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A giant boring in a Silurian stromatoporoid analysed by computer tomography

LYDIA BEUCK, MAX WISSHAK, AXEL MUNNECKE, and ANDRÉ FREIWALD



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This study describes the largest known Palaeozoic boring trace, *Osprioneides kampto* igen. et isp. nov., found within a stromatoporoid *Densastroma pexisum* from the Upper Visby Formation (lower Wenlock, Silurian) on the island of Gotland, Sweden. Differences between the physical properties of the stromatoporoid and the dense micritic infilling of the borings allowed the application of the CT-scan technology for the 2D and 3D-visualisation of this rare trace. The additional application of a stereoscopic technique on these CT images and movies enhances its value for unravelling spatial orientations. This non-destructive method has a great potential for future macro- as well as microboring analyses. The trace maker, most likely a worm, infested the hosting colony post-mortem with up to 120 mm long borings measuring 5–17 mm in diameter. Smaller forms of *Trypanites* and *Palaeosabella* within the same stromatoporoid preferentially occur in the outer coenosteum and occasionally in abandoned borings of *O. kampto*. The stratigraphic position of *O. kampto* follows the "Great Ordovician Biodiversification Event" in time, and reflects the increase in diversity of boring species. Borings with penetration depths of 120 mm are, however, unique findings for the Palaeozoic and were not exceeded until some 260 million years later (Bajocian, Middle Jurassic) when the "Mesozoic Marine Revolution" led to convergent reinventions as a result of enhanced predation, grazing pressure, and ecospace competition.

Key words: Bioerosion, trace fossil, *Osprioneides*, stromatoporoid, computed tomography, Silurian, Gotland.

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Introduction

During the Early Palaeozoic, major evolutionary adaptive radiations—referred to as the "Cambrian Explosion" (Gould 1989) and the "Great Ordovician Biodiversification Event" (Webby et al. 2004; Harper 2006)—produced a burst in marine invertebrate biodiversity. This general increase is also reflected in the ichnodiversity of trace fossils as indicated by the first appearance of many ichnogenera during the Ordovician (Kobluk et al. 1978; Mángano and Droser 2004). This trend holds especially true for borings in lithic substrates, where the "Ordovician Bioerosion Revolution" led to the appearance of many new ichnogenera in concert with a significant increase in the intensity of bioerosion (Ekdale and Bromley 2001; Bromley 2004; Wilson and Palmer 2006). However, even though the density of bioerosion was greatly enhanced, most macroborings were comparatively shallow, only rarely reaching 50 mm in penetration depth. In this context, we would like to present the unexpected finding of unusually large and deeply penetrating macroborings—a new ichnogenus presumably produced by a cavity-boring worm in a Silurian stromatoporoid.

Institutional abbreviation.—NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden.

Material and methods

The stromatoporoid host.—One piece of the stromatoporoid *Densastroma pexisum* (Yavorsky, 1929) was found in the locality "Halls Huk 3" (see Laufeld 1974) on Gotland, Sweden (Fig. 1). This locality is situated ca. 4 km NE of the Hall church (Swedish Grid: 6425681/1674742, topographical map 66C Tingstäde). The specimen is in the collections of the Naturhistoriska Riksmuseet, Stockholm, Sweden (inventory number NRM-Cn 69062). The colony is 240 mm in diameter and with a maximal height of 175 mm in the central part of its coenosteum. The surface of the coenosteum is smooth but exhibits a high number of small pit holes filled with carbonate mud. The colony is high dome-shaped (sensu Kershaw 1990), and is broken along the vertical middle axis. Furthermore, the surface is partly broken off along the laminae. The fracture zones expose several endolithic traces of different size, all filled with fine carbonate mud.

CT scan analysis.—Computer Tomography (CT) was chosen for its direct, non-destructive characteristics and for analysing the spatial distribution of bodies with different densities and shapes within the stromatoporoid. A Siemens SOMATOM Sensation 64® in the Medical Solution Centre Forchheim, Germany, was used in this study. The data acquisition occurred at

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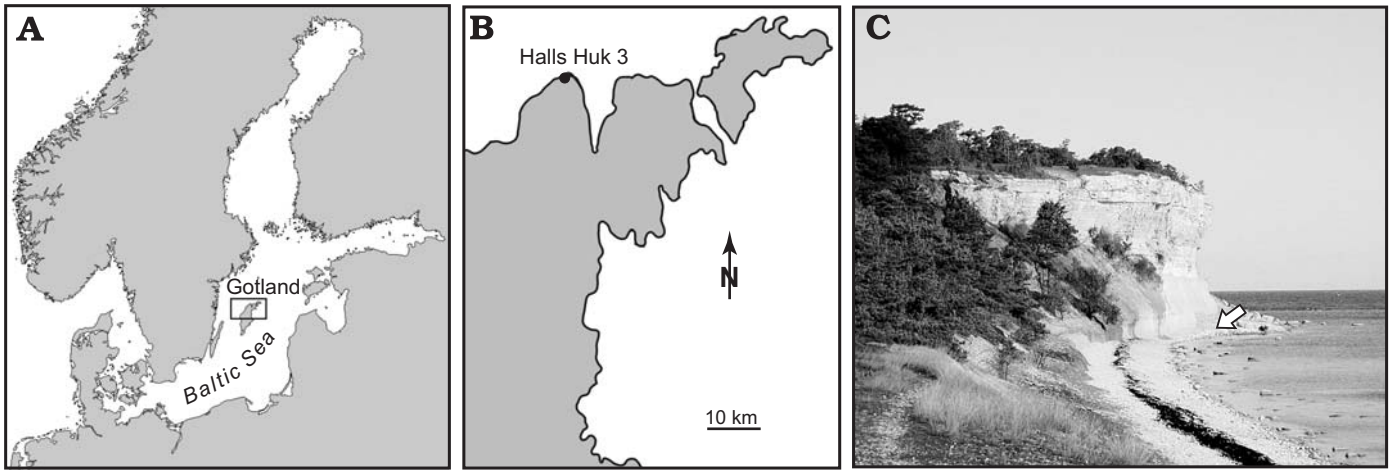


Fig. 1. Study area. **A**. Overview showing the position of Gotland in the Baltic Sea. **B**. Geographic position of the "Halls Huk 3" locality. **C**. Field photograph indicating where the stromatoporoid specimen was found (arrow).

