

First record of the ichnofossil *Podichnus centrifugalis* from the Maastrichtian of northeast Belgium

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Abstract

In spite of the fact that Campanian-Maastrichtian (Upper Cretaceous) strata in the extended Maastrichtian type area (southeast Netherlands, northeast Belgium, Aachen area, Germany) locally yield common and fairly diverse brachiopod assemblages, there are no previous records of pedicle etching traces assignable to the ichnotaxon *Podichnus centrifugalis* BROMLEY & SURLYK, 1973. Here we report the first examples of this type of trace fossil, in a test of the echinoid *Echinocorys* gr. *conoidea* (GOLDFUSS, 1829) from the Lixhe 1 Member (Gulpen Formation; lower Upper Maastrichtian), as exposed at the CPL SA quarry (Haccourt, province of Liège, Belgium). Overall size (c. 1.0 and 0.5 mm, respectively; the smaller example possibly representing the attachment trace of a juvenile or a different species of brachiopod) and structure suggest these traces to have been produced by a brachiopod pedicle with relatively few papillae. Of brachiopod species known to date from the same stratigraphic level, either the terebratulids *Neoliothyria obesa* and *Carneithyris* sp. or the platidiid *Aemula* may be considered as agents but this is, of course, highly conjectural, at least for the time being.

Keywords: Cretaceous, Maastrichtian, Belgium, brachiopods, ichnofossils, *Podichnus*.

Résumé

En dépit du fait que les dépôts Campaniens-Maastrichtiens de la zone du Maastrichtien type au sens large (sud-est des Pays-Bas, nord-est de la Belgique) ont localement livré une faune abondante et diversifiée de brachiopodes, il n'existe encore aucune mention de traces produites par le pédoncule d'un brachiopode que l'on puisse assigner à l'ichnotaxon *Podichnus centrifugalis* BROMLEY & SURLYK, 1973. Nous rapportons ici les deux premiers exemples de ce type de traces fossiles, préservées dans le test d'un *Echinocorys* gr. *conoidea* (GOLDFUSS, 1829), collecté dans la

craie du Membre Lixhe-1 (Formation de Gulpen, partie inférieure du Maastrichtien supérieur) de la carrière CPL SA (Haccourt, province de Liège, Belgique). Tant la taille que la structure (respectivement 1,0 et 0,5 mm, le plus petit exemplaire pouvant représenter les traces d'attachement d'un spécimen juvénile du plus grand exemplaire ou des traces dues à une autre espèce plus petite de brachiopode) suggèrent que ces traces ont été produites par le pédoncule d'un brachiopode dont la base était ornée d'un petit nombre de papilles. Parmi les brachiopodes connus de ce niveau stratigraphique, les terebratulides *Neoliothyria obesa* et *Carneithyris* sp. ou le platidiide *Aemula* sont des espèces responsables possibles mais ceci reste purement conjectural.

Mots-clefs: Crétacé, Maastrichtien, Belgique, brachiopodes, ichnofossiles, *Podichnus*.

Introduction

Brachiopods, in particular rhynchonelliforms (cyclothyridids, tetrarhynchiids), terebratuloids (terebratulids, gibbithyridids) and kingenoids (kingenids), are comparatively common in the Zeven Wegen, Vijlen and Lixhe 1-3 members of the Gulpen Formation (early Late Campanian to early Late Maastrichtian; see JAGT, 1999 for discussion) in the extended type area of the Maastrichtian Stage. At least sixteen taxa are now known from the Vijlen and Lixhe 1-3 members alone (see Table 1); associated craniids of the genera *Crania*, *Ancistrocrania* and *Isocrania* (*sensu* LEE & BRUNTON, 1986, 2001) are not considered here, since they are cemented to the substrate, either wholly or partially. Moreover, as demonstrated by NIELSEN (1991) for the Recent species *Novocrania anomala* (O.F. MÜLLER, 1776), this craniid lacks a pedicle throughout ontogeny.

Despite this diversity, and a wide range of available hard calcareous substrates for brachiopods to attach to and etch into (*e.g.*, molluscan shells, echinoid tests, rostra of belemnitelid coleoids and

Order/Suborder	Brachiopod species	Stratigraphy	Adaptive group (<i>sensu</i> JOHANSEN, 1987)
Rhynchonellida	<i>Cretirhynchia (Homaletarhynchia) limbata</i>	Lixhe	Ic
	<i>C. (H.) undulata maastrichtiensis</i>	Vijlen	Ib
Terebratulidina	<i>Nerthebrochus ovalis</i>	Vijlen	Ib
	<i>N. sulcata</i>	Vijlen	Ib
	<i>Neoliothyris obesa</i>	Lixhe	Ib
	<i>Carneithyris subcardinalis</i>	Vijlen-Lixhe	II
	<i>C. sp.</i>	Vijlen-Lixhe	Ib
	<i>Terebratulina gracilis</i>	Vijlen	II
	undescribed new cancellothyridinid species	Lixhe	Ia
Terebratellidina	<i>Kingena limburgica</i>	Vijlen	Ib
	<i>Maastrichtiella costellata</i>	Vijlen	Ib
	<i>Aemula inusitata</i>	Lixhe	Ia
	<i>Magas chitoniformis</i>	Vijlen	II
	<i>Kingenella pseudohebertiana</i>	Vijlen	Ib
	<i>Kingenella popielae</i>	Vijlen	Ib
	<i>Mosaethyris felderi</i>	Vijlen	Ib

