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Trace fossils from the Maastrichtian chalk of the Isle of Rügen, north-east Germany

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Review

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Abstract

The lower Maastrichtian chalk of the Isle of Rügen was deposited in a pelagic setting in the aphotic zone. Its rich fossil content has attracted research attention for centuries, whereas its ichnological characteristics remain poorly understood, even though horizons with intense bioturbation and occurrences of trace fossils in flint are common. The enhanced colour contrast of smooth chalk faces reveals repeated phases of benthic colonisation; larger burrows are commonly subject to silicification, while flint nodules also can preserve burrows in chalk. A total of 37 ichnogenera, including 47 ichnospecies of bioturbation and bioerosion trace fossils have been recognised; these are here briefly described, in addition to indeterminate material. Many ichnotaxa are recorded for the first time from the Rügen chalk. Bioerosion is restricted mainly to local hardgrounds in the form of biogenic components (such as shells and belemnite guards).

Introduction

The iconic chalk cliffs of the Jasmund Peninsula, unique in Germany, have always been an inspiration to artists such as the romantic painter Caspar David Friedrich (1774–1840) or the classical composer Johannes Brahms (1833–1897), but also to natural scientists, especially geologists and palaeontologists. Likewise, ichnological research on Rügen has a long tradition that started in the eighteenth century with the work of Friedrich von Hagenow (1797–1865) and was continued in the twentieth century by Gerhard Steinich (1934–2021), to mention just two of the most active scientists. Meanwhile, the chalk cliffs along the coast of the Jasmund Peninsula are protected as a national park and have been declared a geosite of national relevance. The small museum 'Kreidemuseum Gummanz' informs visitors about different aspects of the chalk. In addition to professional scientists, many private fossil collectors have contributed to the reconstruction of the unique depositional environment of the Late Cretaceous chalk sea.

Approximately 1,400 fossil taxa are known from the Rügen chalk (Reich & Frenzel, 2002); however, an actual assessment of the ichnofauna and an overview of ichnotaxa recognised is still missing. The intention of our contribution is to provide an inventory of common ichnotaxa preserved in the chalk and flint concretions embedded therein, within the frame of outlining present knowledge concerning the ichnology of the Rügen chalk in general.

Geological setting

During the Late Cretaceous, an epeiric sea with chalk sedimentation covered large parts of north-west Europe because of global sea level rise and thermal subsidence. The chalk sea was connected in the north with the Arctic, to the south-east with the Tethys and to the south-west with the Atlantic Ocean (Surlyk et al., 2003; Boussaha et al., 2017). Lower Maastrichtian chalk is exposed in cliffs of the north-east German Isle of Rügen, where it occurs in Pleistocene glaciotectonic complexes (Fig. 1). The chalk was deposited at an approximately 45°N palaeolatitude within the Danish-Polish Trough, about 50 km south-west of the Tornquist Zone. Sedimentation took place in a bathymetric position below the storm-wave base in the aphotic zone. The pelagic sediment is rich in fossils of benthic taxa (Nestler, 2002; Reich & Frenzel, 2002; Reich et al., 2018). Autochthonous sediments are dominated by matrix-supported, completely bioturbated mudstone to wackestone. Packstone uncommonly occurs as infill of burrows.

During the Turonian to Maastrichtian, the study area was influenced by syndepositional tectonics. Accordingly, the sea floor west of the Tornquist Zone was tilted towards the north-east, and adjoining faults such as the Wiek (Seidel et al., 2018) and Nord Jasmund faults were reactivated. Uplifted blocks triggered local mass-wasting processes and guided the direction and strength of regional bottom currents in the Maastrichtian. The pelagic background sedimentation was modified by periods of erratic deposition, omission and erosion, resulting from intermittent contouritic bottom currents (Hübscher et al., 2019). The upper part of the Rügen succession contains seven allochthonous layers displaying primary depositional fabrics with varying diagenetic features (Steinich, 1972), as well as syndepositional decollement

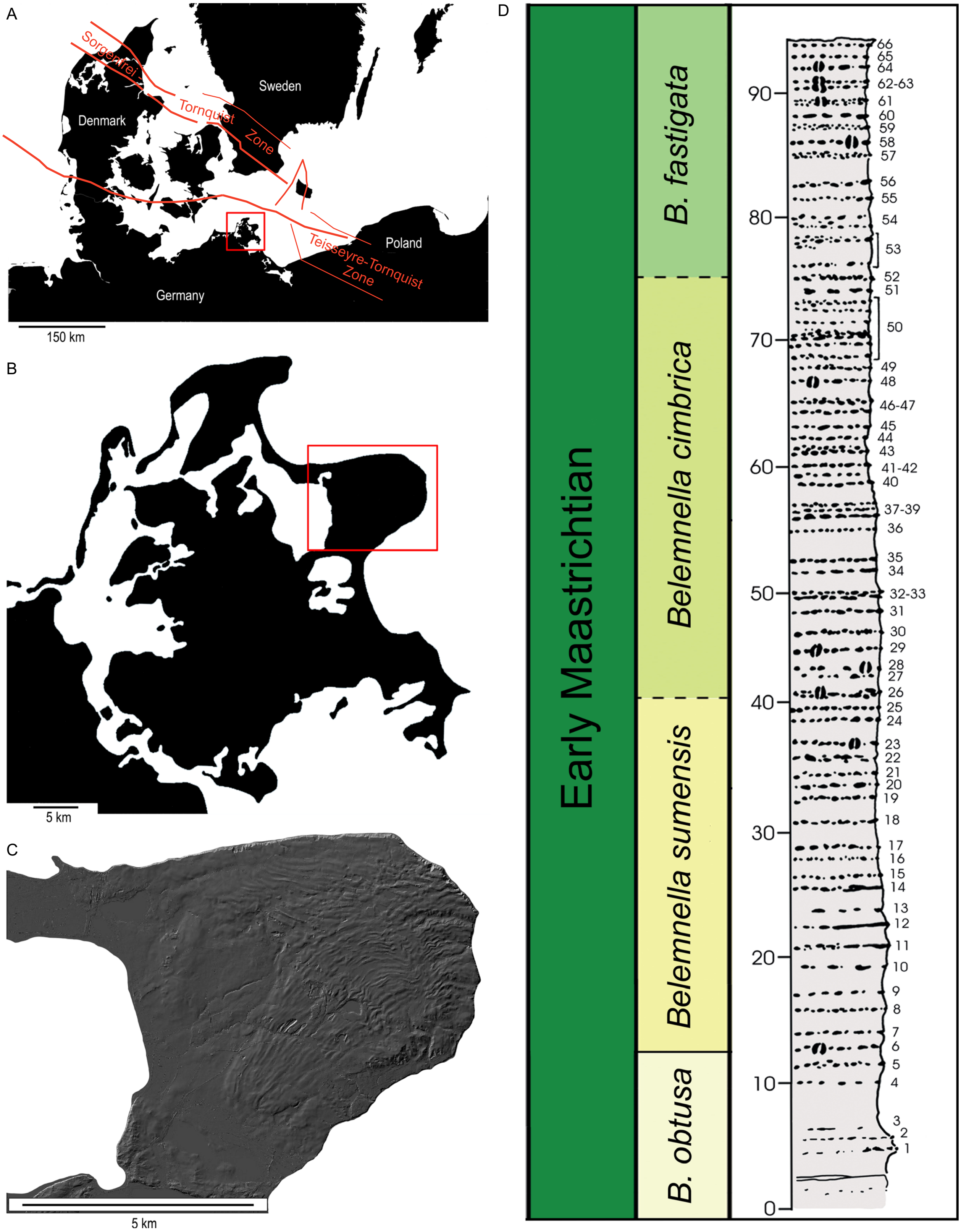

Figure 1. Study area and generalised section. **A.** Location of the Isle of Rügen in the south-western Baltic (framed). **B.** Jasmund Peninsula in the north-eastern part of Rügen, with the largest outcropping chalk complex. **C.** Morphology of the Jasmund glaciotectonic complex which exposes the Rügen chalk in cliff sections along the eastern coast and at quarries in the central part of the Jasmund Peninsula (source: GeoPortal.MV, modified). **D.** Stratigraphical and lithological synopsis of the Rügen chalk with scale in metres and numeration of flint layers (modified from Reich et al., 2018, fig. 6).

horizons that indicate erosional events. The allochthonous units comprise a broad spectrum of types and scales, ranging from large-scale (i.e., metre-size), non-bioturbated debrites with basal erosion, to small-scale (i.e., centimetre size), superficially bioturbated sediment covers of rather turbiditic origin. A common feature of the buried sedimentary surfaces is a highly dispersed pyrite impregnation of the chalk, caused by bacterial desulphurisation. However, the interpretation of sedimentary fabrics previously described as 'clouds', lumps and laminations as seismites (Steinich, 1972; Frenzel et al., 1998; Herrig, 2004; Reich et al., 2018) requires further investigation.

There are different types of flint concretions in the Rügen chalk, such as nodular flint, paramoudra flint, flint steinkerns of larger fossil skeletons and discordantly arranged flint plates. Nodular flint is the most common variant, occurring in 66 discrete horizontal layers with different densities (Steinich, 1972; Fig. 1). In addition to flint layers that consist of individual nodules surrounded by chalk, there are also layers of interconnected flint nodules (e.g., networks), as well as unusual massive concordant flint plates. In many cases, the formation of flint nodules started from burrow infills that originally had enhanced permeability and vertical connectivity. Because of a general tendency to over-mineralisation, the silicification does not conform exactly with the initial burrow but rather extends into the surrounding sedimentary rock (Savrda, 2007). The silicification process was initiated by microbial decomposition of organic matter and took place during periods of a stationary redox boundary, probably caused by reduced sedimentation or omission (Bromley et al., 1975; Clayton, 1983; Madsen & Stemmerik, 2010).

History of research

The palaeontological research of the Rügen chalk has a long history. Since the first description by Kosegarten (1794), many workers have provided information on its fossil content. Two scientists need to be highlighted here in view of their important contributions to ichnology: Friedrich von Hagenow and Gerhard Steinich. In the last decades, contributions to the ichnology of the Rügen chalk were provided by Nestler (1960, 1965), Kutscher (1972), Schnick (1992), Hofmann & Vogel (1992), Schmidt (1996), Bromley et al. (1999a), Herrig (2004), Neumann et al. (2008), Buchholz (2010) and Schlembach (2023). Reich and Frenzel (2002) presented the most recent overview of the fossil flora and fauna from the Rügen chalk, inclusive of 19 ichnotaxa.