140kV, 545 eff. mAs, 0.6 pitch and with an isotropic resolution of 1 mm. The spiral data set was visualised in syngo® CT.3D with 2D and 3D post-processing tools at the Institute for Medical Physics in Erlangen, Germany. The common view of acquired slices on a monitor is from caudal, resulting in a mirrored view. For the analysis of the borings, only the density range of the micritic fillings was imaged. CT scan analysis figures of this study were taken by screenshots from the monitor and were not mirrored. For printable 3D visualisation, the stereoscopic technique was applied on selected images. Therefore, two images were superimposed intergrading in a perspective angle of 6°, were coloured in Adobe Photoshop® (red/blue) and one image was given a transparency of 50% for examination with anaglyph glasses (red-blue glasses). Additionally, three types of movies were produced: serial sections in 2D throughout the entire specimen were created from individual section images with an interval of 1 mm; rotating 3D sample movies were created from 360 serially produced images within syngo® CT.3D, showing the object from all possible angles in a defined rotation axis and movies created for anaglyph glasses were produced from the dataset of the latter by superimposing two movies with a six frame offset (equal to 6°). The conversion from images to movies was done with the software VideoMach® 3.1.7. The anaglyph technique for the 3D movies was undertaken in Adobe Premiere® 1.5 by colouring the individual movies (red/blue) and rendering the compound movie with a transparency of 50% of the upper one (see also Beuck et al. 2007). The movies are stored in the data repository of Acta Palaeontologica Polonica (see Supplementary Online Material at http://app.pan.pl/acta53/app53-Beuck_etal_SOM.pdf).

Stable carbon isotope analysis.—In order to stratigraphically date the sample, $\delta^{13}C_{carb}$ analyses have been carried out on 5 micrite samples drilled from the fillings of three different borings. Carbonate powders were reacted with 100% phosphoric acid (density >1.9, Wachter and Hayes 1985) at 75°C using a Kiel III online carbonate preparation line connected to a ThermoFinnigan 252 mass-spectrometer at the Geological Institute in Erlangen (Germany). All values are reported in per mil relative to V-PDB by assigning a $\delta^{13}C_{carb}$ value of +1.95‰ to NBS19. Reproducibility was checked by replicate analysis of laboratory standards and is better than ± 0.02 (1s).

Results

Stratigraphic position.—The stromatoporoid was found at the locality termed "Halls Huk 3" (Fig. 1). This locality is characterised by an up to 30 m high cliff section. Just below modern sea level the Lower Visby Formation (uppermost Llandovery to lowermost Wenlock) crops out. The cliff itself comprises the Upper Visby Formation (lowermost Wenlock) in the lower part, and the Högklint Formation in the upper part (lower Wenlock). The Lower and Upper Visby Formations represent the oldest rocks on Gotland. They developed as a prograding limestone-marl alternation. The Lower Visby Formation was deposited below storm-wave base and below the photic zone in a distal shelf environment, whereas the overlying Upper Visby Formation was deposited in shallower water, probably between storm-wave base and fair-weather wave base as indicated by an increased abundance of packstones and grainstones, ripple marks, and the occurrence of calcareous algae (Samtleben et al. 1996; Calner et al. 2004). The Upper Visby Formation contains numerous small decimeter-sized reef-mounds. The main reef builders are tabulate corals and stromatoporoids, but also rugose corals. The overlying Högklint Formation consists of coarse-grained bioclastic limestones rich in crinoids, trilobites, brachiopods, and molluscs. Abundant oncolites and oncolitic crusts indicate deposition well within the photic zone.

Since the stromatoporoid was found as a loose specimen at the foot of the cliff, the exact stratigraphic position was unknown. However, on Gotland—but also on a global scale—

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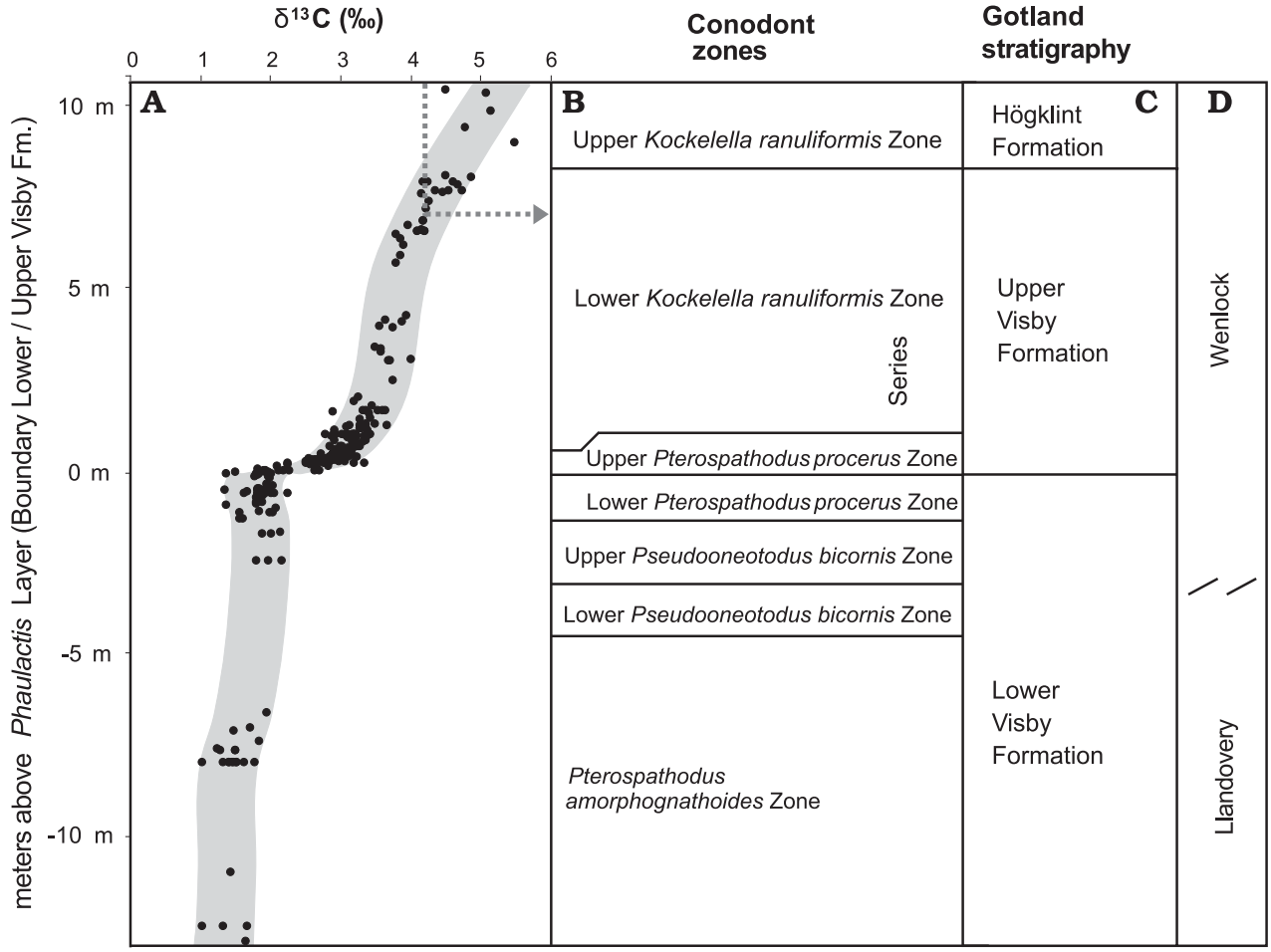


Fig. 2. **A**. Stable carbon isotope stratigraphy across the Silurian Lower/Upper Visby Formation boundary (metres according to the Ireviken type section; after Munnecke et al. 2003). **B**. Conodont stratigraphy after Jeppsson (1997). **C**. Formations on Gotland. **D**. Series. $\delta^{13}C_{carb}$ data from micritic material indicate a stratigraphic position within the upper part of the Lower *Kockelella ranuliformis* Conodont Zone.

the Llandovery–Wenlock boundary is characterised by a pronounced positive shift in $\delta^{13}C_{carb}$ values (Samtleben et al. 1996), which can be correlated exactly with the conodont stratigraphy (Fig. 2; Jeppsson 1997; Munnecke et al. 2003). The mean $\delta^{13}C_{carb}$ value of +4.18‰ indicates a stratigraphic position within the upper part of the Lower *Kockelella ranuliformis* Conodont Zone, i.e., in the upper part of the Upper Visby Formation (Fig. 2).