Table 1 — Brachiopod species known to date from the Vijlen and Lixhe 1-3 members (Gulpen Formation) in southern Limburg (The Netherlands) and from the Haccourt-Lixhe area (Liège, northeast Belgium), as compiled from SIMON (1993, 1998, 2005), SIMON & OWEN (2001), JAGT & SIMON (2004) and SIMON (unpubl. data). The adaptive groups (*sensu* JOHANSEN, 1987, pp. 46-50) are: **Ia** – minute, pedically attached form; **Ib** – larger forms attached with a pedicle to hard substrate; **Ic** – medium-sized forms with pedicle rooted in sediment; **II** – larger, free-living species with attached juvenile stages.

other brachiopods) at the same stratigraphic level, we know of no previous record of the typical brachiopod pedicle trace fossil genus *Podichnus*. Here we record the first examples (Plate 1), in a test of *Echinocorys* gr. *conoidea* (*sensu* JAGT, 2000) from the upper Lixhe 1 Member as exposed at the CPL SA quarry, Haccourt (Liège, northeast Belgium). These specimens bring the number of ichnofossil genera from the area which are assignable to the ethologic class fixichnia (*sensu* DE GIBERT *et al.*, 2004) to six (Table 2).

The present examples of *Podichnus centrifugalis* are the first to be recognised amongst several hundreds of tests of the genus *Echinocorys* LESKE, 1778, both well-preserved and fragmentary, diagenetically deformed ones. Material housed at the Natuurhistorisch Museum Maastricht as well as in several private collections (W. van Rijsselt, P. van Knippenberg, M. Deckers) have been examined, and any epi- and endoskeletobionts (*sensu* TAYLOR & WILSON, 2002) noted. Although no statistical analysis of these data has yet been performed, the paucity of this trace fossil appears genuine. Currently, hard substrates from other stratigraphic members (of

different facies) are being screened, and statistics will be presented and discussed at a later date.

Ichnotaxonomy

The following abbreviations are used to denote the repositories of material referred to in the text: NHM – The Natural History Museum, Department of Palaeontology, London; NHMM – Natuurhistorisch Museum Maastricht (PK = Paul Van Knippenberg Colln.).

Ichnogenus *Podichnus* BROMLEY & SURLYK, 1973

Type ichnospecies: Podichnus centrifugalis BROMLEY & SURLYK, 1973, p. 364, fig. 13, by original designation.

Podichnus centrifugalis BROMLEY & SURLYK, 1973
Pl. 1

*1973 — *Podichnus centrifugalis* BROMLEY & SURLYK, p. 364, figs 6-13.

Domichnia (borings)	<i>Caulostrepsis</i> <i>Entobia</i> <i>Gastrochaenolites</i> <i>Maeandropolydora</i> <i>Rogerella</i> <i>Talpina</i> <i>Trypanites</i>	VOIGT (1971), BROMLEY & D'ALESSANDRO (1983) DONOVAN & JAGT (2006) VOIGT (1972, 1975, 1978) DONOVAN & JAGT (2004)
Fixichnia (superficial attachment structures)	<i>Centrichnus</i> <i>Flosculichnus</i> <i>Lacrimichnus</i> <i>Leptichnus</i> <i>Podichnus</i> <i>Renichnus</i>	JAGT & DORTANGS (2000), JAGT (2003) DONOVAN & JAGT (2005b) JAGT (2007) TAYLOR <i>et al.</i> (1999), JAGT & DORTANGS (2003) <i>present paper</i> JAGT (2003)
Pascichnia (raspings/ scratchings)	<i>Gnathichnus</i> <i>Radulichnus</i>	VOIGT (1977), JAGT (2003)
Praedichnia (drill holes, durophagous scars, bitemarks)	<i>Oichnus</i>	DONOVAN & JAGT (2002, 2005a)

Table 2 — Ichnofossil genera from the Campanian-Maastrichtian of the Maastrichtian type area (pers. obs.), assignable to four (out of five) ethological classes of DE GIBERT *et al.* (2004, fig. 3). Selected literature sources are indicated; examples of the remaining ichnofossil genera will be described and illustrated by BROMLEY, DONOVAN & JAGT (work in progress). Planorbulinid foraminifera locally are common encrusters of ostreid and gryphaeid bivalves, so that examples of the recently erected ichnogenus *Camarichnus* (fixichnia; see SANTOS & MAYORAL, 2006) may also be expected to occur in the study area.

- 1977 — *Podichnus centrifugalis* – RADWAŃSKI, p. 249.
 1982 — *Podichnus centrifugalis* BROMLEY & SURLYK, 1973
 – MARTINELL, p. 93, pl. 1, figs 4-8; pl. 2, figs 1, 2.
 1990 — *Podichnus* isp. – BROMLEY & D'ALESSANDRO, p.
 48, fig. 16.
 1993 — *Podichnus* – PALMER & PLEWES, p. 141, fig. 9C.
 1996 — *Podichnus centrifugalis* BROMLEY & SURLYK, 1973
 – HOFMANN, p. 54, pl. 2, figs 2, 3.
 1999 — *Podichnus centrifugalis* BROMLEY & SURLYK, 1973
 – TADDEI RUGGIERO, p. 169, fig. 11, J.
 2002 — *Podichnus centrifugalis* BROMLEY and SURLYK
 – TADDEI RUGGIERO & ANNUNZIATA, p. 48, pl. 3,
 figs 1-6.
 2004 — *Podichnus centrifugalis* BROMLEY & SURLYK
 – BROMLEY, p. 464, fig. 1.
 2004 — *Podichnus centrifugalis* – DE GIBERT *et al.*, p. 436,
 fig. 6B.
 2004 — *Podichnus centrifugalis* BROMLEY & SURLYK, 1973
 – DONOVAN & LEWIS, p. 368, figs 2, 3.
 2006 — *Podichnus centrifugalis* – BROMLEY & HEINBERG,
 p. 444, fig. 12A, B.