Friedrich von Hagenow (1797–1865)

The polymath and entrepreneur Friedrich von Hagenow mapped the Isle of Rügen in the years 1825 to 1828 and published the first detailed map in 1829. Recognising the potential economic value of the chalk, von Hagenow leased all existing chalk pits and began chalk mining along the outer coast of Jasmund Peninsula. The excavated chalk was brought to Greifswald harbour for further manufacturing in the first German whiting factory founded by von Hagenow in 1832. Besides the whiting, exceptionally preserved fossils were concentrated as residues in the production process. Within seven years of chalk processing, von Hagenow gathered more than 100,000 fossil specimens. Based on this lot, he published the three-volume work entitled 'Monographie der Rügen´schen Kreideversteinerungen' (von Hagenow, 1839, 1840, 1842). Unfortunately, von Hagenow was unable to accomplish the fourth volume of his monograph, because he suffered from eyesight deterioration. For comparative purposes, von Hagenow visited other chalk occurrences in Europe, for instance Maastricht, in 1851. To promote exact scientific drawing, von Hagenow developed in the same year a new optical instrument based on the camera lucida principle. This 'dikatopter' became widely disseminated among palaeontologists at the time.

There is an interesting contribution to ichnology made by von Hagenow. He published a comprehensive description of endolithic trace fossils preserved in belemnite rostra. Unfortunately, he did not add any drawings to illustrate his descriptions. Despite the loss of von Hagenow's original collection during the World War II, lectotypes have recently been designated using von Hagenow's specimens that survived the wartime in other collections (Wisshak et al., 2017a).

Gerhard Steinich (1934–2021)

Gerhard Steinich started his scientific career as palaeontologist at the Universität Greifswald. He established a five-stage brachiopod zonation, a stratigraphical framework applicable not only to the Isle of Rügen but to the entire Danish Basin and beyond. Furthermore, he mapped all relevant sedimentological features such as flint layers and certain ichnofabrics, as well as allochthonous units at the Rügen stratigraphical standard section and later from one outcrop to the next across the entire island. Supplemented by the local ostracod stratigraphy of Herrig (1966), the Steinich stratigraphical scheme became the standard for classifying palaeontological, ichnological, sedimentological and structural data of the Rügen chalk. In addition, Steinich (1967) developed an innovative contrast-enhancing preparation technique for chalk, in which low-contrast ichnofabrics could be made visible with high resolution by applying a synthetic resin impregnation. Applying this technique, Steinich was able to verify the predominance of ichnofabrics and several resedimentation events at specific positions within the Rügen chalk sequence. Moreover, Steinich's stratigraphical work provided the basis for understanding the architectural and structural evolution of the Jasmund glaciotectonic complex (Steinich, 1972; Gehrmann, 2018).

In the early 1970s, Richard G. Bromley contacted Steinich to have a joint excursion on Rügen. In preparation of his article 'Trace fossils at omission surfaces' (Bromley, 1975a), Bromley was interested in seeing the 'Pseudo-hardgrounds' described by Steinich (1972). They made an appointment and Bromley came together with his wife, Ulla Asgaard, by ferry from Sweden. After passing the impressive Rügen chalk cliffs, both arrived at Sassnitz Ferry Port, but only Danish citizen Ulla was allowed to leave the ferry. Richard, holding a British passport, had to return to Sweden on the same ferry without touching the Rügen chalk and personal contact with Gerhard Steinich, because of the limited diplomatic relations between the UK and East Germany in the Cold War era.

Preservation of trace fossils in chalk and embedded flint

Burrows

Chalk is a porous carbonate rock that originates from the accumulation of minute calcitic shells, mostly from disarticulated calcareous algae, so-called coccoliths. It commonly formed on the shelf and in deeper marine environments during Cretaceous time, for instance, in western Europe and North America. Chalk is frequently affected by silicification, leading to the formation of flint concretions (nodules). Flint is micro- to cryptocrystalline quartz that occurs in horizons subparallel to the bedding at roughly regular intervals.

Different degrees of silicification can be distinguished in the flint layers from scattered distribution of single nodules to interconnected networks and massive flint plates. It often seems to be related to burrows, foremost of the ichnogenus *Thalassinoides*, which occur at certain intervals representing colonisation (omission) surfaces. In addition to the flints occurring at these horizons, there are silicified internal moulds (steinkerns) of macrofossils (echinoids, oysters and brachiopods) and internal micro-silicifications of calcite skeletons (belemnite rostra and inoceramid shell fragments) occurring in the chalk between the flint layers. Early diagenetic cementation is suggested because the decay of organic matter is invariably involved. For example, there is vague evidence of the original brachiopod musculature that is preserved as a 'shadow' in transparent flint steinkerns (Steinich, 1965).

The chalk succession of the Isle of Rügen is intensively bioturbated. However, the lack of contrast in colour and/or grain size between burrows and their host substrate often prohibits quantitative and qualitative assignments. Sediment composition is a key factor in the visibility of biogenic sedimentary structures (e.g., Savrda, 2012), which in parts relates to the behaviour of the tracemaker (e.g., dwelling, deposit-feeding or gardening). For example, pure white chalk in the matrix *versus* greyish marly chalk as burrow fill can be the reason for a significant colour contrast.

Burrow composition and subtle changes in grain size promote guided fluid pathways, resulting in subsequent mineralisation with unique cementation patterns (Bromley & Ekdale, 1984; Ekdale & Bromley, 1984b). Burrow mineralisation commonly takes place at an early phase of diagenesis and is promoted by localised geochemical conditions and the contribution of micro-organisms (Knaust, 2021a). Apart from non-silicified bioturbated chalk, four stages of quartz cementation can be recognised, i.e., partial, complete, inverse and pervasive. The taphonomic and diagenetic modifications provide a challenge for the identification of trace fossils in chalk.

Bioerosion

There are no true lithic hardgrounds in the Rügen chalk and bioerosion is restricted to skeletal fragments, which in fact acted as island-like substrates in a desert of soft sediment. The largest substrates available for bioeroders were shells of inoceramid bivalves that reached overall sizes of up to one metre and more. Moreover, there were exoskeletons of many other epibenthic organisms such as oysters, brachiopods, echinoids and sponges, as well as endoskeletons of nektonic belemnites. The difference between endo- and exoskeletons must be emphasised. The latter possess protective structures against endolithic infestation such as external and internal conchiolin structures, vesicular shell layers, skeletal cavities, etc., whereas such structures are absent from endoskeletons. Therefore, belemnite rostra are particularly suitable test specimens for determination of quality and quantity of bioerosion.

Sediment particles are affected by diagenetic processes according to their primary mineralogical composition. Most aragonitic skeletons or skeletal components are lost because of dissolution. The original existence of an inner aragonitic nacreous layer of inoceramid shells is obvious by cross sections of sponge borings at the inner surface of outer calcite prismatic layers. Possible is also 'steinkern-on-steinkern preservation', which concerns sediment fills of borings in subsequently diagenetically dissolved cephalopod shells on top of their internal moulds. In addition, there is diagenetic formation of calcite cement on the internal surfaces of borings that may lead to superposition on the original surface and complete sealing of narrow endolithic voids. Vertebrate bones, scales, teeth and wood acted as bioerosion substrates as well. Driftwood may either occur silicified or have completely disappeared because of the well-oxygenated environment but evidenced indirectly by calcite linings of wood-boring bivalves in flint.

Systematic ichnology

Based on a literature review, Reich & Frenzel (2002) provided a list of trace fossils recorded from the Rügen chalk. In the present section, the focus is on the most common ichnotaxa of that succession; a critical review of the ichnofauna is beyond the scope of this contribution. Bioturbation trace fossils (softground and firmground) are most prominent, both in form of flint nodule inclusions on the beach as well as in situ in the chalk cliff. In contrast, bioerosion trace fossils include macro- and microborings in hard substrate, which often require special preparation techniques to reveal their morphologies.

Bioturbation trace fossils

Balanoglossites triadicus Mägdefrau, 1932 (Fig. 2A–C)
Several horizons of firmground occur within the Rügen succession, which served as colonisation surfaces for burrowers that produced relatively large and complex burrow systems with a passive fill. Such burrow systems can be observed in the chalk some decimetres below such surfaces, which may be accompanied by intraformational chalk clasts. The burrows contrast from the white chalk matrix by their grey chalky fill, partly incorporating subangular to rounded white chalk clasts. Some burrow portions became the subject of reburrowing, whereas others were affected by silicification. Sectional views reveal complex burrow systems with three-dimensional branching and common U- or Y-shaped elements, as well as blind-ending terminations. Burrow diameter is highly variable between a few millimetres to several centimetres. Burrow margins are sharp and serrated. Parts of *B. triadicus* burrows are also preserved in flint nodules, where they contrast from the flint with their white chalky fill.

The ichnogenus *Balanoglossites* is defined as follows (Knaust, 2008, p. 352): 'Branched galleries with several openings and acorn-, bulb- or lance-shaped side branches. Tunnels are elliptical or circular in cross sections, margin is unlined and locally striated; tunnel size varies in the order of several magnitudes within a single gallery system'. *Balanoglossites triadicus* includes '... predominantly deep U- or Y-shaped tunnel elements' (Knaust, 2008, p. 355). *Balanoglossites* is a common constituent of shallow-marine carbonates, ranging throughout the Phanerozoic and occurring globally (Knaust, 2021b). It has often been confused with ichnospecies of *Thalassinoides*, from which it differs by its very irregular three-dimensional architecture and highly varying burrow diameter, as well as a predominance of U- and Y-shaped elements (Knaust, 2021c, 2024). *Balanoglossites triadicus* was produced mainly by polychaetes with a burrowing and partly bioeroding ability, which might also have been the case for the examples recorded from Rügen for the first time.

Figure 2. Bioturbation trace fossils – Part 1. Scale bars equal 50 mm (A, J, K), 10 mm (B, C, G–I, L), 100 mm (E, F); in D, the person is *c.* 150 cm tall. **A.** Ichnofabric with *Balanoglossites triadicus* preserved in chalk. **B, C.** *Balanoglossites triadicus* preserved in flint. **D.** Parts of *Bathichnus paramoudrae* with a thick flint halo (arrows). **E.** Close-up view of D showing the cross section of the dark burrow in the centre (arrow). **F.** Flint concretion of *B. paramoudrae* used as flowerpot ('Sassnitzer Blumentopf'). **G, H.** *Chondrites intricatus* on the rind of a flint nodule. **I.** *Chondrites recurvus* on the surface of a flint nodule. **J, K.** Chalk with *Chondrites targionii* as reburrows in *Thalassinoides paradoxicus* (grey fill). **L.** *Chondrites targionii* in a flint nodule.

Bathichnus paramoudrae Bromley et al., 1975 (Fig. 2D–F)
This famous and giant trace fossil with the local nickname 'Sassnitzer Blumentopf' (flowerpot of Sassnitz) comprises a narrow vertical tube surrounded by a thick rim of flint. The burrow-flint-consortium commonly exceeds several metres in length and has an inner and outer diameter of *c.* 5–10 cm and 20–40 cm, respectively (Steinich, 1972). The narrow slender burrow itself is hardly visible and only the pronounced flint cementation around it penetrates the layered chalk perpendicular to it. Silicification is not uniform but rather occurs in irregular intervals. Bromley et al. (1975) were able to show the original cylindrical burrow in some cases, which is only *c.* 0.5 cm in diameter, whereas Nygaard (1983) also recognised irregularly diverging side branches.