Characterisation of the ichnocoenosis.—The surface of the investigated *Densastroma pexisum* is highly pitted by circular holes between 1 and 4 mm in diameter (Figs. 3, 4C). These are the apertures of borings referred to as ichnogenera *Palaeosabella* and *Trypanites* (see also Kershaw 1980). Both are cylindrical boring traces of up to few centimetres in length as seen in the fracture surface (Fig. 4D). Surface-boring density is very high and increases towards the apex of the host. Although most of these borings originated from the surface of the stromatoporoid, some traces were recognised deep within the host as revealed by CT scan analysis (Figs. 5B, D, F, 6C–F, 7C). Most prominent are, however, exceptionally large traces (Figs. 3–8), which we describe below as a new ichnospecies.

Systematic ichnology

(L. Beuck and M. Wisshak)

Ichnogenus *Osprioneides* Beuck and Wisshak, nov.

Type and only ichnospecies: *Osprioneides kampto* nov.

Derivation of the name: From Greek *osprion*, legume; *-eides*, alike.

Diagnosis.—Unbranched, elongate boring in lithic substrate with oval cross-section, single-entrance and straight, curved or irregular course.

Discussion.—The morphological characteristics of *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. are distinguished from the emended diagnosis of *Trypanites* Mägdefrau, 1932 as given by Bromley and D'Alessandro (1987) by being oval in cross-section and by being somewhat variable in width. In addition, *Trypanites* is generally smaller in dimension (the diameter of *Trypanites weisei* is usually only about 1 mm; Mägdefrau 1932; Bromley 1972), and the only ichnospecies reaching comparable penetration depths is *T. fosteryeomani* which is, however, always oriented vertical and has a smaller diameter (3.9–4.9 mm; Cole and Palmer

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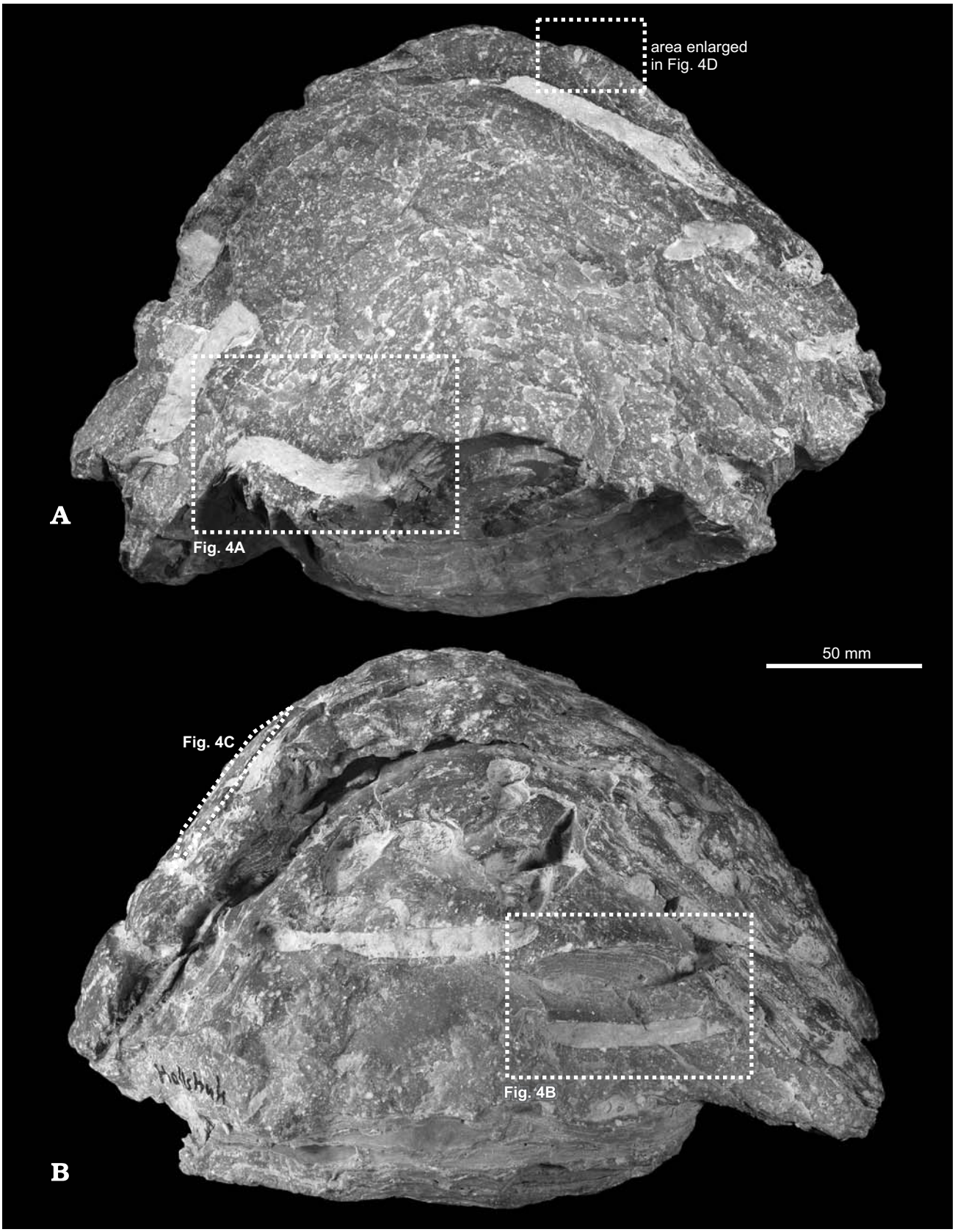


Fig. 3. Large stromatoporoid *Densastroma pexisum* from the Upper Visby Formation at "Halls Huk 3" of Gotland, Sweden, with multiple macroborings (dashed rectangles indicate close-ups illustrated in Fig. 4). **A**. Transverse fracture surface showing dense host skeleton with concentric growth laminae, and large *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. macroborings filled with a fine micrite matrix. **B**. Densely pitted, partly eroded surface of the stromatoporoid with numerous unroofed *O. kampto* Beuck and Wisshak, igen. et isp. nov. macroborings, occasionally truncating each other.