Type

NHM B 51163 (A. Rowe Colln), on the gibbithyridid brachiopod *Carneithyris carnea* (J. SOWERBY, 1812) from the 'Belemnitella mucronata Zone', i.e., Upper Campanian *sensu lato* (compare CHRISTENSEN, 1995) of Mousehold, Norwich (England) (see BROMLEY & SURLYK, 1973, fig. 13).

Material

Two examples, NHMM PK 1488a, b, in a large-sized test (length 93 mm, width 78 mm, height 80 mm) of the echinoid *Echinocorys* gr. *conoidea*; upper Lixhe 1 Member (Gulpen Formation); CPL SA quarry, Haccourt (Liège, Belgium).

Description

Both examples of *P. centrifugalis* occur in the anterior, left-hand portion of the echinoid test, the larger one (NHMM PK 1488a) at the ambitus, in the median portion of interambulacrum 3, and the smaller one (NHMM PK 1488b) in ambulacrum IV at mid-test height, being 30.5 mm apart. The larger example is a slightly asymmetrical cluster of pits, measuring 1.0 by 0.9 mm, and comprising at least seventeen perforations, the (sub)central ones of which are (near)circular, perpendicular to the test surface, and *c.* 0.1 mm (or less) in diameter. Peripheral perforations are larger, oblique, comma- or elongate teardrop-shaped, and measure between 0.2 and 0.3 mm in length. There is a clear clustering on one side, and this side also comprises the largest, oblique perforations, reflecting the growth of the brachiopod and deeper penetration of larger papillae into the substrate, diverging centrifugally.

The smaller example (not illustrated) is much fainter, *c.* 0.5 mm in greatest diameter, and consists of *c.* 10 round to slightly elongate perforations of a type comparable to the ones seen in the (sub)central portion of the larger trace.

Associated episkeletozoans (*sensu* TAYLOR & WILSON, 2002) include bourgueticrinid root structures, a single juvenile pycnodonteine oyster, dimyid bivalves arranged in clear encrustation patterns, as well as at least five species of cyclostome and cheilostome bryozoans, and pits, especially apically, of the type described by MÜLLER (1969) and BROMLEY (1981).

Discussion

These etching traces are clearly those left by brachiopod pedicles; size and structure indicate that there were not too many papillae. In fact, the larger example is closely comparable to a specimen from the Lower Campanian of Roger's Whitening Pit, Fareham (England), illustrated by BROMLEY & SURLYK (1973, fig. 11, upper row, second example from the left). The smaller trace may have been left either by a different species of brachiopod or by a juvenile of the same taxon which produced the larger example here illustrated. At least, the agent must be sought amongst representatives of adaptive groups (*sensu* JOHANSEN, 1987, pp. 46-50) Ib or II (Table 1), which include larger forms with pedicle openings suitable for functional pedicles, and which are confined to large, hard substrates or include medium-sized to large, free-living species which have pedically attached juvenile stages, respectively. Potentially,

the sixteen species known to date from the Vijlen and Lixhe members (Gulpen Formation; see Table 1), cannot equally be held responsible for the trace fossil *Podichnus centrifugalis* documented herein. These brachiopod species can be classified according to two criteria, the first being the adaptive group (*sensu* JOHANSEN, 1987), which must be either Ib or II. Species of these groups, all relatively large, possessed a functional pedicle, at least during the juvenile stage. The species referred to in Table 1 as 'undescribed new cancellothyridinid species' is extremely abundant (125 individuals/5 kg chalk) in the Lixhe 1 Member; it is a diminutive brachiopod which lived attached with a tiny pedicle. Such a micromorphic species cannot be considered a good candidate for constructing a 'large' trace of a width of 1.0 mm.

The larger example of *Podichnus centrifugalis* documented here is much too wide to have been produced by early juvenile individuals of *Magas chitoniformis* (VON SCHLOTHEIM, 1813) or by juveniles of *Terebratulina gracilis* (VON SCHLOTHEIM, 1813). If the size of the foramen is taken into account, the width of the juvenile pedicle of these two species was much too reduced. Moreover, these species rapidly turned into free-living forms already at young growth stages.

Amongst free-living species at adult growth stages, *Carneithyris subcardinalis* (SAHNI, 1925) remains a valid candidate because young specimens might have possessed a pedicle with a base width of 1 mm.

Cretirhynchia (Homaletarhynchia) limbata (VON SCHLOTHEIM, 1813) can also be excluded because, as shown by SIMON (1998, pp. 184-185), this species probably lived rooted to the sea floor with its dorsal valve down. The rapid development of a dorsal fold in this form was an adaptation to elevate continuously the commissure above the substrate level, thus avoiding the negative effects of rapid sedimentation. Because of this, *C. limbata*, which did not occur on hard substrates, could not be responsible for producing *Podichnus* traces.

All other species listed in Table 1 under group Ib remain possible candidates.