Bathichnus paramoudrae is diagnosed as follows (Bromley et al., 1975, p. 27: 'Burrows comprising a vertical shaft 0.2–0.6 cm in diameter and 5–9 m long. Side branches radiate irregularly from all parts of the shaft and have the same diameter as the shaft but are rarely traceable for more than 10 cm sub-horizontally'. Paramoudras occur in different Upper Cretaceous chalk successions of north-west Europe and have received attention since the seventeenth century (Bromley et al., 1975). This extremely long burrow with the characteristic flint rim around it is comparable to similar burrows such as *Tisoa siphonalis* and *Paratisoa contorta* (see Breton, 2006; Knaust, 2019). Its penetration of deeply buried anoxic sediment with local concentration of organic matter promoted local pyritisation, glauconitisation, carbonate cementation, silica redistribution and concentration around the burrow conduit (Bromley et al., 1975). Paramoudra burrows have been assumed to be domichnia of a predatory or filter-feeding nemertean worm or pogonophoran, although polychaetes with a chemosymbiotic lifestyle may also be considered as agents.

Chondrites intricatus (Brongniart, 1823) (Fig. 2G, H)
This minute ichnospecies is occasionally preserved in flint margins. The radiating burrow systems are silicified, with centimetre-sized diameter and a sub-millimetric burrow diameter. The dichotomously branched, sub-horizontal to oblique branches are mainly straight and are connected to the surface by a shaft.

The ichnogeneric diagnosis of *Chondrites* has been revised by Baucon et al. (2020, p. 3) as follows: 'Regularly branching tunnel system consisting of a small number of sub-vertical master-shafts, connected to the ancient sediment-water interface, that branches at depth to form a dendritic network. Fill can be active or passive'. *Chondrites intricatus* comprises 'small *Chondrites* composed of numerous downward radiating, mostly straight branches. The angle of branching is usually less than 45°'. (Uchman, 1999, p. 90).

Chondrites recurvus (Brongniart, 1823) (Fig. 2I)
This ichnospecies comprises curved, bifurcated branches with a width of 2–4 mm. The branches originate from a master branch and bend away from it only in one direction.

Chondrites recurvus comprises 'branches only at one side of the master branch, all bent in one direction; branching occurs up to the 3rd order'. (Uchman, 1999, p. 93; Baucon et al., 2020, p. 5).

Chondrites targionii (Brongniart, 1828) (Figs. 2J–L, 4M, 5F)
This ichnospecies occurs ubiquitously in the chalk, where its dark grey burrows are closely associated with *Thalassinoides*, *Zoophycos* and *Taenidium*, partly leading to their reburrowing. In flint nodules, the burrows are preserved as flint in chalk or *vice versa*. Burrow width is in the range of 2 to 4 mm.

Chondrites targionii is characterised by 'well-expressed primary successive branching and few secondary branches. Branching angle is acute. Curved branches are common' (Baucon et al., 2020, p. 5). It is the product of a vermiform organism that likely thrived in dysoxic pore waters (Bromley & Ekdale, 1984). Reworking by the *Chondrites* producer of previously emplaced larger burrows, such as *Thalassinoides*, is a common feature and relates to the elevated organic matter in such burrows (Baucon et al., 2020).

Lamellaecylindrica paradoxica (Woodward, 1830) (Figs. 3A–D, 5F)
These relatively large burrow systems occur as ramified burrows with a thick layer of concentrically laminated grey chalk and an inner cylindrical core with a passive fill of white chalk. Bulbous burrow extensions may occur. Cross sections reveal a serrated outer burrow margin, suggesting longitudinal ornamentation. Burrow diameter ranges between 1 and 2 cm. *Lamellaecylindrica paradoxica* is rarely preserved in flint nodules, in which case the concentric lamination is well pronounced on account of an alternation of chalk and flint layers.

The ichnogenus *Lamellaecylindrica* consists of a 'horizontal to oblique, ramified cylindrical burrow with a thick, concentrically laminated muddy wall and a passively filled sandy core'. (Knaust, 2021c, p. 183). *Lamellaecylindrica paradoxica* has 'longitudinal striae (ornamentation) on the external surface'. (Knaust, 2021d, p. 1864). It was originally described from the Albian of southern England (Webster, 1814; Knaust, 2022), but was later confused with *Thalassinoides paradoxicus*, with which it may intergrade (Knaust, 2021c). It is a characteristic element of Cretaceous shelf deposits, possibly produced by a holothurian, polychaete or crustacean.

Lamellaeichnus imbricatus Šimo & Tomašovych, 2013 (Fig. 3E)
This relatively rare ichnotaxon was recognised based on a few specimens on the margin of a flint nodule, where it occurs in form of a slightly curved basal tube, from the upper of which numerous stacked, convex-up, gutter-shaped lamellae with spike-like tips emerge in regular distances. The diameter of the burrow is *c.* 6–8 mm.

Lamellaeichnus imbricatus is 'composed of inclined lamellae that protrude at an acute angle from horizontal basal cylinder' (Šimo & Tomašovych, 2013, p. 361). It was first described from Lower Jurassic hemipelagic limestones in the Carpathians, where it occurs in the organic-rich, shallow part of the substrate. It is the product of a deposit-feeding organism. The specimens from Rügen are the first record of the present ichnotaxon outside its type area and from the Cretaceous.

Lepidenteron lewesiensis Mantell, 1822 (Fig. 3F, G)
This rare ichnotaxon occurs in chalk and comprises horizontal, unbranched burrows densely lined with fish scales and bones. It is several centimetres long and has a diameter of *c.* 2 cm.

Lepidenteron is diagnosed as 'unbranched tubular structure without a wall, partly lined with bioclasts. Orientation to the bedding variable; terminations mostly diffuse, not associated with any discontinuity surface' (Jurkowska & Uchman, 2013, p. 614). In *L. lewesiensis*, the 'bioclasts are composed of fish scales and bones in varying proportions' (Jurkowska & Uchman, 2013, p. 617). It is common in Upper Cretaceous marly and biocalcarenitic sedimentary rocks in Europe (Suhr, 1988; Jagt, 2019). Eunicid polychaetes preying on fish have been suggested as the producers of this ichnotaxon (Bieńkowska-Wasiluk et al., 2015).

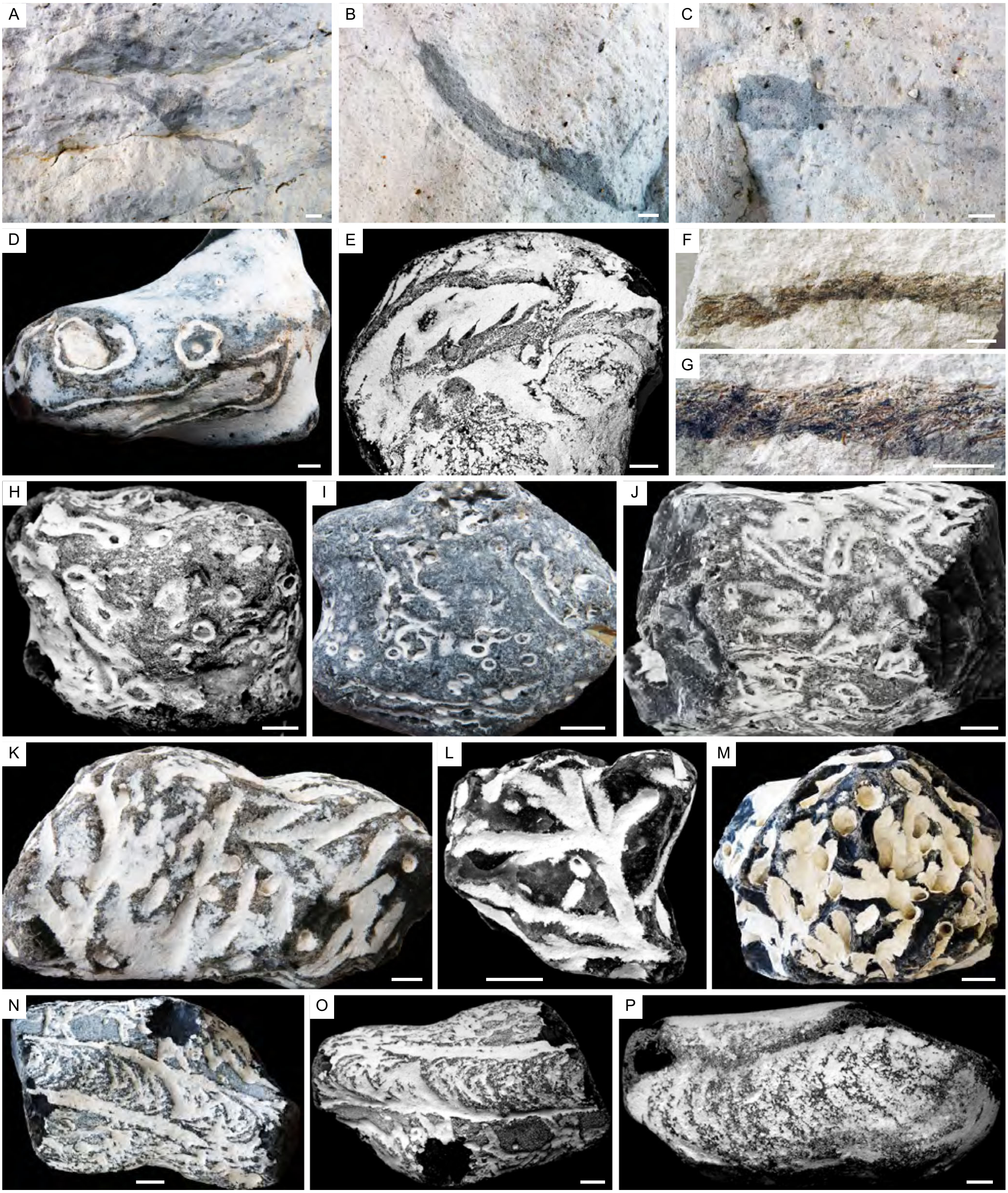

Figure 3. Bioturbation trace fossils – Part 2. Scale bars equal 10 mm. **A–C.** Chalk with *Lamellaecylindrica paradoxica* in oblique (A), longitudinal (B) and transverse sections (C). **D.** *Lamellaecylindrica paradoxica* preserved in flint. **E.** *Lamellaeichnus imbricatus* preserved in flint. **F.** *Lepidenteron lewesiensis* preserved in chalk. **G:** Close-up view of F. **H–J.** *Palaeophycus heberti* preserved in flint. **K–M.** *Phymatoderma granulata* preserved in flint. **N–P.** *Rhizocorallium commune* preserved in flint.