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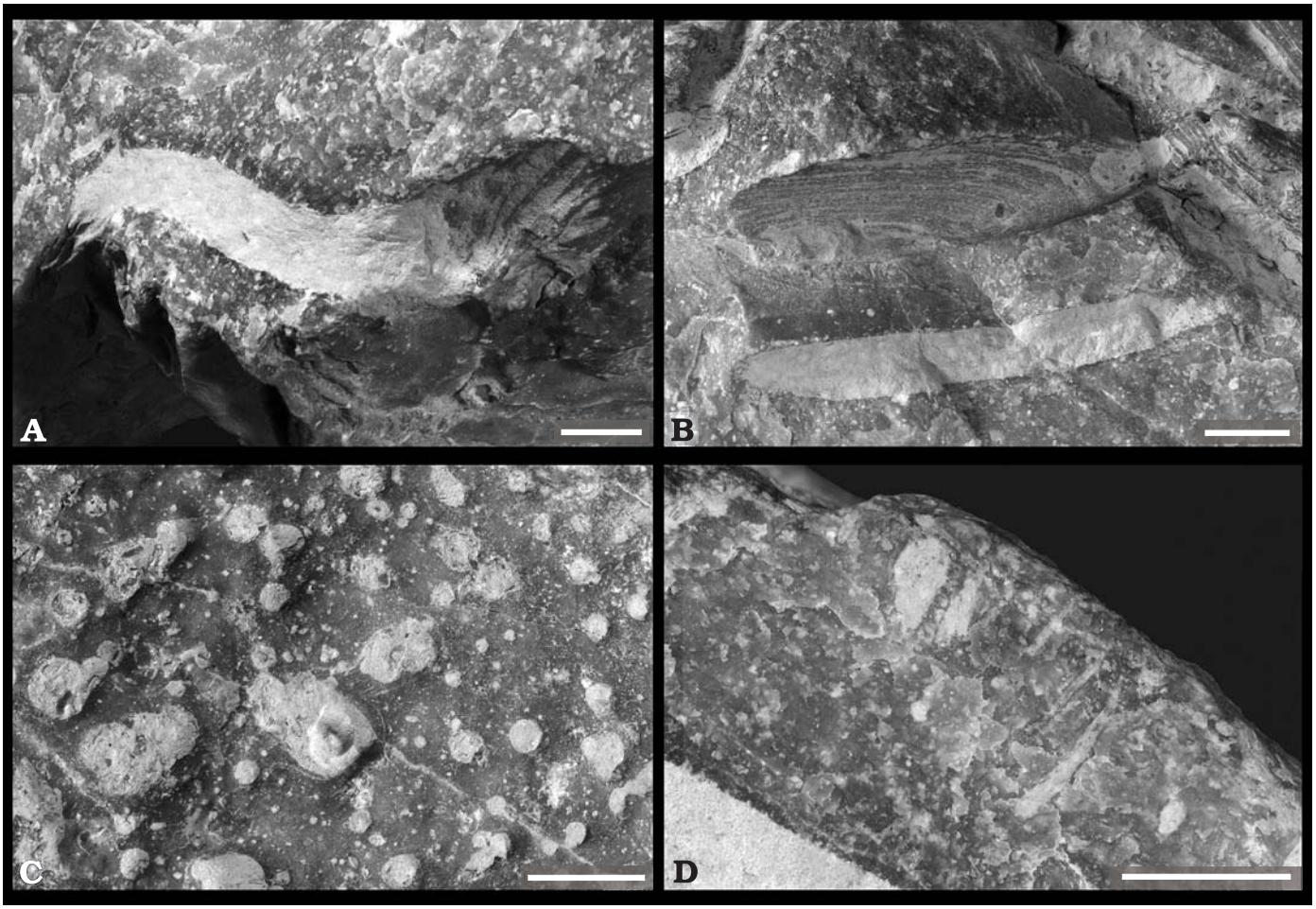


Fig. 4. Close-ups of the bored *Densastroma pexisum* stromatoporoid (positions indicated by dashed lines in Fig. 3). **A**. Undulating course of a deeply penetrating *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. in longitudinal section. **B**. Two unroofed *O. kampto* Beuck and Wisshak, igen. et isp. nov. specimen, one of which showing the growth increments of the host stromatoporoid on the boring walls where the micritic infill is eroded. Boring direction was from the eroded aperture at the right towards the left hand side. **C**. The densely pitted outer surface of the stromatoporoid showing circular apertures of *Trypanites* and *Palaeosabella* of various size. **D**. The nearby fracture surface, exposing longitudinal to oblique sections of small *Trypanites* and *Palaeosabella* borings. Scale bars 10 mm.

1999). The related ichnogenus *Palaeosabella* Clarke, 1921 is distinguished from *Trypanites* and *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. by widening towards its distal limit. Furthermore, *Palaeosabella* features a circular cross-section and is also commonly much smaller (e.g., Bromley 2004). The ichnogenus *Gastrochaenolites* Leymarie, 1842 is a clavate boring that may reach comparable penetration depths but exhibits an aperture size always significantly smaller than the traces maximum width, and it additionally shows lower length/width ratios (Kelly and Bromley 1984). There is some apparent affinity to *Petroxestes pera* Wilson and Palmer, 1988 where traces of *O. kampto* Beuck and Wisshak, igen. et isp. nov. are uncovered by erosion. *Petroxestes* is, in contrast, much longer than deep and is usually connected to the substrate surface along its entire length forming an elongated groove rather than a tube-shaped boring (Wilson and Palmer 1988; Tapanila and Copper 2002).

Osprioneides kampto Beuck and Wisshak, isp. nov.

Fig. 3–8.

1982 "Gekronkelde boring"; Stel and Stoep 1982: 22–23, text-figs. 11, 12.
1970 "Macroscopic borings"; Newall 1970: 337, pl. 1; 341, pl. 2.
2001 *Petroxestes pera* Wilson and Palmer, 1988; Tapanila 2001: 90–91, pl. 3: 1–4.
2001 *Trypanites* Mägdefrau, 1932; Tapanila 2001: 86–87, pl. 1: 3.

Derivation of the name: From Greek *kampto*, bent.

Holotype: Boring trace within the stromatoporoid *Densastroma pexisum* (NRM-Cn 69062) revealed by computer tomography (see Figs. 6G, 7B).

Type locality: "Halls Huk 3", Gotland, Sweden.

Type horizon: Lower *Kockelella ranuliformis* Conodont Zone, Upper Visby Formation, lower Sheinwoodian, Wenlock, Gotland, Sweden.