The second criterion is the actual presence of a brachiopod candidate species at the same stratigraphic level and site from where the echinoid test with *Podichnus centrifugalis* was collected. *Nerthebrochus ovalis* SIMON, 2005, *N. sulcata* SIMON, 2005, *Kingena limburgica* SIMON, 2005, *Maastrichtiella costellata* SIMON, 2005, *Kingenella pseudohebertiana* (PERON, 1895), *Kingenella popielae* SIMON, 2005 and *Mosaethyris felderi* SIMON, 2005 are all species

known to date only from the basal Vijlen Member (equivalents of the *Belemnella sumensis* Zone; Lower Maastrichtian) in southern Limburg (The Netherlands). Amongst species listed in Table 1, only *Carneithyris subcardinalis*, *Carneithyris* sp., *Neoliothyryna obesa* SAHNI, 1925 and *Aemula inusitata* STEINICH, 1968 have been collected from the Lixhe 1 Member at the CPL SA quarry. *Creterhynchia* (*Homaletarhynchia*) *undulata maastrichtiensis* SIMON & OWEN, 2001 is common in the upper Vijlen Member exposed there, and is found associated with *Terebratulina gracilis*. So far, *Aemula inusitata* is the only non-craniid brachiopod found *in situ* on echinoid tests in the Lixhe 1-3 members (see JAGT & SIMON, 2004). In specimens of *Aemula* illustrated in the literature by their dorsal valves (STEINICH, 1968; SURLYK, 1972; SIMON, 1998), the diameter of the foramen (which could be related to the size of the potentially attached base of the pedicle) varies between 1.34 mm and 1.8 mm for a dorsal valve width of 5 mm (maximum size observed). *Aemula* specimens generally are smaller, but the range of their foramen size fit the width of *Podichnus centrifugalis* documented here. However, the larger *Podichnus* shows a clear clustering on one side which indicates possible growth of the pedicle with deeper penetration of larger papillae into the substrate. This is not really compatible with the development of a small individual of *Aemula inusitata* living with its dorsal valve firmly appressed to the substrate. The type of growth of this example of *P. centrifugalis* better matches a brachiopod species which was obliged to increase its attachment strength relative to its increased weight during growth. Thus, the best candidates are *Neoliothyryna obesa* and *Carneithyris* sp. If current records of brachiopod species and of *Podichnus centrifugalis* are considered in conjunction, *Neoliothyryna obesa* would appear the best candidate to have produced these traces. This is a comparatively rare species in the Lixhe 1-3 members and examples of *Podichnus* also are extremely scarce.

However, this analysis, based as it is on two essential criteria, remains highly speculative and, in fact, all species known from the Vijlen and Lixhe 1-3 members remain possible agents. Only the discovery *in situ* of a brachiopod responsible for a *Podichnus* trace can settle this matter. Specimens of *Aemula inusitata* attached to *Echinocorys* might be carefully removed in order to document any possible traces under the excavated dorsal valves; in view of the limited material currently available, we refrain from such destructive action for now.

BROMLEY (2005a, p. 9) noted that the trace fossil *P. centrifugalis* was based originally on Recent and Cretaceous examples only, and that at the time it was unknown that brachiopod etching of carbonate substrates was in fact much more widespread than previously thought, and in fact dates back to the Silurian. Consequently, various groups of brachiopods can be held responsible for producing this type of this trace. Despite this wide taxonomic range of agents, trace morphology is remarkably constant throughout its range, and it therefore appears advisable to use but a single ichnotaxon name for it (see also BROMLEY, 2004). However, BROMLEY (2005b) also expressed the hope that minor variations in traces might be linked to specific brachiopod types, e.g., those with divided pedicle, or those with a massive one, armed either with short or long attachment papillae. Only in cases where brachiopods are found preserved *in situ*, and where careful preparation may reveal the underlying etching trace of the pedicle or where assemblages are monospecific, can examples of *Podichnus* clearly be linked to specific brachiopod types. Illustrating the latter is material from the Middle Triassic (Muschelkalk) of the Opole area (southwest Poland), from where MALKOWSKI (1975) recorded a new ichnospecies, *P. silesiacus*, ascribed to the 'terebratuloid' *Coenothyris vulgaris* (VON SCHLOTHEIM, 1820).

In the same abstract volume which contains BROMLEY's (2005b) paper, ROBINSON (2005, p. 26) noted that there are at least three distinct types of brachiopod 'footprint', that is, pedicle etching trace, related to pedicle type, which appear to be correlated with distinct brachiopod orders or suborders, and date back to at least the Cretaceous. The same author redefined *P. centrifugalis* and proposed two additional ichnospecies of *Podichnus*. As far as we know, these have not yet been validly introduced, which is why we adopt the name *P. centrifugalis* for the present examples from Haccourt.

Occurrence

TAYLOR & WILSON (2003, table 2) noted that *Podichnus* ranged from the Carboniferous to the Recent, and referred specifically to MICHALÍK (1977), VOGEL *et al.* (1987) and ALEXANDER (1994) for examples. Later, BROMLEY (2004) extended the range down into the Silurian, and made reference to SCHMIDT (1992), GLAUB & SCHMIDT (1994) and BUNDSCHUH (2000) for examples. Recently described examples of this trace fossil include those by HANGER (1992; Albian of Texas), REICH & FRENZEL (2002;

Lower Maastrichtian of Rügen, northern Germany), BROMLEY (2003; Pleistocene of Rhodes, Greece), BLISSETT & PICKERILL (2004; Middle Eocene to Middle Miocene of Jamaica), RADLEY (2004; Lower Jurassic of England) and FÖRSTERRA *et al.* (2005; Recent, off central Chile).