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Palaeophycus heberti (de Saporta, 1872) (Fig. 3H–J)
Palaeophycus heberti is best preserved and visible in flint, where it appears in densely associated sub-horizontal burrows with an empty or passive (silicified) fill surrounded by a thick chalky lining. Burrow diameter ranges from 0.3 to 1.2 cm.

The ichnogenus *Palaeophycus* refers to 'sub-horizontal, essentially cylindrical, straight or slightly curved burrows with a lining and passive fill. The burrows are typically unbranched' (Knaust, 2017, p. 101). *P. heberti* is a 'smooth, unornamented, thickly lined cylindrical burrow' (Pemberton & Frey, 1982, p. 861). It is a common trace fossil with a wide stratigraphical and environmental distribution. Dwelling or predaceous annelids (e.g., polychaetes) and enteropneusts constitute likely producers.

Phymatoderma granulata (von Schlotheim, 1822) (Fig. 3K–M)
This is one of the most common ichnotaxa, typically preserved as chalk-filled or empty burrows in flint. It consists of dense, complex, three-dimensional burrow systems that in some cases produce a very cavernous fabric. Individual tunnels are first- and second-order bifurcated, some of which show an internal backfill structure. Burrow margins are often serrated, probably because of dense packing with faecal pellets, which, however, are rarely preserved. Burrow width is between 0.3 and 0.5 mm, whereas entire systems reach a size of several centimetres. Many burrow systems occupy predefined tubular or globular flint structures, the latter apparently being reburrowed larger ichnotaxa (e.g., *Thalassinoides paradoxicus*).

The ichnogenus *Phymatoderma* is a 'horizontal to sub-horizontal trace fossil composed of irregularly branched lobes spreading out from one point. Edges of the lobes are irregular and can show palmate termination. The lobes are commonly filled with pellets arranged perpendicularly to the longer axes of the lobes' (Uchman & Gaździcki, 2010, p. 85). *Phymatoderma granulata* is a 'dendritic, densely branched burrow system with clearly visible faecal pellets in the wall and along the diffuse margin' (Fu, 1991, p. 29). It is common in organic-rich epicontinental, shelfal and deep-marine deposits. Echiuran polychaetes deposit-feeding at the surface are likely tracemakers (e.g., Izumi & Yoshizawa, 2016).

Rhizocorallium commune Schmid, 1876 (Fig. 3N–P)
A small form of this ichnospecies is occasionally found preserved in flint, where it reaches a length of 5 to 8 cm and a width of 1.5 to 3 cm. The horizontal burrows clearly show the U-shaped marginal tube surrounding the spreite laminae. The spreiten traces appear to have similar widths to the marginal tube, *c.* 0.5 to 0.6 cm. Some specimens preserve sub-millimetric ellipsoidal pellets, probably faecal pellets (*Coprulus oblongus*).

The ichnogenus *Rhizocorallium* is a 'horizontal to oblique, U-shaped spreite burrow' (Knaust, 2013, p. 6). *Rhizocorallium commune* includes 'unbranched, rarely branched burrows with a preferred sub-horizontal orientation. The burrows are elongate, band-like, straight or winding, and may have subparallel longitudinal scratches on the wall. Faecal pellets (*Coprulus* isp.) are common within the actively filled spreite and the marginal tube' (Knaust, 2013, p. 19). It is most likely the product of deposit-feeding polychaetes and commonly occurs in shallow-marine environments (Knaust, 2013).

cf. *Rosselia erecta* (Torell, 1870) (Fig. 4A–C)
Some silicified beds are pierced by vertical burrows with a funnel-shaped aperture and a thick wall, whereas the burrow fill is passive or empty. The diameter of the burrow aperture is in the range of 0.6 to 1.0 cm and burrow length can reach several centimetres. No termination at the bottom has been observed. The burrow diameter becomes gradually smaller downwards and the wall disappears. Although the wall appears to be structured, in some cases, clear lamination is difficult to discern, probably due to strong silicification. Therefore, this form is tentatively assigned to *R. erecta*.

The ichnogenus *Rosselia* comprises a 'vertical to inclined, downward tapering, straight or curved burrow with a funnel-shaped, bulbous or fusiform aperture containing a thick concentric, spiralled or eccentric lining around one or several, passively filled, cylindrical tube(s)' (Knaust, 2021d, p. 1850). *Rosselia erecta* is defined as 'unbranched, sub-vertical *Rosselia* with a funnel-shaped aperture, in which the passively filled cylindrical tube is enlarged to occupy a major fraction of the funnel. Adjacent sedimentary laminae are commonly deflected downward' (Knaust, 2021d, p. 1851). It is common in Lower Cambrian shallow-marine sandstone and occurs throughout the Palaeozoic and Mesozoic. It was probably produced by suspension-feeding polychaetes (Knaust, 2021d).

Schaubcylindrichnus coronus Frey & Howard, 1981 (Fig. 4D–F)
Some flint nodules contain clustered or aligned oblique burrows with a thick chalky lining that apparently belongs to shallow arcuate burrow systems. Individual branches are identical to *Palaeophycus heberti*.

Schaubcylindrichnus coronus 'is characterized by three distinct parts: a funnel, a sheaf of converging thickly lined tubes, and a faecal mound' (Löwemark & Nara, 2010, p. 186). A more recent diagnosis provided by Evans & McIlroy (2016, p. 252) also includes isolated burrows (i.e., *P. heberti*), which is not followed herein, because it is not based on an evaluation of the type specimens of *P. heberti*. It is a common element of lower shoreface to shelf deposits (Knaust, 2017) and is assumed to have been produced by funnel-feeding enteropneusts or polychaetes (Löwemark & Nara, 2010; Kikuchi et al., 2016).

Sulcolithos variabilis Knaust, 2020 (Fig. 4G–I)
Various silicified bedding planes contain elongate, straight or curved grooves, which are 0.5 to 1.5 cm wide and several centimetres long. The grooves have a smooth to sharp, somewhat irregular margin, indicating firm to hard substrate. Some of the grooves are connected to irregular burrows in the subsurface, typically *B. triadicus*, or follow incipient fractures. Others are associated with shallow circular pits, *c.* 0.1 to 1.0 cm in diameter.

The ichnogenus *Sulcolithos* is diagnosed as 'superficial burrow or boring with an elongate, groove-like, straight or curved course' (Knaust, 2020, p. 197) and *Sulcolithos variabilis* includes 'grooves unbranched or with short acorn-, bulb- or lance-shaped side-branches' (Knaust, 2020, p. 199). It was originally described from shallow-marine Triassic carbonates, in which it also occurs together with *B. triadicus* and shallow pits with an irregular elliptical outline (Knaust, 2020). Burrowing and boring polychaetes are assumed to have been the tracemakers.

Taenidium irregulare Li, 1993 (Fig. 4J–L)
This common form is preserved in chalk and flint nodules and consists of unlined, unbranched, cylindrical burrows with a winding course and an active, meniscate fill. Sediment packets are variable, parabolic or chevron-shaped, generally asymmetrical, with the apex of the parabola or chevron offset from the midline of

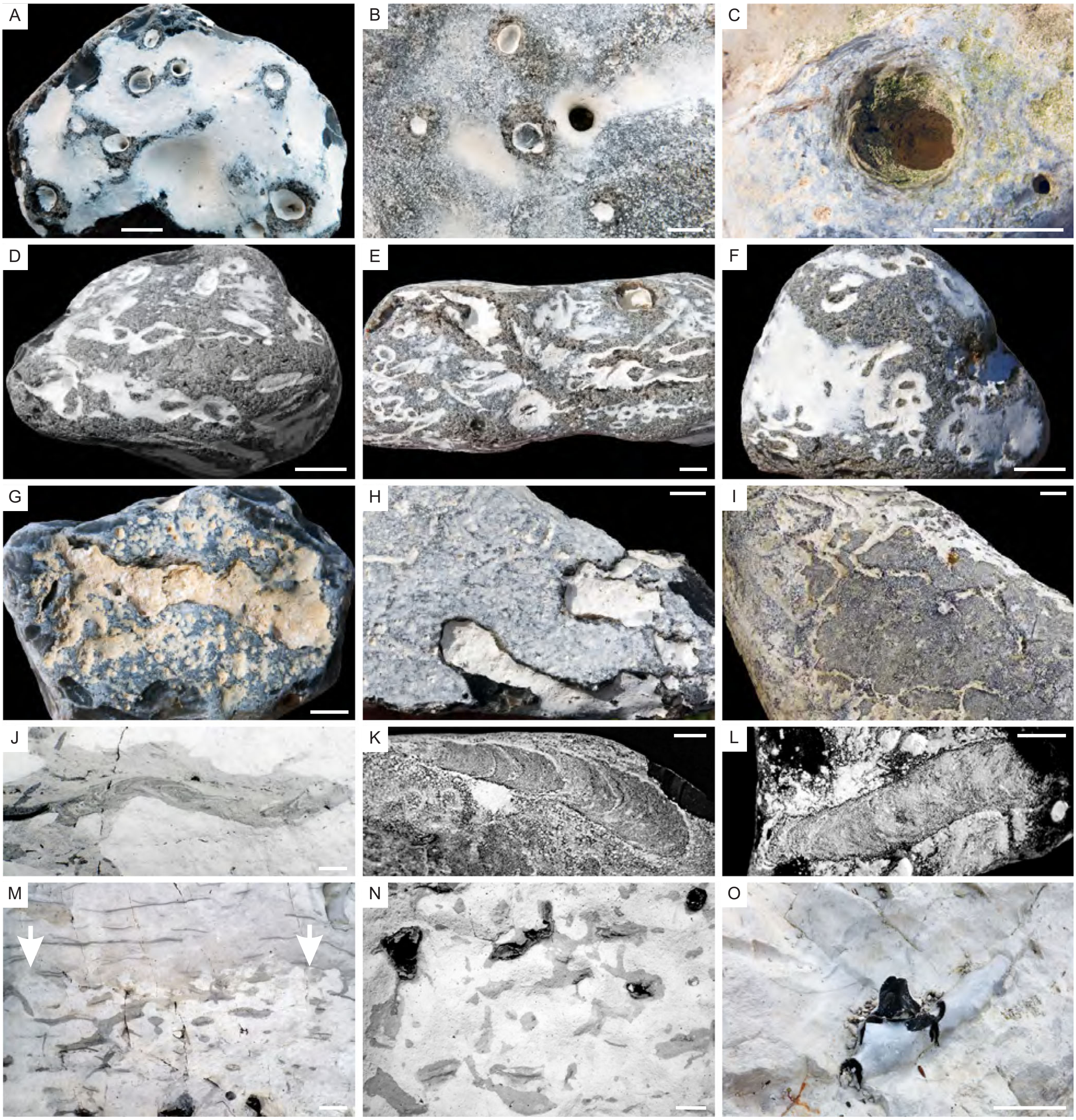

Figure 4. Bioturbation trace fossils – Part 3. Scale bars equal 10 mm (A–L), 50 mm (M–O). **A–C.** cf. *Rosselia erecta* in chalk. **D–F.** *Schaubcylindrichnus coronus* preserved in flint. **G, H.** *Sulcolithos variabilis* preserved in flint. **I.** Flint surface with incipient fractures that are partly overprinted by *Sulcolithos variabilis*. **J.** *Taenidium irregulare* preserved in chalk. **K, L.** *Taenidium irregulare* preserved in flint. **M.** Omission surface (arrows) in white chalk with *Thalassinoides paradoxicus* in the firmground below, filled and overlain by grey chalk. The softground above contains *Zoophycos* isp. (dark streaks) and *Chondrites targionii* (dark spots). **N.** Ichnofabric with *T. paradoxicus* in chalk; portions of the burrow systems are silicified (dark flint). **O.** Silicified burrow part of *T. paradoxicus* in chalk.

the fill. Burrow width is between 0.7 and 1.3 cm, the length can reach several centimetres.