Material.—Large *Densastroma pexisum* specimen (NRM-Cn 69062) with multiple borings including the holotype (Figs. 3, 4). Section of a small *Densastroma* cf. *pexisum* stromatoporoid (NRM-Cn 69063) found in the upper part of the Slite Group (locality "Odvalds 1", "*Pentamerus gothlandicus* Beds",

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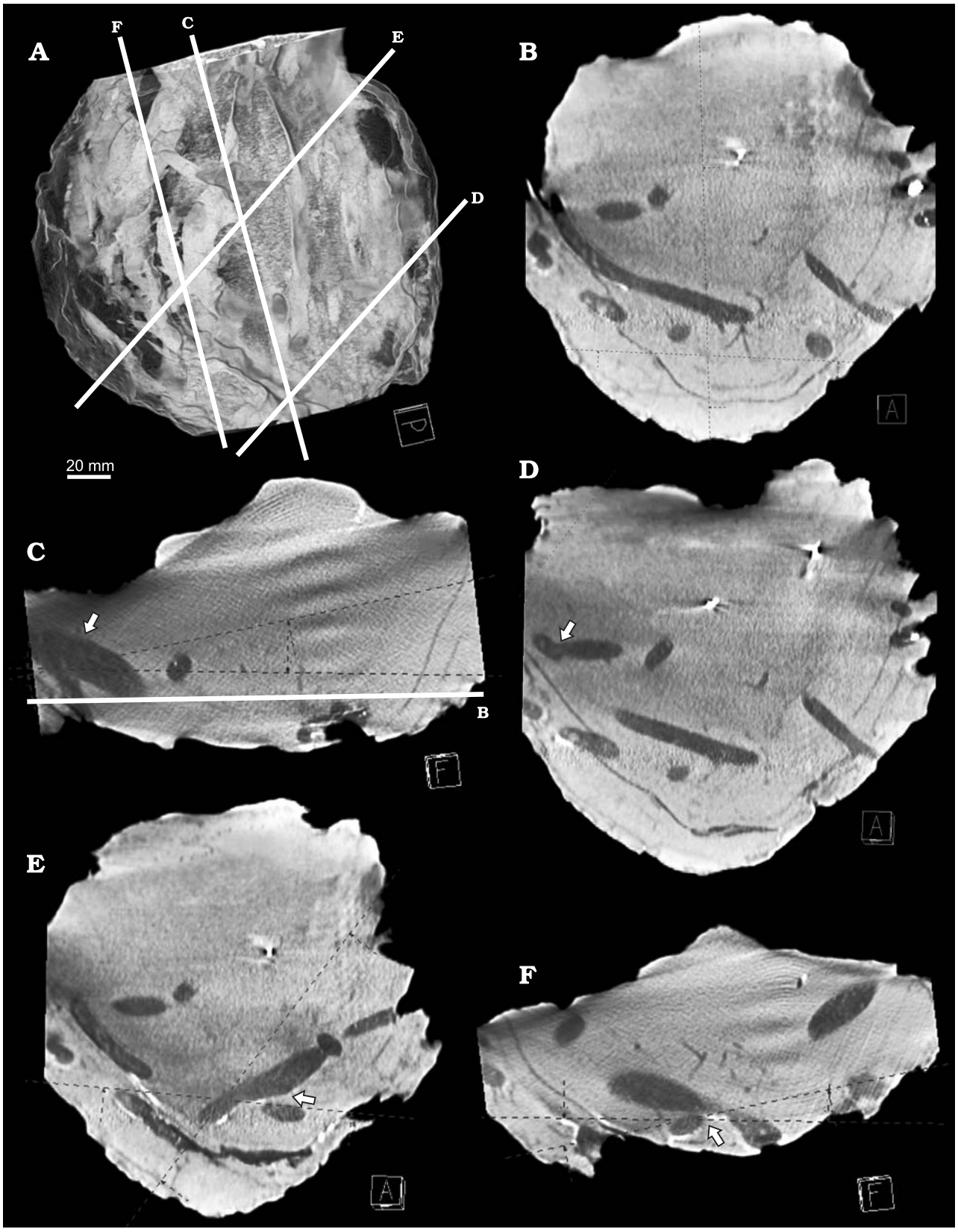


Fig. 5. Spatial distribution of traces (CT scan analysis). Cubes indicating the spatial orientation of sample based on medical terms; grey-dashed lines indicate further virtual sections that have been visualised parallel but are not pictured. **A**. 3D reconstruction of *Densastroma pexisum* with semi-transparent adjustment of it's skeleton, exposing trace fillings. White lines indicate the section planes of C–F. Cutting sites of C/D and E/F show meeting points of individual *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. **B**. Virtual section partially exposing a 120 mm long trace of *O. kampto* Beuck and Wisshak, igen. et isp. nov. **C**. White line indicating section plane of B. **C**–**F**. *O. kampto* Beuck and Wisshak, igen. et isp. nov. traces feigning ramification (see arrows).

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Ozarkodina sagitta sagitta Conodont Zone, lower Homerian, Wenlock) in the Silurian of Gotland (Sweden) exhibiting one oblique oval cross-section of a boring (21 × 10 mm).

Diagnosis.—Large, straight to irregularly bent, unlined boring of variable length entering the substrate perpendicular to subparallel; cross-section oval; roughly constant oval diameter; terminus tapered to rounded.

Description.—From a single oval aperture, the unbranched borings are sharply incised in the dense host skeleton, showing no deflections of the host growth increments (Fig. 4A, B), and are filled with a micritic matrix (Figs. 3, 4). The borings enter the substrate in a perpendicular to subparallel manner and follow primarily a straight course but may as well slightly curve or undulate (e.g., Fig 6C). Individual traces measure up to 120 mm in length (Fig. 5B) with an oval cross-section of averaging 7 (min. 5) × 13 (max. 17) mm in diameter, with a max/min ratio in excess of 2/1 (Fig. 6, 7). Individual borings have a tapered to rounded terminus (Fig. 6D, E). Due to the high-abundance of traces within the sample analysed, borings occasionally truncate each other, occasionally resembling a branching pattern (Figs. 5A, C–F, 6F). Neither scratch marks nor any internal lining were observed. An idealised schematic drawing of the trace is given in Fig. 8.

Discussion.—As for genus.

Stratigraphic and geographic range.—In the tabulate coral *Heliolites interstinctus* from the Aymestry Limestone in the Upper Silurian (Ludlow) of the Welsh Borderlands, Newall (1970: pls. 1, 2) describes a similar boring under the informal name "Macroscopic borings" having corresponding diameters but a maximum penetration depth of 42 mm (due to substrate limitation). Another occurrence was reported among other boring traces by Stel and Stoep (1982: fig. 12A, D) under the informal name "gekronkelde boring" found in the stromatoporoid *Densastroma pexisum* from the Visby Formation (Wenlock, Lower Silurian) at Ireviken on Gotland, Sweden. From the Lower Silurian (Llandovery) of Anticosti Island, eastern Canada, Tapanila (2001) and Tapanila et al. (2004) report large, vertical *Trypanites* borings in the tabulate coral ?*Propora conferta* and in stromatoporoids. The latter authors give a size range with a maximum length of 52.8 mm at a diameter of 9.5 mm, indicating an affinity to the present material. In addition, Tapanila (2001: pl. 3: 1–3) depicts large *Petroxestes pera* borings in the stromatoporoid *Clathrodictyon* which closely mirror unroofed *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. A boring tentatively attributed as ?*Gastrochaenolithes* (Tapanila 2001: pl. 3: 4) possibly represents an obliquely sectioned specimen of the new ichnospecies. Furthermore, similar borings are found from the Silurian of Estonia by Olev Vinn (Mark Wilson, personal communication 2007).