Conclusion

In comparison to other ethologic classes, fixichnia are rare in Upper Cretaceous strata of the study area, and include mainly examples of the ichnogenera *Centrichnus*, *Renichnus* and *Leptichnus*. So far, *Podichnus centrifugalis* has proved to be exceedingly rare, which is surprising in view of the common occurrence of brachiopods and the ubiquity of calcareous substrates for attachment at the same stratigraphic levels. All possible substrates need to be screened carefully, in order to record more examples and additional substrate types, especially from those levels where certain rhynchonelliform, terebratuloid and kingenoid brachiopods are common and diverse.

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References

- ALEXANDER, R.R., 1994. Distribution of pedicle boring traces and the life habit of Late Paleozoic leiorhynchid brachiopods from dysoxic habitats. *Lethaia*, **27**: 227-234.
- BLISSETT, D. & PICKERILL, R.K., 2004. Aspects of micro- and macroborings from the White Limestone Group, Jamaica, West Indies. *Geological Society of America, Abstracts with Programs*, **36**: 111.
- BROMLEY, R.G., 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geológica Hispánica*, **16**: 55-64.
- BROMLEY, R.G., 2003. Bioerosion of Pleistocene *Lophelia*, Rhodes, Greece. In: FREIWALD, A. & SCHULBERT, C. (Editors). 2nd International Symposium on Deep-sea Corals, September 8th-13th 2003, Erlangen. *Erlanger geologische Abhandlungen, Sonderband*, **4**: 24.
- BROMLEY, R.G., 2004. A stratigraphy of marine bioerosion. In: MCILROY, D. (Editor). The application of ichnology to palaeoenvironmental and stratigraphic analysis. *Geological Society London, Special Publication*, **228**: 455-479.
- BROMLEY, R.G., 2005a. *Podichnus centrifugalis* Bromley & Surlyk, 1973 revisited: attachment scars of brachiopods. In: HARPER, D.A.T., LONG, S.L. & MCCORRY, M. (Editors). *Fifth International Brachiopod Congress, Copenhagen 2005, Abstracts*. Copenhagen, Geological Survey of Denmark and Greenland, p. 9.
- BROMLEY, R.G., 2005b. Preliminary study of bioerosion in the deep-water coral *Lophelia*, Pleistocene, Rhodes, Greece. In: FREIWALD, A. & MURRAY, J.W. (Editors). *Cold-water corals and ecosystems*. Springer Verlag, Berlin/Heidelberg, pp. 587-606.
- BROMLEY, R.G. & D'ALESSANDRO, A., 1983. Bioerosion in the Pleistocene of southern Italy: ichnogenera *Caulostrepsis* and *Maeandropolydora*. *Rivista italiana di Paleontologia e Stratigrafia*, **89**: 283-309.
- BROMLEY, R.G. & D'ALESSANDRO, A., 1990. Comparative analysis of bioerosion in deep and shallow water, Pliocene to Recent, Mediterranean Sea. *Ichnos*, **1**: 43-49.
- BROMLEY, R.G. & HEINBERG, C., 2006. Attachment strategies of organisms on hard substrates: a palaeontological view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**: 429-453.
- BROMLEY, R.G. & SURLYK, F., 1973. Borings produced by brachiopod pedicles, fossil and Recent. *Lethaia*, **6**: 349-365.
- BUNDSCHUH, M., 2000. Silurische Mikrobohrspuren – ihre Beschreibung und Verteilung in verschiedenen Faziesräumen (Schweden, Litauen, Großbritannien und USA). Johann Wolfgang Goethe Universität, Frankfurt am Main (unpubl. PhD thesis) (not seen).
- CHRISTENSEN, W.K., 1995. *Belemnitella* from the Upper Campanian and Lower Maastrichtian Chalk of Norfolk, England. *Special Papers in Palaeontology*, **51**: 1-84.
- DE GIBERT, J.M., DOMÈNECH, R. & MARTINELL, J., 2004. An ethological framework for animal bioerosion trace fossils upon mineral substrates with proposal of a new class, fixichnia. *Lethaia*, **37**: 429-437.
- DONOVAN, S.K. & JAGT, J.W.M., 2002. *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. & JAGT, J.W.M., 2004. Taphonomic and ethologic aspects of the ichnology of the Maastrichtian of the type area (Upper Cretaceous, The Netherlands and Belgium). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **74**: 119-127.
- DONOVAN, S.K. & JAGT, J.W.M., 2005a. An additional record of *Oichnus excavatus* Donovan & Jagt from the