The ichnogenus *Taenidium* is diagnosed as ‘unlined or very thinly lined, unbranched, straight or sinuous cylindrical trace fossils containing a segmented fill articulated by meniscus-shaped partings’, and *T. irregulare* contains variable, parabolic or chevron-shaped, asymmetrical menisci longer than wide, with the apex of the parabola or chevron offset from the midline of the fill (Li, 1993, p. 103; Bromley et al., 1999a, p. 47). This form was described as *Taenidium crassum* from upper Maastrichtian chalk of Denmark by Bromley et al. (1999a). It probably represents a dwelling or feeding trace of a vermiform organism or arthropod.

Thalassinoides paradoxicus Kennedy, 1967 (Fig. 4M–O)
These are complex burrow systems, reaching several decimetres in depth, originating from some omission and erosion surfaces within the chalk succession. The cylindrical burrows are X-, Y- and T-shaped branched, partly with extended junctions, and have a

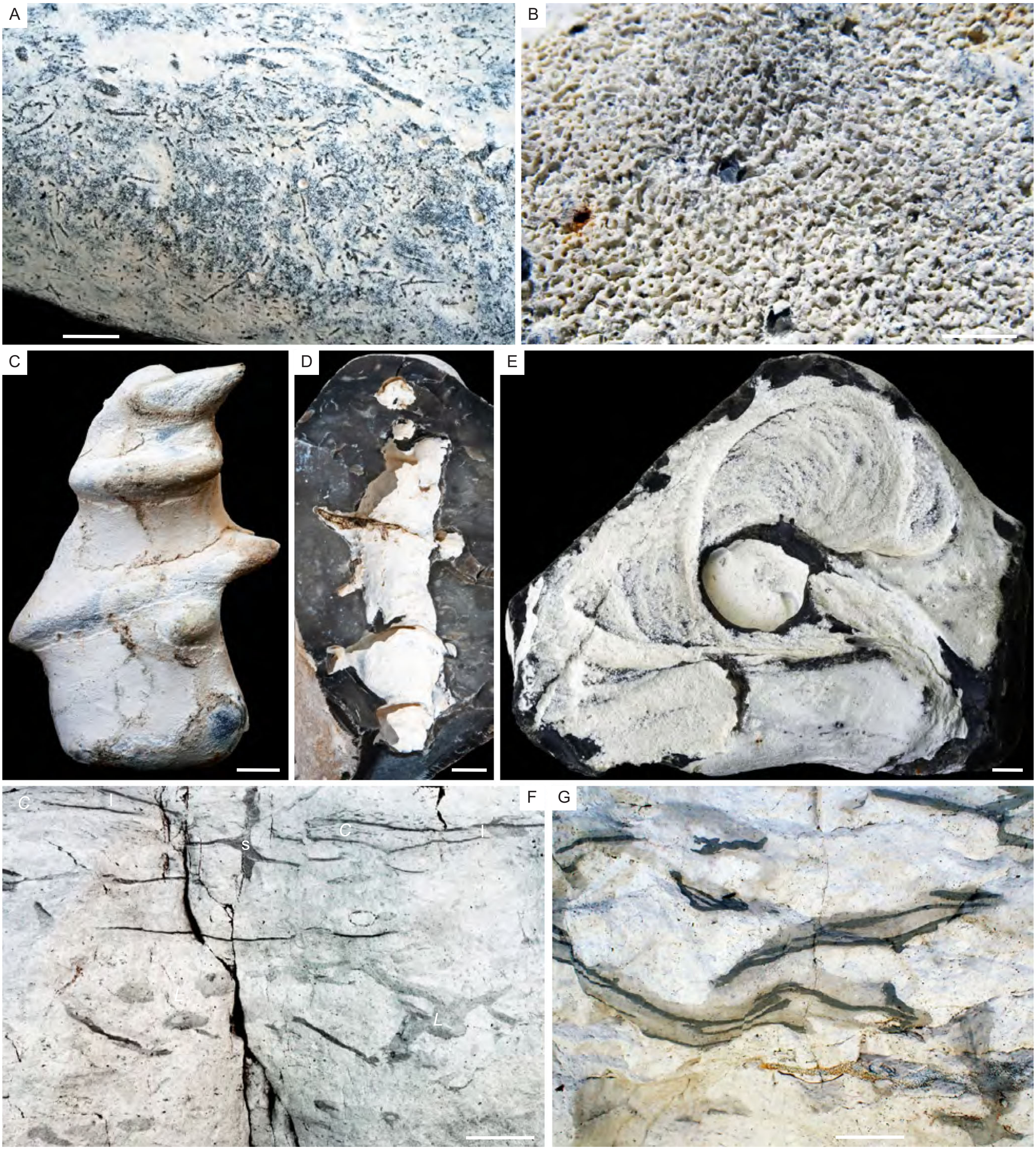

Figure 5. Bioturbation trace fossils – Part 4. Scale bars equal 10 mm (A–E), 50 mm (F, G). **A, B.** *Virgaichnus undulatus* preserved in flint. **C, D.** Spindle-shaped axial shaft of *Zoophycos* isp. preserved in flint (C) and as chalk within a flint concretion (D) together with parts of the adjacent shirt-shaped lobes. **E.** Lobes of *Zoophycos* isp. (flint preservation) emerging from a central shaft (chalk preservation). **F.** Chalk section with an ichnofabric containing a *Zoophycos* isp. burrow system (s = shaft, l = lobes), *Chondrites targionii* (*C*) and *Lamellaecylindrica paradoxica* (*L*). **G.** Chalk section with extensive lobes of *Zoophycos* isp. (dark grey) overprinting a completely bioturbated fabric.

diameter of 1 to 2 cm. Their grey, passive, chalky fill contrasts with the whitish chalk matrix. Burrow cross sections are circular or slightly flat-elliptical. Reburrowing (e.g., *Chondrites, Zoophycos*) is common. Some burrow portions are silicified and preserved as flint nodules. Co-occurrence and intergradation with *Lamellaecylindrica paradoxica* are frequent.

Thalassinoides paradoxicus is a 'medium-sized *Thalassinoides*, with irregular, very extensive horizontal burrow network, occurring at several levels, connected by vertical shafts' (Kennedy, 1967, p. 142). It was originally described from Albian–Cenomanian chalk of south-east England; it is common in shallow-marine Cretaceous chalk deposits of north-west

Europe. Based on finds of body fossils within the burrows and modern analogues, dwelling decapod crustaceans (foremost callianassid shrimp) were likely producers (Knaust, 2024).

Virgaichnus undulatus Knaust, 2010 (Fig. 5A, B)

This tiny ichnospecies is preserved at the margin of flint nodules, where it occurs as an irregularly branched, undulating burrow system. Individual segments have pinch-and-swell-like features that lead to bulbous enlargements and alternating blade-like contractions. The flint-filled burrows have a diameter between 0.01 and 0.05 cm.

The ichnogenus *Virgaichnus* is a 'complex, three-dimensional, irregular burrow system with horizontal and inclined elements, "Y"-shaped and/or "T"-shaped branching and smooth-walled and passively filled burrows' (Knaust, 2010, p. 83). *Virgaichnus undulatus* has 'undulating burrow sections leading to bulbous enlargements and alternating blade-like contractions' (Knaust, 2010, p. 83). It is probably the product of a highly flexible vermiform organism such as a nemertean, with a dwelling, feeding and predatory lifestyle (Knaust, 2010, 2017). It is a common part of chalk successions (Knaust et al., 2020; Blinkenberg et al., 2020).

Zoophycos isp. (Figs. 4M, 5C–G)

This characteristic form consists of a spindle-shaped axial shaft, from which shirt-shaped lobes emerge in a spiral manner. Preservation is complex and can be as grey chalk or as flint, or a combination of both. Preserved parts of the axis can be 10 cm or more in depth, 1 to 3 cm in diameter and contain four to five rounds of whorls of various lengths and widths. In plan view, the lobes display concentric lamination (so-called spreite) surrounded by a marginal master tunnel (*c.* 0.6 cm in width). Both spreite and tunnel are densely packed with faecal pellets (*Coprulus oblongus*). Besides idiomorphic burrow systems, some lobes are concentrated in the fill of *Thalassinoides paradoxicus*, where they appear in vertical section as elongated stripes with closely spaced chevrons (compare Ekdale & Bromley, 1983).

The ichnogenus *Zoophycos* includes 'spreiten structures consisting of numerous J- or U-shaped protrusive burrows of variable length and width. The spreiten form laminae bordered by a marginal tube, spirally coiled around a central "virtual" axis, constructed upward or downward, furrowed by numerous lamellae (primary and secondary). In section, the laminae show the typical backfill structure, formed during the lateral displacement of the marginal tube' (Olivero, 2007, p. 226). *Zoophycos* isp. is common in deeper shelf chalk (Ekdale & Bromley, 1984a, 1991). It was produced by a deposit-feeding worm, which perhaps had a chemosymbiotic relationship with microbial colonies (Bromley et al., 1999b; Zhang et al., 2015).

Bioerosion trace fossils

Abeliella procera Mägdefrau, 1937 (Fig. 6A)

Phosphatic remains are rare in the Rügen chalk, but the few fish teeth and scales commonly show infection with rosette-shaped borings that have been known since the mid-nineteenth century (Rose, 1855; von Kölliker, 1860). Mägdefrau (1937) introduced two distinct ichnospecies that significantly differ from each other in general appearance and relative branch diameter. *Abeliella procera* is the more filigree and slender one. Because of its occurrence in strata laid down in the aphotic zone, it is inferred that both ichnospecies of *Abeliella* were produced by heterotrophic thallophytes.