In summary, the known stratigraphical range of *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. is currently restricted to the Silurian (Llandovery–Ludlow), and the known host substrates comprise stromatoporoids and tabulate corals.

Discussion

CT scan analysis as visualisation tool.—When investigating boring trace fossils, one is often confronted with the problem of proper three-dimensional visualisation of the structures in question. As a result, destructive methods such as serial thin-sectioning (Van der Pers 1978) or epoxy-cast embedding techniques (Golubic et al. 1970) were utilised. For relatively thin substrates, such as mollusc shells, this problem was partly solved by applying x-ray analysis, allowing a two-dimensional visualisation of boring traces where significant density contrasts are present between cavity and substrate (Bromley 1970; Bromley and Tendal 1973; Schönberg 2001). Only with the advent of sophisticated (micro-) Computer Tomography (CT), it is now possible to produce three-dimensional views, not only of empty Recent and/or fossil borings (Schönberg 2001; Beuck 2002; Beuck et al. 2007; Bromley et al. in press; Schönberg and Shields in press) but even of filled cavities (see also Tapanila in press). In the present study the borings are filled with a dense matrix, which contains clay minerals and has a slightly higher density than calcite. With the aid of new image analysis software, the raw data can be processed and visualised in form of virtual sections, x-ray simulations, three-dimensional views and animations (see Figs. 5–7 and Supplementary Online Material at http://app.pan.pl/acta53/app53-Beuck_etal_SOM.pdf). Additional application of the anaglyph technique on CT images and movies clearly shows the shape and spatial orientation of the traces. Even subtle density contrasts are sufficient for distinguishing between substrate (pure calcite) and boring (calcite plus clay), providing adequate settings are chosen. However, some of the *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. borings show unclear, blurred termini (Figs. 6G, 7). This might be an indicator of traces that are only partly filled by fine-grained sediment (geopetal fillings), because the sparite fillings at the end of such traces would be indistinguishable in terms of density from the surrounding stromatoporoid since both are composed of pure calcite. In addition, as the soft sediment inside the borings was protected from mechanical compaction prior to lithification by the rigid stromatoporoid framework, the distal part of the sedimentary fillings was characterised by very high initial porosity with probably up to 80% water in the pore space. During the cementation of the sediment, this pore space was filled by calcite, resulting in comparatively high carbonate contents of the micritic filling close to the sediment-sparite boundary, and consequently producing low density contrasts, which might be the reason for the blurred termini.

This study is a successful attempt to use this non-destructive method to characterise lithified boring patterns with low density differences in fossil material. We consider CT scan analysis to be of high potential for future bioerosion studies on both fossil and Recent material. With increasing hardware performance it can be expected that the resolution of the

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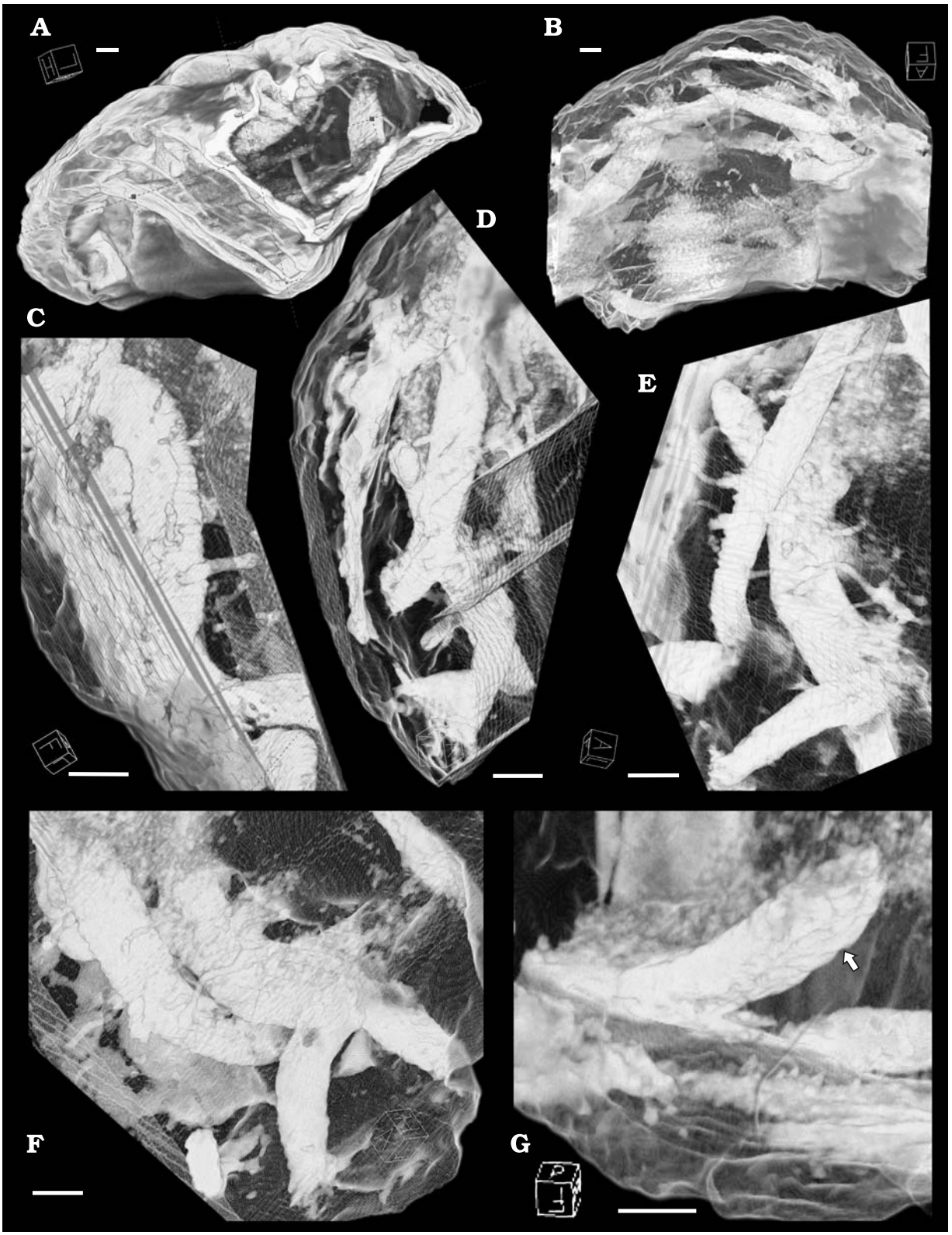


Fig. 6. 3D reconstruction of *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. (CT scan analysis). Cubes indicating the spatial orientation of sample based on medical terms. **A**. Semi-transparent visualisation of the of stromatoporoid's surface and the micritic matrix of its boring infill. Grey-dashed lines indicate virtual sections that have been visualised parallel but are not pictured. **B**. *O. kampto* Beuck and Wisshak, igen. et isp. nov. mainly located in the upper part of host substrate. **C**. *O. kampto* Beuck and Wisshak, igen. et isp. nov. gently curved and presumably secondarily settled by *Trypanites weisei*. **D**. Tapered and rounded terminus of *O. kampto* Beuck and Wisshak, igen. et isp. nov. **E**. *O. kampto* Beuck and Wisshak, igen. et isp. nov. interwoven with *Trypanites* isp. **F**. Three traces of *O. kampto* Beuck and Wisshak, igen. et isp. nov. meet. **G**. Holotype of *O. kampto* Beuck and Wisshak, igen. et isp. nov. showing a strongly oval cross-section and a slightly bent course (arrow). Scale bars 10 mm.