- Maastrichtian (Upper Cretaceous) of southern Limburg, The Netherlands. *Scripta Geologica*, **129**: 147-150.
- DONOVAN, S.K. & JAGT, J.W.M., 2005b. *Flosculichnus tectus*, an etched attachment scar from the Upper Cretaceous (Maastrichtian) of The Netherlands. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **75**: 207-210.
- DONOVAN, S.K. & JAGT, J.W.M., 2006. Opmerkelijke Luiks-Limburgse Krijtfofossielen. Deel 10. Xenoglyfen – sporenfofossielen met iets extra's. *Natuurhistorisch Maandblad*, **95**: 228-230.
- DONOVAN, S.K. & LEWIS, D.N., 2004. Palaeoecology in the museum gift shop. *Proceedings of the Geologists' Association*, **115**: 367-370.
- FÖRSTERRA, G., BEUCK, L., HÄUSSERMANN, V. & FREIWALD, A., 2005. Shallow-water *Desmophyllum dianthus* (Scleractinia) from Chile: characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications. In: FREIWALD, A. & ROBERTS, J.M. (Editors). *Cold-water corals and ecosystems*. Springer Verlag, Berlin/Heidelberg, pp. 937-977.
- GLAUB, I. & SCHMIDT, H., 1994. Traces of endolithic microboring organisms in Triassic and Jurassic bioherms. *Kaupia*, **4**: 103-112.
- GOLDFUSS, A., 1826-1844. Petrefacta Germaniæ tam ea, quae in museo universitatis regiae Borussicae Fridericiae Wilhelmae Rhenanae servantur quam alia quae cunque in museis hoeninghusiano, muensteriano aliisque extant, iconibus et descriptionibus illustrata. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzenden Länder, unter Mitwirkung des Herrn Grafen Georg zu Münster. Arnz & Co., Düsseldorf, viii + 1-76, pls. 1-12 (1826); 77-164, pls. 26-50 (1829); 165-240, pls. 51-71 (1831); 242-252 (1833); 1-68, pls. 72-96 (1833); 69-240, pls. 97-121 (1836); 141-224, pls. 122-146 (1840); 225-312, pls. 147-165 (1837); iv + 1-128, pls. 166-200 (1844).
- HANGER, R.A., 1992. *Podichnus centrifugalis* (Bromley and Surlyk, 1973) in the Cretaceous (Albian) Duck Creek Formation, Tarrant County, Texas. *Texas Journal of Science*, **44**: 252-254.
- HOFMANN, K., 1996. Die mikro-endolithischen Spurenfofossilien der borealen Oberkreide. *Geologisches Jahrbuch*, **A136**: 3-153.
- JAGT, J.W.M., 1999. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 1: Introduction and stratigraphy. *Scripta Geologica*, **119**: 1-57.
- 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., 2007. A Late Cretaceous gastropod homing scar (possibly ichnogenus *Lacrimichnus*) from southern Limburg, The Netherlands. *Scripta Geologica*, **134**: 19-25.
- JAGT, J.W.M. & DORTANGS, R.W., 2000. Opmerkelijke Luiks-Limburgse Krijtfofossielen. Deel 4. Goedzittende paardezadels. *Natuurhistorisch Maandblad*, **89**: 183-186.
- JAGT, J.W.M. & DORTANGS, R.W., 2003. Opmerkelijke Luiks-Limburgse Krijtfofossielen. Deel 6. Mosdiertjes vermist. *Natuurhistorisch Maandblad*, **92**: 28-29.
- JAGT, J.W.M. & SIMON, E., 2004. A pedunculate brachiopod population preserved *in situ* (Late Maastrichtian, NE Belgium). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **74**: 97-103.
- JOHANSEN, M.B., 1987. Brachiopods from the Maastrichtian-Danian boundary sequence at Nye Kløv, Jylland, Denmark. *Fossils and Strata*, **20**: 1-99.
- LEE, D.E. & BRUNTON, C.H.C., 1986. *Neocrania* n. gen., and a revision of Cretaceous-Recent brachiopod genera in the family Craniidae. *Bulletin of the British Museum (Natural History), Geology Series*, **40**: 141-160.
- LEE, D.E. & BRUNTON, C.H.C., 2001. *Novocrania*, new name for the genus *Neocrania* Lee and Brunton, 1986 (Brachiopoda, Craniida); preoccupied by *Neocrania* Davis, 1978 (Insecta, Lepidoptera). *Bulletin of the Natural History Museum, Geology Series*, **57**: 5.
- LESKE, N.G., 1778. Jacobi Theodori Klein Naturalis dispositio Echinodermatum, edita et descriptionibus novisque inventis et synonymis auctorum aucta. G.E. Beer, Lipsiae, xxii + 278 pp.
- MAŁKOWSKI, K., 1975. Attachment scars of the brachiopod *Coenothyris vulgaris* (Schlothheim, 1820) from the Muschelkalk of Upper Silesia. *Acta Geologica Polonica*, **25**: 275-282.
- MARTINELL, J., 1982. Borings produced by presumed Pliocene brachiopods from L'Empordà (Catalonia, Spain). *Bulletin del Institut Catalyuna de Historia natural*, **(3)48**: 91-97.
- MICHALÍK, J., 1977. Systematics and ecology of *Zeilleria* Bayle and other brachiopods in the uppermost Triassic of the West Carpathians. *Geologica Carpathica*, **28**: 323-346.
- MÜLLER, A.H., 1969. Zur Ökologie und Biostratinomie eines *Echinocorys* (Echinoidea) mit eigentümlichen Naticiden-Befall aus der Oberkreide. *Monatsberichte der deutschen Akademie der Wissenschaften Berlin*, **11**: 672-684.
- MÜLLER, O.F., 1776. Zoologiae Danicae. Prodromus seu animalium daniae et norvegiae indigenarum characteres,

nomina et synonyma imprimis popularium. Typis Hallageriis, Havniae, xxxii + 282 pp.

NIELSEN, C., 1991. The development of the brachiopod *Crania (Neocrania) anomala* (O.F. Müller) and its phylogenetic significance. *Acta Zoologica*, **72**: 7-28.