Wisshak (2017, p. 48) provided an emended diagnosis, as follows: 'Dichotomous ramification in acute angles and with long internodes. Tunnels of constant diameter and slightly meandering course'.

Abeliella riccioides Mägdefrau, 1937 (Fig. 6A)

This is the second rosette-shaped boring occurring in phosphatic substrates from the Rügen chalk. It shows a more regular dichotomous branching pattern and appears less slender than *A. procera*. It may be characterised as follows (Wisshak, 2017, p. 50): 'Distinctly regular and bilateral symmetrical ramification pattern, strictly dichotomous and prostrate, with angle of bifurcations decreasing towards the periphery of the trace. Nearly constant tunnel diameter and only weakly widened gallery terminations'.

Apectoichnus longissimus (Kelly & Bromley, 1984) (Fig. 6B)

In general, the well-oxygenated shelf of the Rügen chalk was inappropriate for wood preservation. Therefore, silicified wood with calcite-lined bivalve borings is preserved only in very few instances. The use of the ichnogenus *Teredolites* Leymerie, 1842 for clavate borings in lignic substrates was recommended by Kelly & Bromley (1984), including the ichnospecies, *T. longissimus*. Emendation, according to advanced ichnotaxonomic principles by Donovan (2018), led to a new combination, *A. longissimus*.

Belichnus monos Pether, 1995 (Fig. 6C)

This trace fossil describes holes of irregular outline in molluscan shells that are smaller on the outside than on the inside. These are interpreted as predation traces of pointed impacts on exoskeletons. Shell-smashing stomatopod crustaceans in basinal marine sites have been mentioned as potential tracemakers (see overview in Cadée & de Wolf, 2013). *Belichnus monos* rarely occurs in echinoid tests from the Rügen chalk. It is likely that this irregular kind of shell damage is commonly overlooked or misinterpreted.

Calcideletrix anomala (Mägdefrau, 1937) (Fig. 6D–E)

This refers to a rosette-shaped bioerosion trace that regularly occurs in chalk deposited below the photic zone. As such, this trace is considered to have been produced by a heterotrophic invertebrate or thallophyte. The ichnotaxon originally established as *Dendrina anomala* Mägdefrau, 1937 was subsequently designated as belonging to the ichnogenus *Calcideletrix* Mägdefrau, 1937 by Wisshak (2017, p. 41).

Wisshak (2017, p. 35) provided an emended diagnosis of the ichnogenus *Calcideletrix*, as follows: 'Dendritic boring system in calcareous skeletal substrates with a series of main axes that give the trace a lobed appearance. Inner branches may anastomose or leave blind-ending branches. Trace closely prostrates and with many contacts to the substrate surface'. The emended diagnosis for the ichnospecies (Wisshak, 2017, p. 40) is specified: 'Main branches may curve in a sinuous fashion and in small individuals may be devoid of smaller side-branches along some length of the curve. From these closely prostrate main axes, with usually smooth surface texture, branches divide, may form anastomoses and gradually decrease in diameter to fine pointed ends that connect to the substrate surface'. This ichnogenus needs further investigation for refining both, regular differential diagnoses as well as ontogenesis reconstructions of individual ichnospecies.

Figure 6. Bioerosion trace fossils – Part 1. Scale bars equal 0.1 mm (A), 10 mm (B, C, F–I, K, L), 1 mm (D, E, J, M). **A.** *Abeliella procera* (*p*) and *A. riccioides* (*r*) in a tooth of *Hexanchus* sp. (image courtesy of Max Wisshak). **B.** *Apectoichnus longissimus* with the preservation of calcite linings in a flint nodule. The wooden host substrate decayed due to oxygenation. **C.** *Belichnus monos* with bioerosion holes in the apical area of an irregular echinoid displaying their ragged marginal zone. **D.** Group of *Calcideletrix anomala* together with *Dendrina dendrina* rosettes in the shallow bioerosive zone of a belemnite rostrum. **E.** Irregular ramification pattern of a *C. anomala* rosette in a belemnite. **F.** Cluster of *Caulostrepsis* isp. at the lower surface of an irregular echinoid test that was infested *post-mortem*. The interior of the borings is exposed by grazing of regular echinoids. **G.** *Caulostrepsis biforans* on a belemnite rostrum, recognised by groups of paired pits that are visible immediately distal of the aperture and interpreted as brood chambers. **H.** *Caulostrepsis cretacea* on a belemnite rostrum. **I.** *Centrichnus eccentricus*, byssus attachment trace (b) and shell margin trace (s) on a belemnite rostrum, probably produced by an anomiid bivalve. **J.** Group of *D. dendrina* rosettes on a belemnite rostrum showing a great variability of morphological features. **K, L.** *Entobia cretacea* in oyster shells. The sectional image of the boring system is caused by the dissolution of the aragonitic nacreous layer on the internal surface of the shell. **M.** *Entobia cretacea* in a belemnite rostrum.

Caulostrepsis isp. (Fig. 6F)

In many cases, the skeletal fragments available were too small for an undisturbed idiomorphic development of larger borings, as defined in exemplary detail by Bromley & d'Alessandro (1984, p. 236) for the ichnogenus *Entobia*, as follows: 'The natural, uninhibited, full growth-form of a sponge boring in an extensive, homogeneous carbonate substrate'. This circumstance equally concerns worm borings in the Rügen chalk. Physical restriction of small and overcrowded substrates led to stenomorphic worm traces that can be identified only at the ichnogenus level. An example is given by an echinoid test densely populated by worms and their traces. An additional specimen of the echinoid

Echinocorys ovata featuring 27 boring traces of the ichnogenus *Caulostrepsis* from Rügen was interpreted as symbiotic association by Wisshak & Neumann (2006).

Caulostrepsis avipes Bromley & d'Alessandro, 1983

This ichnotaxon is interpreted as a dwelling trace of spionid polychaetes in calcareous substrates. The trace is a single-entrance boring with a pouch-shape produced by a U-bend gallery. All ichnospecies of *Caulostrepsis* are determined by lateral boring processes, i.e., advances at the vertex. The distinctive feature of this ichnospecies is the presence of apertural grooves. *Caulostrepsis biforans'* and *C. cretacea* are closely related ichnospecies that are also common in the chalks of north-west Europe.

Bromley & d'Alessandro (1983, p. 291) provided the following diagnosis: '*Caulostrepsis* with or without a vane, dumbbell-shaped to flattened-oval in cross section, characterised by the possession of two to four grooves branched out from the aperture. In some cases, the branching occurs beneath the surface so that each diverging branch bears its own aperture'.

Caulostrepsis biforans (Gripp, 1967) (Fig. 6G)

This ichnospecies is considered a polychaete-dwelling trace in calcareous substrates. The diagnostic feature of this form is the paired pits close to the aperture, interpreted as brood chambers (Hillmer & Schulz, 1973).

Bromley & d'Alessandro (1983, p. 290) provided the following diagnosis: '*Caulostrepsis* having no vane, normally lacking an axial depression, flattened-oval cross section distally, approaching circular proximally. Immediately distal of the aperture, a series of paired or double-paired pits. Two or four grooves branch out from the aperture, or these branches may be submerged within the substrate, the true apertures (2 or 4) occurring where the branches break the surface'.

Caulostrepsis cretacea (Voigt, 1971) (Fig. 6H)

The third, closely related *Caulostrepsis* ichnospecies of the Rügen chalk is also regarded as a polychaete-dwelling trace in calcareous substrates. It is the simplest form, lacking any further ichnologically important features.

The diagnosis provided by Bromley & d'Alessandro (1983, p. 291) reads as follows: 'Galleries bent in a long, narrow U-form with the inward-facing walls of the limbs fused by complete removal; the original position of the median wall is sometimes indicated by a very shallow axial depression along the structure. Vane absent. Transverse section always flattened-elliptical but showing gradual decrease in width toward the aperture. Shape of aperture flattened-oval'.

Centrichnus eccentricus Bromley & Martinell, 1991 (Fig. 6I)

This is the most common attachment trace on calcareous substrates of the Rügen chalk, attributed to saddle oysters (Anomiidae). The trace enhanced firm attachment and increased shear defence against shell-crushing vertebrate predators, as indicated by associated biting marks (Neumann et al., 2015).

Neumann et al. (2015, p. 542) provided the following diagnosis: 'Teardrop-shaped *Centrichnus* comprising a bundle of bow-shaped grooves, concave toward the pointed anterior of the trace. A facultative lateral and posterior feature are faint to progressively more deeply carved eccentric grooves with the outermost and often longest and most deeply carved groove marking the margin of the trace. The anterior delineation may be formed by two linear series of pits, sometimes fused to elongate grooves, deepening outwards on both sides of the trace's longitudinal axis'.

Dendrina dendrina (Morris, 1851) (Fig. 6D, J)

This probably is the most conspicuous bioerosion trace in the Maastrichtian chalks of north-west Europe. It is a trace that functionally can be compared with a foraminiferan test, and a test-less foraminiferan species is considered to be the trace-making organism (Schnick, 2017, p. 240). Rediscovered original specimens of the von Hagenow Collection prove that he already had recognised that trace and labelled it as *Talpina foliacea*. Since it was never formally published and figured, it must be regarded as a *nomen nudum* (Wisshak et al., 2017a).

The ichnogenus *Dendrina* Quenstedt (1849) is defined by Wisshak (2017, p. 14) as follows: 'Rosetted boring system, developed closely parallel to surface of calcareous skeletal substrates, with a circular to irregular outline, originating from a single point at the end of a tubular inlet tunnel. Individual galleries vary in width at constant height, ramify and may anastomose or fuse to form a flat central cavity. Fine galleries connect the rosette with the substrate surface, preferentially towards the rounded distal terminations'. Most of the Rügen specimens conform to the emended diagnosis given by Wisshak (2017, p. 18) for the ichnospecies *Dendrina dendrina* (Morris, 1851): 'Rosette of irregular to sub-circular outline, with loosely spaced galleries radiating from the centre in meandering fashion, ramifying with widened bi- and trifurcations of various angles, only rarely forming anastomoses. In larger individuals, additional tiers may develop'.

The successive morphological development of *D. dendrina* (Morris, 1851) sensu Wisshak (2017) is currently under examination to prove the applicability of the ichnogeny concept (Belaústegui et al., 2016; Bertling et al., 2022).

Dendrina lacerata Hofmann, 1996

This is a rosette-shaped microboring in calcareous substrates, occurring commonly accompanied by *Dendrina dendrina* and *Calcideletrix flexuosa* in the Rügen chalk. Wisshak (2017, p. 21) gave the following emended diagnosis: 'Rosette of irregular outline and with wide and lobed galleries, common fusion, and only few ramifications. Inlet tunnel relatively short and often entirely obscured by the rosette'.

It cannot be ruled out that this ichnospecies represents an early ichnogenetic phase of *D. dendrina* based on its morphological similarity but smaller size according to data from Hofmann (1996) and its reinterpretation in the revision of Wisshak (2017).