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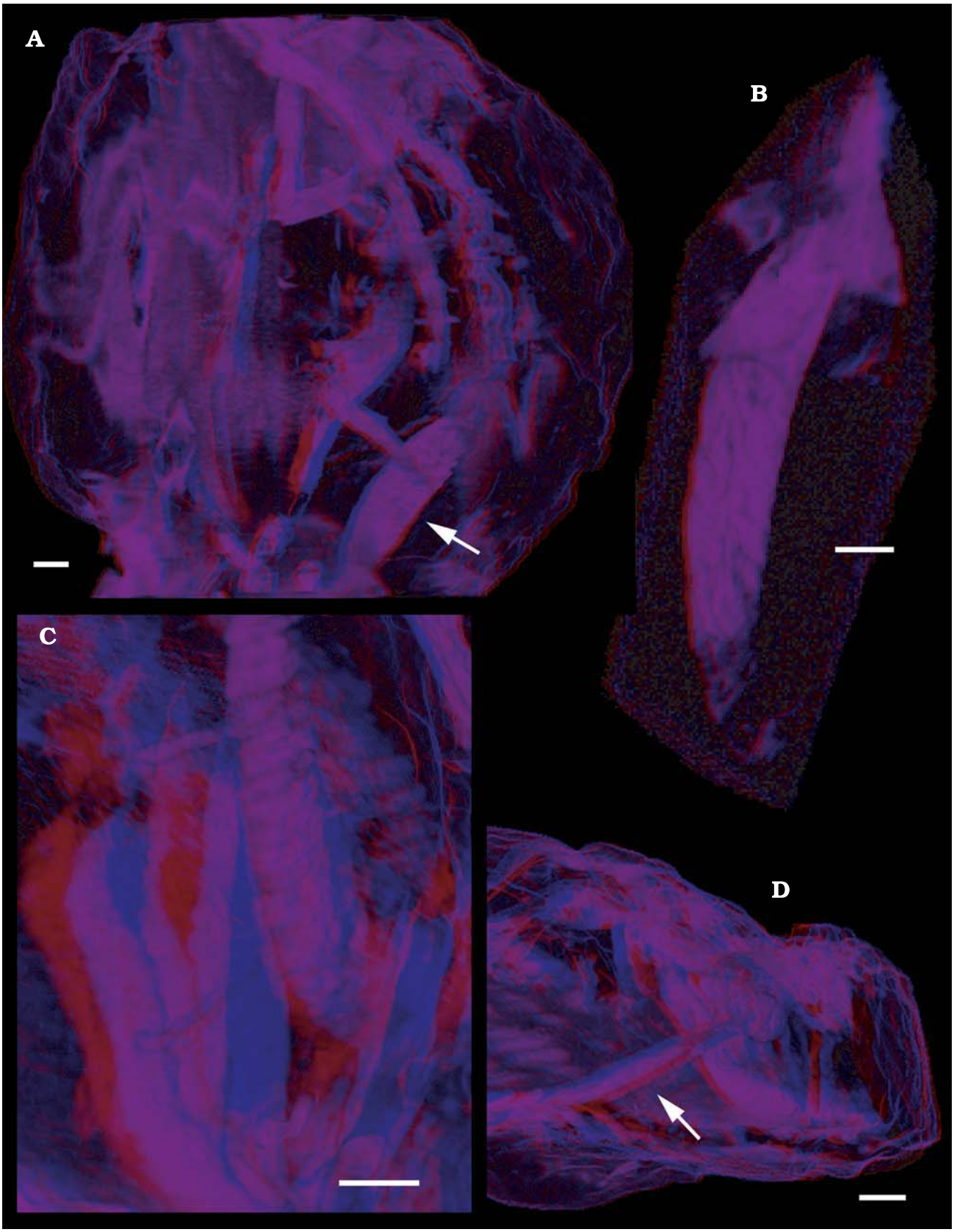


Fig. 7. 3D reconstruction of traces visualised for observation with anaglyph glasses (red/blue). **A**. Borings filled by micritic material within *Densastroma pexisum*. Arrow indicating holotype. **B**. Holotype of *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. showing a maximal diameter of 17 mm. **C**. Micritic matrix of boring infills with interfering micritic compounds augmented in the host skeleton. **D**. Holotype of *O. kampto* Beuck and Wisshak, igen. et isp. nov. indicated by arrow. Scale bars 10 mm.

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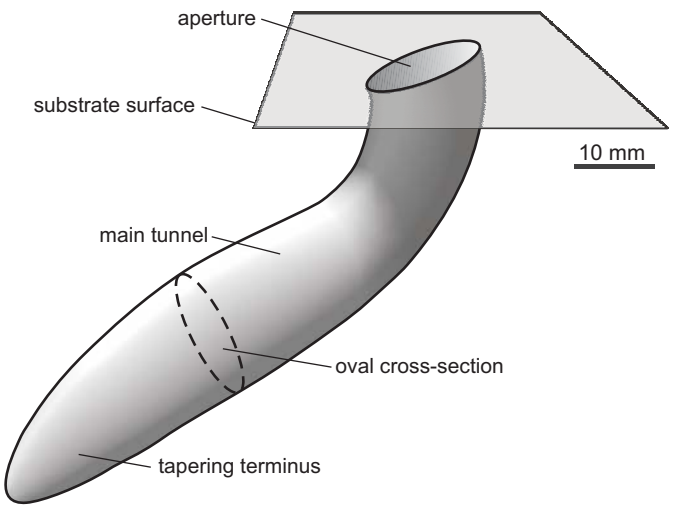


Fig. 8. Idealised schematic drawing of *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov.

method will be further enhanced, as will be the image analysis software, which might soon contain also stereoscopic features and become more affordable as a standard tool for bioerosion analyses.