PALMER, T. & PLEWES, C., 1993. Borings and bioerosion in fossils. *Geology Today*, **9**: 138-142.

PERON, A., 1895. Les brachiopodes du terrain Crétacé supérieur de Ciplly (Belgique). *Association Française pour l'Avancement des Sciences*, **23**: 453-468.

RADLEY, J.D., 2004. Brachiopod pedicle attachment scars (*Podichnus centrifugalis* Bromley & Surlyk) on Lower Jurassic oysters (Gloucestershire and Warwickshire). *Proceedings of the Cotteswold Naturalists' Field Club*, **43**: 18-19.

RADWAŃSKI, A., 1977. Present-day types of trace in the Neogene sequence; their problems of nomenclature and preservation. In: CRIMES, T.P. & HARPER, J.C. (Editors). *Trace Fossils 2*. Seel House Press, Liverpool, pp. 227-264.

REICH, M. & FRENZEL, P., 2002. Die Fauna und Flora der Rügener Schreiekreide (Maastrichtium, Ostsee). *Archiv für Geschiebekunde*, **3**: 73-284.

ROBINSON, J., 2005. Brachiopod pedicle traces: redefinition of *Podichnus centrifugalis* to differentiate three types of trace. In: HARPER, D.A.T., LONG, S.L. & MCCORRY, M. (Editors). *Fifth International Brachiopod Congress, Copenhagen 2005, Abstracts*. Copenhagen, Geological Survey of Denmark and Greenland, p. 26.

SAHNI, M.R., 1925. Morphology and zonal distribution of some Chalk terebratulids. *Annals and Magazine of Natural History*, **(9)15**: 353-385.

SANTOS, A. & MAYORAL, E., 2006. Bioerosive structures of sclerozoan foraminifera from the lower Pliocene of southern Spain: a contribution to the palaeoecology of marine hard substrate communities. *Palaeontology*, **49**: 719-732.

SCHLOTHEIM, E.F. VON, 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. *Leonhard's Taschenbuch für die gesammte Mineralogie*, **7**: 3-134.

SCHLOTHEIM, E.F. VON, 1820. Die Petrefaktenkunde auf ihrem jetzigen Standpunkte, durch die Beschreibung seiner Sammlung versteinertes und fossiler Überreste des Thier- und Pflanzenreiches der Vorwelt erläutert. Becker, Gotha, lxii + 437 pp.

SCHMIDT, H., 1992. Mikrobohrspuren ausgewählter Faziesbereiche der tethyalen und germanischen Trias (Beschreibung, Vergleich und bathymetrische Interpretation). *Frankfurter geowissenschaftliche Arbeiten*, **A12**: 1-228.

SIMON, E., 1993. Possible presence of *Cretirhynchia*

undulata (Pusch, 1837) in the Vijlen Chalk (Upper Maastrichtian) from Hallembaye (Belgium) and neighbouring area. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **63**: 73-97.

SIMON, E., 1998. Maastrichtian brachiopods from Ciplly: palaeoecological and stratigraphical significance. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **68**: 181-232.

SIMON, E., 2005. New Lower Maastrichtian brachiopods (Gulpen Formation, Vijlen Member) from southern Limburg (The Netherlands). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **75**: 127-165.

SIMON, E. & OWEN, E.F., 2001. A first step in the revision of the genus *Cretirhynchia* Pettitt, 1950. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **71**: 53-118.

SOWERBY, J., 1812-1822. The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the earth. The author, London, 1, pls. 1-9 (1812); pls. 10-44 (1813); pl. 45-78 (1814); pls. 79-102 (1815); 2, pls. 103-114 (1815); pls. 115-150 (1816); pls. 151-186 (1817); pls. 187-203 (1818); 3, pls. 204-221 (1818); pls. 222-253 (1819); pls. 254-271 (1820); pls. 272-306 (1821); 4, pls. 307-318 (1821); pls. 319-383 (1822).

STEINICH, G., 1968. Neue Brachiopoden aus der Rügener Schreiekreide (Unter-Maastricht). II. Die Platidiidae Thomson. *Geologie*, **17**: 192-209.

SURLYK, F., 1972. Morphological adaptations and population structures of the Danish Chalk brachiopods (Maastrichtian, Upper Cretaceous). *Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, **19**: 1-57.

TADDEI RUGGIERO, E., 1999. Bioerosive processes affecting a population of brachiopods (Upper Pliocene, Apulia). *Bulletin of the Geological Society of Denmark*, **45**: 169-172.

TADDEI RUGGIERO, E. & ANNUNZIATA, G., 2002. Bioerosion on a *Terebratula scillae* population from the Lower Pleistocene of Lecce area (Southern Italy). *Acta Geologica Hispanica*, **37**: 43-51.

TAYLOR, P.D. & WILSON, M.A., 2002. A new terminology for marine organisms inhabiting hard substrates. *Palaios*, **17**: 522-525.

TAYLOR, P.D. & WILSON, M.A., 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews*, **62**: 1-103.

TAYLOR, P.D., WILSON, M.A. & BROMLEY, R.G., 1999. A new ichnogenus for etchings made by cheilostome bryozoans into calcareous substrates. *Palaeontology*, **42**: 595-604.

VOGEL, K., GOLUBIC, S. & BRETT, C.E., 1987. Endolith associations and their relation to facies distribution in the Middle Devonian of New York State. *Lethaia*, **20**: 263-290.

