. 1999. An overview of Late Cretaceous and Early Palaeogene echinoderm faunas from Liège-Limburg (Belgium, The Netherlands). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **69 (Suppl. A)**: 103-118.

JAGT, J.W.M., 2000. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium - Part 4: Echinoids. *Scripta Geologica*, **121**: 181-375.

JAGT, J.W.M., 2003. The ichnofossil genera *Radulichnus* and *Renichnus* in the Maastrichtian of The Netherlands and Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **73**: 175-184.

JAGT, J.W.M., DONOVAN, S.K., DECKERS, M.J.M., DORTANGS, R.W., KUYPERS, M.M.M. & VELTKAMP, C.J., 1998. The late Maastrichtian bourgueticrinid crinoid *Dunnocrinus aequalis* (d'ORBIGNY, 1841) from The Netherlands and Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **68**: 129-154.

KAUNHOWEN, F., 1898. Die Gastropoden der Maestrichter Kreide. *Paläontologische Abhandlungen*, n.s., **4**: 1-132.

LESKE, N.G., 1778. Iacobi Theodori Klein naturalis dispositio echinodermatum, edita et descriptionibus novisque inventis et synonymis auctorum et aucta a N. G. Leske. G.E. Beer, Lipsiae, xxii + 278 pp.

MÄGDEFRAU, K., 1937. Lebensspuren fossiler "Bohr"-Organismen. *Beiträge zur Naturkundeforschung Südwestdeutschlands*, **2**: 54-67.

MATTHEWS, S.C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, **16**: 713-719.

MAYER, G., 1952. Lebensspuren von Bohrorganismen aus dem unteren Hauptmuschelkalk des Kraichgau. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1952**: 450-456.

NIELSEN, J.K. & NIELSEN, K.S.S., 2002. Pattern versus process or informative versus ininformative (*sic*) ichnotaxonomy: reply to Todd and Palmer. *Ichnos*, **9**: 83-84.

NIELSEN, K.S.S. & NIELSEN, J.K., 2001. Bioerosion in Pliocene to late Holocene tests of benthic and planktonic foraminiferans, with a revision of the ichnogenera *Oichnus* and *Tremichnus*. *Ichnos*, **8**: 99-116.

NIELSEN, K.S.S., NIELSEN, J.K. & BROMLEY, R.G. (in press). Palaeoecological and ichnological significance of microborings in Quaternary Foraminifera. *Palaeontologica Electronica*.

PICKERILL, R.K., 1994. Nomenclature and taxonomy of invertebrate trace fossils. In: DONOVAN, S.K. (Editor), *The Palaeobiology of Trace Fossils*: 3-42. Wiley, Chichester.

PICKERILL, R.K. & DONOVAN, S.K., 1998. Ichnology of the Pliocene Bowden shell bed, southeast Jamaica. In: DONOVAN, S.K. (Editor), *The Pliocene Bowden shell bed, southeast Jamaica. Contributions to Tertiary and Quaternary Geology*, **35**: 161-175.

QUENSTEDT, F.A., 1858. *Der Jura*. Fuess, Tübingen, 842 pp.

REINECK, H.-E., 1980. Steinkerne in der Entstehung. *Natur und Museum*, **110** (2): 44-47.

SCHLOTHEIM, E.F. VON, 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. In: LEONHARD, C.C. von, *Taschenbuch für die gesammte Mineralogie mit Hinsicht auf die neuesten Entdeckungen herausgegeben von Dr. Carl Caesar Leonhard, Jahrgang 7* (1): 3-134.

STENZEL, H.B., 1971. Oysters. In: MOORE, R.C. (Editor), *Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia 3*(3): N953-N1224. Geological Society of America and University of Kansas Press, Boulder and Lawrence.

STEPHENSON, L.W., 1952. Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. *U.S. Geological Survey Professional Paper*, **242**: 226 pp.

TODD, J.A., 1993. The bivalve shell as a preservation trap, as illustrated by the Late Jurassic gryphaeid, *Deltoideum delta* (Smith). *Scripta Geologica, Special Issue*, **2**: 417-433.

TODD, J.A. & PALMER, T.J., 2002. Pattern versus process or informative versus ininformative (*sic*) ichnotaxonomy: comments on Nielsen and Nielsen, 2001. *Ichnos*, **9**: 81-82.

VOIGT, E., 1971. Fremdsulpturen an Steinkernen von Polychaeten-Bohrgängen aus der Maastrichter Tuffkreide. *Paläontologische Zeitschrift*, **45**: 144-153.

VOIGT, E., 1973. Cretaceous burrowing bryozoans. *Journal of Paleontology*, **47**: 21-33.