Entobia cretacea Portlock, 1843 (Fig. 6K–M)

This ichnotaxon is a sponge-dwelling trace common in biogenic carbonate substrates, such as belemnites, oysters and large inoceramids. The endolithic growth of the sponge is a sequence of consecutive growth phases to optimise substrate utilisation. Commonly, the entire substrate is infested by *E. cretacea* or the trace shows a stenomorphic development. It is the largest and most prominent bioerosion trace fossil of the Rügen chalk.

Entobia cretacea comprises networks of boxworks of chambers that are interconnected by intercameral canals. The endolithic system is connected with the substrate surface by numerous apertural canals whereas fine exploration threads investigate the substrate interior for further extension. The inner surface of the boring exhibits the typical verrucous microsculpture of clionaid sponges (Bromley, 1970).

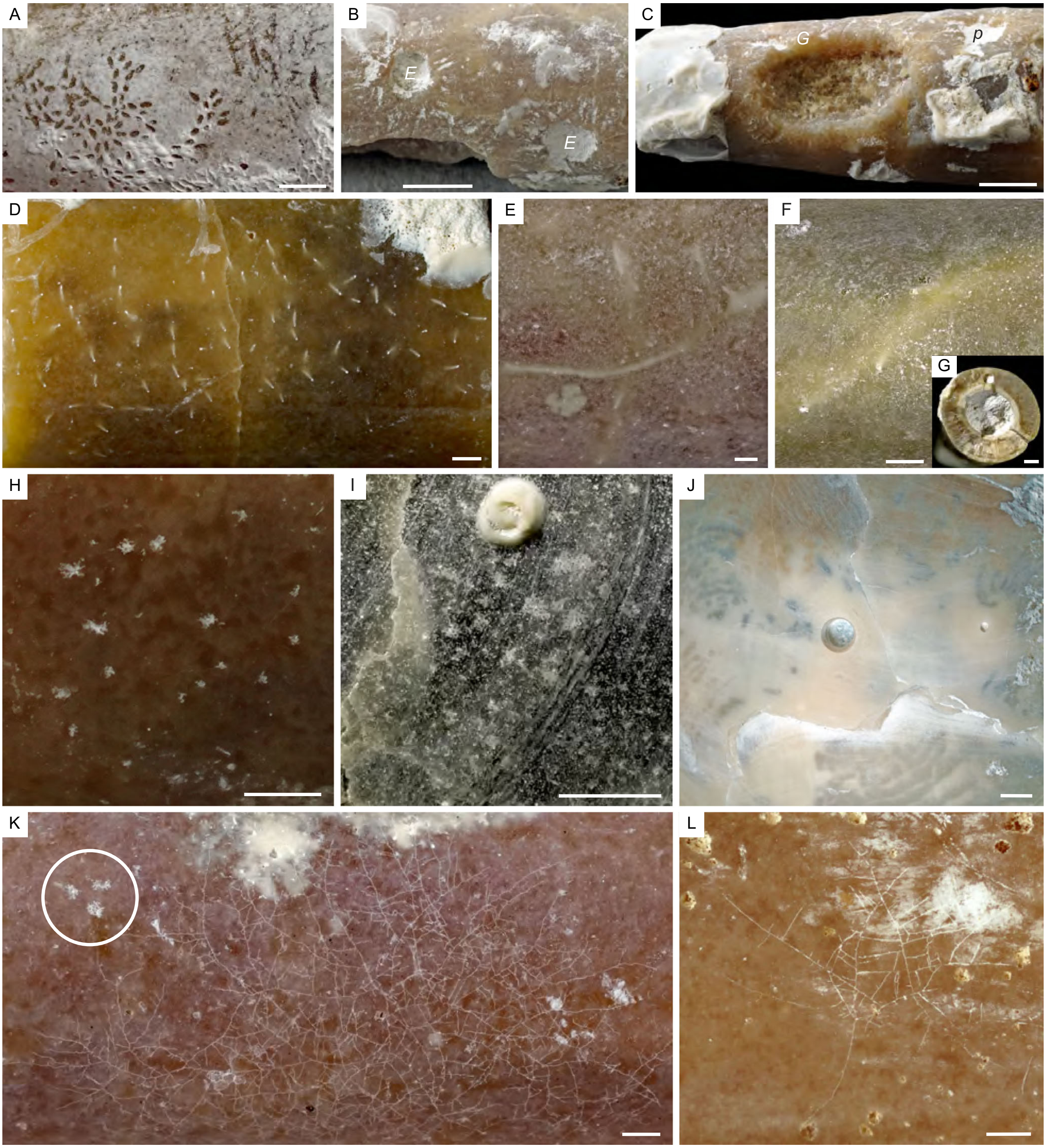

Figure 7. Bioerosion trace fossils – Part 2. Scale bars equal 1 mm (A, D–M) and 5 mm (B, C). **A.** *Finichnus dromeus* on a belemnite rostrum after partial removal of the bryozoan skeleton. **B.** *Gnathichnus pentax* surrounding the apertures of sponge borings (*Entobia* isp., *E*) on a belemnite rostrum. **C.** Groove-like *Gnathichnus* isp. (*G*) together with the more superficial scratches of *G. pentax* (*p*). **D.** *Iramena* isp. arranged linearly along interconnecting tubular tunnels of µm-scale (invisible). **E, F.** *Maeandroplydora sulcans* in belemnite rostrum. Trace of an axial boring worm with several apertures that runs top-down (E) or diagonal (F). **G.** Circular cross section of *M. sulcans* without a vane that is diagnostic of laterally bored worm traces (image courtesy of Max Wisshak). **H, I.** Small rosettes of *Nododendrina incomposita* with irregular central nodes in a belemnite rostrum (H) and a punctate brachiopod shell (I). **J.** *Oichnus simplex* in an oyster shell. **K.** *Orthogonum lineare* in a belemnite rostrum, consisting of isodiametric tunnels with predominant orthogonal ramification, together with tiny *Rhopalondendrina avis* (encircled). **L.** *Orthogonum lineare* in a belemnite rostrum.

Finichnus dromeus (Taylor et al., 2013) (Fig. 7A)

This is an attachment trace of cheilostome bryozoans on calcareous substrates that comprise sub-circular to elongate pits that show a uniserial arrangement. Each pit corresponds to the location of a single zooid in the bryozoan colony. The trace is exceptionally rare in the Rügen chalk. The original ichnogeneric name *Leptichnus* Taylor et al., 1999 had to be replaced because of homonymy by the molluscan genus *Leptichnus* (see Taylor et al., 2013).

The original diagnosis (Taylor et al., 1999, p. 601) reads as follows: '*Leptichnus* with sub-circular, elliptical or pear-shaped pits uniserially arranged, sometimes with a thin groove extending between the pits but never linking them. The pits have their long axes congruent with the linear direction of the series. Series commonly branch to give new uniserial series'.

Gnathichnus pentax Bromley, 1975b (Fig. 7B)
This is a grazing trace produced by the gnawing activity of the lantern of regular echinoids on skeletal fragments, such as belemnite rostra, oysters or inoceramid shells. The trace consists of a regular stellate grouping of five similar grooves, radiating at about 72° (Bromley, 1975b). Potential producers of *G. pentax* from Rügen are cidaroid, saleniid and phymosomatoid echinoids that lived contemporaneously in the chalk sea (Reich & Frenzel, 2002). The presence of *G. pentax* at apertures of *Talpina ramosa*, *Dendrina dendrina* and *Entobia* isp. indicates a bioerosional succession based on a predator-prey interaction and persistent exposure at the sea floor.

Gnathichnus isp. (Fig. 7C)
The ichnogenus *Gnathichnus* Bromley, 1975b (p. 738) was defined as 'biogenic sculpture consisting of grooves, pits and scratches on hard substrates'. Besides the distinctive type ichnospecies, *G. pentax*, which can easily be recognised by its pentagonal symmetry, there are also traces that surround regular scratch-aureoles the apertures of worm and sponge traces. This trace was probably produced by fishes.

Iramena isp. (Fig. 7D)
This trace is a complex dwelling structure of ctenostome bryozoans. It consists of zooidal penetrations that are interconnected by tubular tunnels of micrometre scale. Only the zooidal borings are visible in reflected light, where they appear as point clouds covering substrate areas of square centimetre size. Besides the visibility problem of thin structures in reflected light, there is also a general need for a taxonomic revision of bryozoan borings (Wisshak et al., 2017b). The presence of bryozoan borings matches the high total amount of bryozoan skeletons in the sediment composition of the Rügen chalk.

Maeandropolydora sulcans Voigt, 1965 (Fig. 7E–G)
This is a relatively large worm-dwelling trace that occurs very rarely in the Rügen chalk, probably because it is more common in ichnofacies of higher water turbulence (de Gibert et al., 2007).

Bromley & d'Alessandro (1983, p. 295) provided the following diagnosis: 'Cylindrical gallery having at least two apertures, irregularly contorted, commonly bent in loops, never showing fusion where walls are in mutual contact; vane absent'. The complex morphology of this trace is caused by stenomorphic reactions of an axial boring worm in relatively small substrates. The boring process can be described as testing behaviour to remain within the protecting substrate, because every contact with the substrate surface would be followed by a corrective contortion.

Nododendrina incomposita (Mägdefrau, 1937) (Fig. 7H, I)
This is a relatively small rosette-shaped boring produced by an invertebrate or thallophyte organism in calcareous substrates. The ichnospecies was established by Mägdefrau based on Rügen specimens preserved in brachiopod shells. While the trace is common in brachiopods, it was found more rarely in belemnites, even though these offer a better visibility of borings. Usually, a substrate is infested by numerous individuals of *N. incomposita*. These may reflect different ontogenetic stages and allow the reconstruction of the trace's ichnogeny (Schnick, 1992). A great similarity in the early developmental phases of ichnospecies of *Nododendrina* is obvious (Wisshak, 2017).

Wisshak (2017, p. 56) presented the following emended diagnosis: 'Prostrate branches diverge from a small and irregularly shaped central node, ramify at various angles, and exhibit an irregular surface texture. Density of branching varies, and anastomosis or complete fusion is common'.

Oichnus isp. (Fig. 7J)
Simple 'small round holes in shells' as introduced into ichnology by Bromley (1981, p. 55) represent truly iconic traces that have triggered fundamental discussions on ichnotaxonomic principles (Zonneveld & Gringas, 2014; Wisshak et al., 2015). According to a refined diagnosis, the ichnogenus *Oichnus* stands for complete or incomplete bioerosive penetrations in calcareous skeletal substrates that are interpreted as praedichnia (Wisshak et al., 2015). The millimetre-scale ichnospecies *O. simplex* and *Tremichnus* cf. *paraboloides* (see below) are common in bivalve and brachiopod shells as well as borings of µm-size in ostracod valves and foraminifer tests. An overview of modern potential producers of *Oichnus* was given by Bromley (1981). In addition to six different gastropod groups, these also comprise octopuses, turbellarians, nematodes and brachiopods.