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

VOIGT, E., 1972. Über *Talpina ramosa* v. Hagenow 1840, ein wahrscheinlich zu den Phoronidea gehöriger Bohrorganismus aus der Oberen Kreide, nebst Bemerkungen zu den übrigen bisher beschriebenen kretazischen „*Talpina*“-Arten. *Nachrichten der Akademie der Wissenschaften in Göttingen, II. Mathematisch-physikalische Klasse*, **7**: 93-126 [1-34].

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

VOIGT, E., 1977. On grazing traces produced by the radula of fossil and Recent gastropods and chitons. In: CRIMES, T.P. & HARPER, J.C. (Editors). *Trace fossils 2*. Seel House Press, Liverpool, pp. 335-346.

VOIGT, E., 1978. Phoronidenbaue (*Talpina ramosa* v. Hagenow) aus der Maastrichter Tuffkreide. *Publicaties van het Natuurhistorisch Genootschap in Limburg*, **28**: 1-6.

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Explanation of Plate 1

PLATE 1

Test of *Echinocorys* gr. *conoidea* (GOLDFUSS, 1829) from the upper Lixhe 1 Member (Gulpen Formation), CPL SA quarry, Haccourt (Liège, Belgium) in posterior, lateral and anterior views (A-C), respectively, and detail (D) of larger specimen of *Podichnus centrifugalis* BROMLEY & SURLYK, 1973 (NHMM PK 1488a) near the ambitus in interambulacrum 3 (circled in B and C). Scale bars equal 10 mm in A-C, and 1 mm in D.

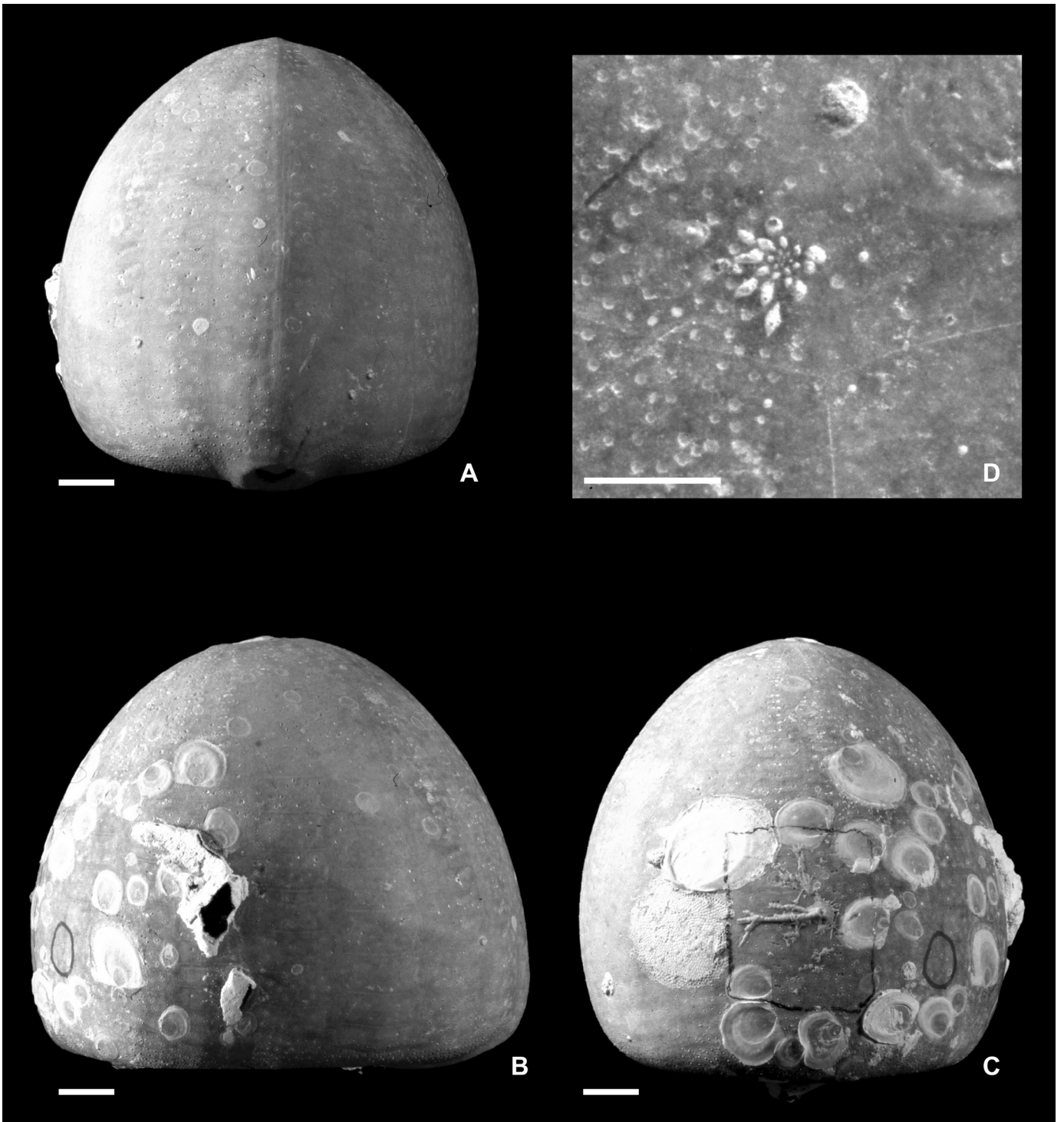


PLATE 1