The identity of the trace maker.—Traces of *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. are sharply incised in the substratum and did not affect the growth of host laminae indicating that the producer penetrated the coenosteum post-mortem and are thus true borings as opposed to embedment structures (e.g., Tapanila et al. 2004). The length of *O. kampto* Beuck and Wisshak, igen. et isp. nov. seems to be only limited by the substrate size (see also Newall 1970). Inside corresponding borings, Newall (1970) detected fossil lingulids. He concluded that *Lingula* occupied preformed sediment filled borings, which in some cases may have lived in symbiosis with *Heliolites*. Our CT scan analysis, however, showed that the boring fills of *Densastroma pexisum* lack any faunal evidence. The occasionally curved to slightly undulating course of the trace, its variable length and sometimes slightly enlarging diameter in central parts as well as the absence of any lining or scratch marks let us presume a soft bodied organism with a primarily chemical mode of penetration—most likely a boring worm—as the potential trace maker. These characters also rule out a bivalve producer such as inferred for *Gastrochaenolites* (Kelly and Bromley 1984) and *Petroxestes pera* (Pojeta and Palmer 1976; Wilson and Palmer 1988). Stel and Stoep (1982) and Newall (1970) came to a corresponding conclusion for the synonymous material. Recent *Trypanites* is known to be produced by sipunculids (Rice 1969) and polychaetes (Bromley 1978), and both bioerosion agents range amongst the most important bioeroders in Recent tropical reefs (Hutchings and Peyrot-Clausade 2002). Corresponding fossil borings were interpreted accordingly (e.g., James et al. 1977 for the oldest *Trypanites* discovered in the Lower Cambrian of Labrador, and Pemberton et al. 1980 from Silurian–Devonian strata in southern Ontario). Moreover, Kobluk and Nemscok (1982) found direct evidence for a polychaete producer in form of scolecodonts detected within the boring infill of *Trypanites* from the Middle Ordovician Verulam Formation at Kirkfield, Ontario.

Temporal pattern of ichnocoenosis development.—It is presumed that *Densastroma pexisum* preferred a marly bottom in calm water (Mori 1969). According to Tapanila et al. (2004), Palaeozoic corals and stromatoporids were also more likely to be bored in muddy facies than in sandy facies with highest boring frequency in high domical host shapes because massive forms are less prone to breakage and burial (see also Kershaw 1984). In addition, shapes that provide optimal water currents, while reducing sediment accumulation, influence the distribution of suspension feeding macroborers (Kobluk and Nemcsok 1982; Nield 1984). Most small *Trypanites* and *Palaeosabella* borings are located in the superficial zone of the coenosteum indicating a post-mortem infestation with the strongest concentration on the higher raised regions of the substrate (see also Kobluk and Nemcsok 1982), which was interpreted by Kershaw (1980) as a larval preference for enhanced current flows. Borings deep inside the host, however, are interpreted to represent either syn-vivo borings overgrown by the recovery of the host bio-substrate (see Tapanila et al. 2004) or, as secondary settlers within abandoned *O. kampto* Beuck and Wisshak, igen. et isp. nov. borings. The latter borings exclusively originate from the host surface and thus represent a post-mortem settlement as well.

Evolution of penetration capabilities.—Both the deeply penetrating nature of the *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. as well as the high density of common *Trypanites* and *Palaeosabella* show a considerable degree of ecospace competition among hardground dwelling organisms during the Silurian. This can be interpreted as a direct result of the "Ordovician Bioerosion Revolution" which led to the appearance of many new ichnogenera in concert with a significant increase in the intensity of bioerosion, peaking in the Late Ordovician and Early Silurian (Tylor and Wilson 2003; Wilson and Palmer 2006). However, a penetration depth of 120 mm is a unique finding for the Palaeozoic (Fig. 9). Even traces exceeding 50 mm did not become abundant before the "Mesozoic Marine Revolution" as demonstrated by an evaluation of animal classes with endolithic representatives throughout the Phanerozoic by Vermeij (1993; see also Fig. 9), even though more recent investigations indicate that some Ordovician to Silurian *Trypanites* and *Gastrochaenolithes* may reach 40 to 60 mm in boring depth (Ekdale and Bromley 2001; Tapanila 2001; Mark A. Wilson, personal communication 2006). During the major Mesozoic evolutionary turnover, enhanced predation and grazing pressure (Vermeij 1977) led to a significant increase in bioerosion intensity reflected for instance in the Palaeo-Reef database (Kiessling et al. 1999; Kiessling 2002; see Fig. 9). The first ichnospecies reaching comparable and even su-

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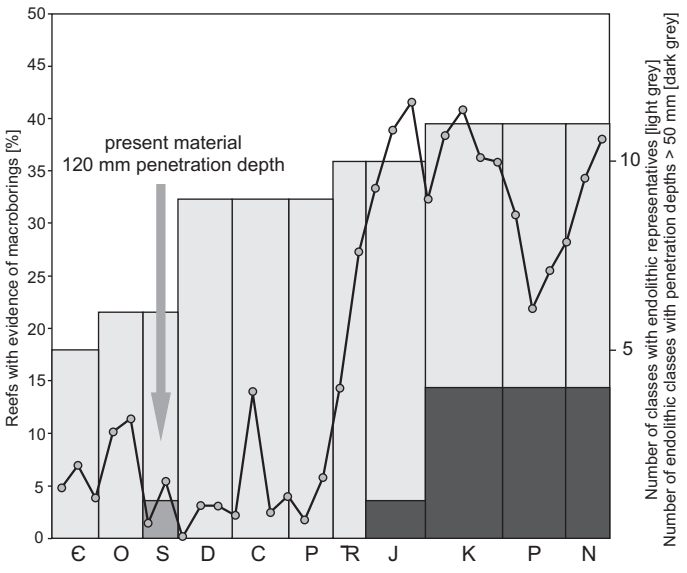


Fig. 9. Evolution of bioerosion intensity and boring depth throughout the Phanerozoic. The line graph (scale at left hand side) illustrates the percentage of reefs with evidence of macroborings, based on the PaleoReefs database (after Kiessling 2002). The shaded columns (scale on right hand side) shows the number of classes with endolithic representatives (light grey) and those reaching penetration depths in excess of 50 mm (dark grey) (after Vermeij 1993). Note the significant increase of boring intensity and penetration depth during the "Mesozoic Marine Revolution".

perior penetration depth is *Trypanites fosteryeomani*, reported from a Middle Jurassic (Bajocian) hardground community by Cole and Palmer (1999). Hence, the present material predates the oldest finding of such a pronounced penetration capability by more than 260 million years, during which this adaptive strategy was abandoned before renewed enhanced ecospace pressure during Mesozoic times led to convergent reinventions.

Conclusions

- *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. is an exceptionally large, straight to irregularly bent, unlined boring of variable length entering the lithic substrate perpendicular to subparallel and with a tapered to rounded terminus. The boring has a constant oval diameter in cross-section. This new ichnospecies represents the deepest boring trace known from the Palaeozoic.
- We presume a soft-bodied organism with a primarily chemical mode of penetration (most likely a boring worm) was the potential tracemaker.
- Both, the deeply penetrating nature of *Osprioneides kampto* Beuck and Wisshak, igen. et isp. nov. as well as the high density of common *Trypanites* and *Palaeosabella* including potential secondary settlement indicate a considerable degree of ecospace competition among hardground dwelling organisms already in the Silurian.
- A penetration depth of 120 mm is a unique finding for the Palaeozoic and was not exceeded until some 260 million years later (Bajocian, Middle Jurassic), when enhanced predation and grazing pressure during the "Mesozoic Marine Revolution" led to convergent reinventions (e.g., *Trypanites fosteryeomani*).
- We consider CT scan analysis, especially in combination with stereoscopic techniques, to be of high potential for future bioerosion studies on both fossil and Recent material.

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