Orthogonum lineare Glaub, 1994 (Fig. 7K, L)
This is one of a few microendolithic traces that can be recognised with sufficient accuracy in reflected light. The trace occurs in calcareous substrates and consists of isodiametric tunnels that run straight closely to the surface and show a predominantly orthogonal branching pattern (Glaub, 1994). The trace was produced by an unknown heterotrophic thallophyte.

Podichnus centrifugalis Bromley & Surlyk, 1973 (Fig. 8A)
Attachment traces of brachiopods in calcareous substrates were recognised and introduced as *P. centrifugalis*. Although brachiopods of different taxonomic groups frequently occur in the Rügen chalk, their etching traces are comparatively rare. This probably can be explained by the ability of some brachiopod species to use different small substrates for their attachment (Bromley & Surlyk, 1973) and may probably explain the common presence of relatively small circular borings in ostracods and foraminifera.

In the context of describing other ichnospecies of *Podichnus*, the original diagnosis provided by Bromley & Surlyk (1973) was emended by Robinson & Lee (2008, p. 223), as follows: 'A cluster of closely spaced holes in hard calcareous substrates, which have a hemispherical to irregular hollow at the shell surface with their edges more or less in contact and with a shaft at the bottom. The smaller hollows/shafts at the centre of the group are more or less perpendicular to the surface; the more peripheral hollows/shafts are typically larger, entering the substrate obliquely or centrifugally. The diameter of the holes is up to ca. 200 µm. The shell surface within the outline of the trace is all or mostly removed'.

Podichnus obliquus Robinson & Lee, 2008 (Fig. 8B)
This is another brachiopod attachment trace introduced subsequently; it comprises groups of centrifugally arranged rootlet groups that are characteristic of brachiopods belonging to the suborder Terebratulidina (Robinson & Lee, 2008). In contrast to *P. centrifugalis*, the pedicle attachment area between the rootlet traces is undisturbed by erosion.

Figure 8. Bioerosion trace fossils – Part 3. Scale bars equal 1 mm (A, B) and 10 mm (C–M). **A.** *Podichnus centrifugalis* on an oyster shell. The shell surface within the outline of the trace is almost completely removed. **B.** *Podichnus obliquus* in a belemnite rostrum. **C.** *Rogerella* isp. on the outer surface of an inoceramid bivalve. Note the preferential settlement within the concentric depressions of the shell. **D.** *Talpina ramosa* in a belemnite rostrum. **E.** Group of *Trypanites solitarius* in a belemnite rostrum. **F.** Group of *Tremichnus* cf. *paraboloides* on the lower surface of an irregular echinoid indicating *post-mortem* settlement of the tracemaker. **G, H.** *Trypanites mobilis* in globular calcareous sponges (*Porosphaera globularis*). **I, J.** Fixichnia (indeterminate), attachment traces. The irregular-oval depression on the lower surface of an echinoid shows a recovery of the original test tuberculation (I), whereas there is no restoration of a similar trace on the outer surface of the spondyloid shell (J). **K.** Praedichnia (indeterminate), bite marks. **L, M.** Pascichnia (indeterminate), grazing traces on a belemnite rostrum.

The diagnosis by Robinson & Lee (2008, p. 223) reads as follows: 'A more or less compact group of circular holes in hard calcareous substrates. The smaller holes at the centre of the group are more or less perpendicular to the surface; the more peripheral holes are typically larger, entering the substrate obliquely or centrifugally. The larger holes are often widely spaced. The diameter of the holes is up to ca. 200 µm. The shell surface between the holes is largely undisturbed'.

Rhopalondendrina avis Wisshak, 2017 (Fig. 7K)

The size of *R. avis* lies in between microscopic and macroscopic scale, but it can be recognised based on a pronounced dichotomous branching pattern and a continuous transition from the primary entrance part into the rosette. The microboring probably was produced by heterotroph invertebrate or thallophyte organisms.

The etymology of the trace is based on the Latin 'avis', for bird (or 'Vogel' in German), acknowledging the ichnological merits of Klaus Vogel and his team in Frankfurt am Main (Wisshak, 2017), also the first investigation of Rügen chalk microborings basing on the cast embedding technique had already been published by Hofmann & Vogel (1992).

Rogerella isp. (Fig. 8C)

This is a macroboring dwelling trace of acrothoracican cirripedes in calcareous substrates. The pouch-shaped borings have rounded to oval- or comma-shaped apertures. However, the interior shape is difficult to assess. *Rogerella* isp. is common in the Rügen chalk on substrates of larger size such as belemnite rostra, inoceramid and oyster shells and shows patchy distributions.

Talpina ramosa von Hagenow, 1840 (Fig. 8D)

This ichnotaxon is recognised as a macroboring dwelling trace of pseudo-colony forming phoronoids in calcareous substrates, mainly in belemnite rostra (Voigt, 1972). This conspicuous ichnotaxon consists of densely ramified cylindrical borings with anastomoses and numerous apertures to the substrate surface. Apertures of *T. ramosa* surrounded by the echinoid grazing trace *Gnathichnus pentax* indicate a predator-prey relationship in some cases.

Talpina ramosa ranks among the most common bioerosion traces of the Rügen chalk. Von Hagenow (1840) gave the first description of this ichnotaxon but failed to illustrate it. The von Hagenow Collection, including the type material of *T. ramosa*, was lost during World War II. Fortunately, some specimens originally identified by von Hagenow survived the wartime in other collections. These were used for a re-examination, inclusive of the designation of a lectotype (Wisshak et al., 2017a).

Tremichnus cf. paraboloides Brett, 1985 (Fig. 8F)

Within the frame of scientific debate over 'small round holes in shells', induced by Bromley (1981), the ichnogenera *Oichnus* and *Tremichnus* were revised by Wisshak et al. (2015). Accordingly, *Tremichnus* refers exclusively to circular pits that are perpendicularly bored and generally wider than deep. In contrast to *Oichnus*, *Tremichnus* is restricted to echinoderm host substrates and does not penetrate the substrate completely and commonly triggers skeletal growth reactions of the host organism. *Tremichnus* represents a domichnion or fixichnion.

Borings of this type commonly occur in groups of similar ichnogenetic status, both in regular and irregular echinoids of the Rügen chalk. In many cases, each single boring is surrounded by a wall-like skeletal deformation representing the growth response of the living host substrate.

Trypanites mobilis Neumann et al., 2008 (Fig. 8G, H)

This most probably represents a particular adaptation of sipunculan worms to the general shortage of hard substrates in softgrounds of the Maastrichtian chalk sea. Bioclasts had been bored and used as mobile shelters in the same way as hermit crabs use empty gastropod shells. The macroboring dwelling trace occurs in medium-sized subspherical calcareous bioclasts, such as the globular calcareous sponge *Porosphaera globularis*, bulbous echinoid spines, as well as asteroid and crinoid ossicles (Neumann et al., 2008; Øhlenschlæger et al., 2022).

Øhlenschlæger et al. (2022, p. 1) defined *T. mobilis* as follows: 'Short, cylindrical, straight or slightly curved *Trypanites* in a calcareous bioclast typically 3 times the diameter of the boring. The boring is in most cases oriented perpendicular to the surface of the bioclast which may or may not be fully penetrated'.

Trypanites solitarius (von Hagenow, 1840) (Fig. 8E)

This ichnospecies was established as *Talpina solitaria* by von Hagenow based on Maastrichtian specimens from Rügen, but he only described this trace, failing to provide illustrations. Furthermore, the type of material was destroyed during World War II. Due to the rediscovery of bioerosion traces originally labelled by von Hagenow, the designation of a lectotype for *T. solitaria* became possible (Wisshak et al., 2017a).

This ichnospecies represents an unbranched cylindrical boring that needs to be included in the ichnogenus *Trypanites* Mägdefrau, 1932. In contrast to other ichnospecies of *Trypanites*, *T. solitarius* follows a sub-horizontal course adapted to the morphology of the substrate surface (Wisshak et al., 2017a; Knaust et al., 2023).

Indeterminate bioerosion trace fossils (Fig. 8I–M)

In addition to the above-listed ichnotaxa, which can be regarded as recurrent in the chalk of the Isle of Rügen, there are numerous trace fossils that do not allow an assignment to existing ichnotaxa, either because of their (poor) preservation or due to weak diagnoses. Further research seems to be necessary for a proper assignment. Superficial and shallow depressions of different sizes and shapes apparently belong to the ethological class of fixichnia. These traces probably were caused by etching of invertebrate epizoans to obtain a fixed position on echinoid tests and bivalve shells (Fig. 8I, J). A similar trace, also from an echinoid test, has been published from the Maastrichtian type area (Donovan et al., 2010, fig. 2). Other traces belong to pascichnia and can be described as superficial scratch traces left by grazing vertebrates, probably fishes (Fig. 8L, M). Finally, there are also predichnia of carnivorous vertebrates that had powerful jaws able to smash oysters and echinoids (Fig. 8K).

Conclusions

The impressive white chalk cliffs of the Isle of Rügen in north-east Germany have attracted landscape painters and natural scientists alike. Friedrich von Hagenow was a pioneer in describing the fossils of the Rügen chalk in the first half of the nineteenth century. Detailed geological, sedimentological and palaeontological investigations with ichnological significance were made by Gerhard Steinich in the middle of the twentieth century, besides contributions of other workers. Despite its wealth of trace fossils, ichnological aspects of the Rügen chalk were only sporadically dealt with, in contrast to work performed in other regions (e.g., Denmark, UK, USA). Reasons for this hiatus might be the high amount of bioturbation with multiple overprinting of different trace-fossil suites, their commonly low contrast in colour and/or grain size, as well as the diagenetic overprint with silica cementation, all of which require special techniques for investigation.

The present overview of trace fossils recognised in the Rügen chalk briefly discusses their preservation within the chalk and as flint concretions, the latter including trace-fossil preservation as chalk in flint or *vice versa*. Bioturbation and bioerosion trace fossils represent two main categories, based on the kind of substrate that is penetrated (e.g., soft- and firmground *versus* hardground). Sixteen bioturbation ichnogenera (including 18 ichnospecies) and 21 bioerosion ichnogenera (including 29 ichnospecies), in addition to indeterminate trace fossils, are recorded and briefly outlined here; many of these are recorded from the Rügen chalk for the first time.

This ichnofauna belongs mainly to the *Zoophycos, Cruziana* and *Glossifungites* ichnofacies with deposits from an offshore environment below the storm-wave base in the aphotic zone. Well-developed hardgrounds with the *Trypanites* Ichnofacies are largely absent and bioerosion chiefly occurred in bioclasts such as shells and belemnites.

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