VOIGT, E., 1975. Tunnelbaue rezenter und fossiler Phoronoidea. *Paläontologische Zeitschrift*, **49**: 135-167.

VOIGT, E., 1978. Phoronidenbaue (*Talpina ramosa* v. Hagenow) aus der Maastrichter Tuffkreide. *Publicaties van het Natuurhistorisch Genootschap in Limburg*, **28**: 3-6.

WILSON, M.A. & TAYLOR, P.D., 2001. Palaeoecology of hard substrate faunas from the Cretaceous Qahlah Formation of the Oman Mountains. *Palaeontology*, **44**: 21-41.

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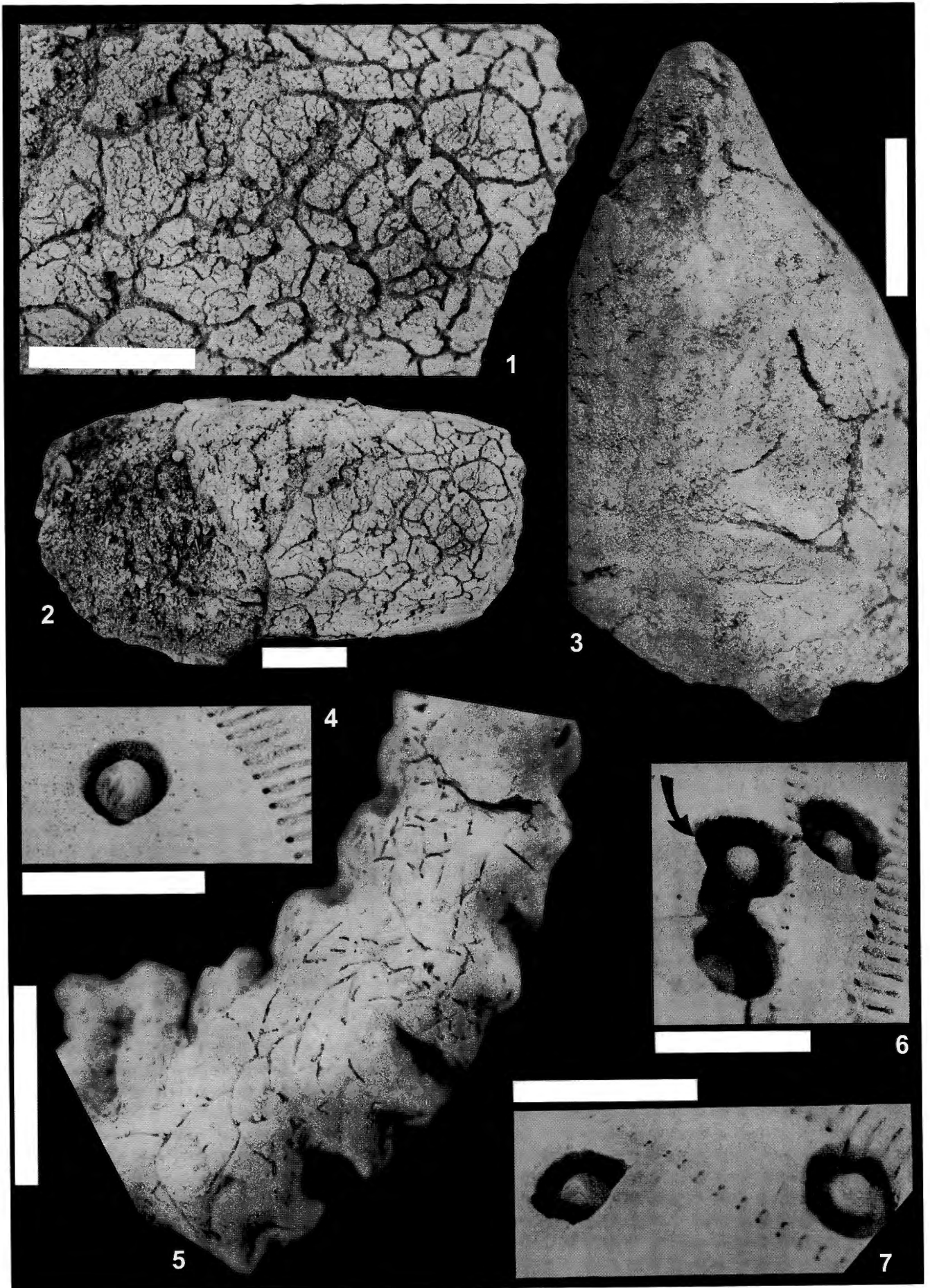


PLATE 1

