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# *Centrichnus eccentricus* revisited: A new view on anomiid bivalve bioerosion

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Saddle oysters (Anomiidae) attach themselves to calcareous hard substrates by means of a calcified byssus that etches an attachment structure, referred to as ichnospecies *Centrichnus eccentricus*. Examination of rich material from the Late Cretaceous of central Europe extends the fossil record of this ichnotaxon and revealed a set of previously unrecognised morphological features which appear to be typical for this time period and the respective anomiid trace maker. Excellent preservation of a large number of trace fossil specimens with a complete set of morphological characters allowed a biometrical analysis and additional observations indicating a distinct substrate preference for belemnite rostra, a strong intra- and interspecific competition for settlement space, as well as interactions with durophaguous predators. Further implications for anomiid palaeobiology and palaeoecology arise from allometric shell growth and an etched outline suture in the substrate along the dorsal, lateral and ventral shell margins. These features enhanced a firm attachment and increased shear resistance, and thus are interpreted as an effective defence mechanism against shell-crushing enemies under the intensified predation pressure in marine environments in the Late Cretaceous.

Key words: Mollusca, Anomiidae, *Centrichnus eccentricus,* belemnite, trace fossil, attachment bioerosion, Cretaceous, Europe.

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## Introduction

Bivalves of the family Anomiidae ("saddle oysters") live permanently attached to hard substrates and secrete an often calcified byssus that serves as an attachment organ (Bromley and Martinell 1991; Bromley and Heinberg 2006). Such a calcified byssus, which protrudes through a byssus gape in the right valve, is unique among the Bivalvia. Equally unique is the etching trace produced by the byssus which has been described as the trace fossil *Centrichnus eccentricus* by Bromley and Martinell (1991) (Fig. 1). Since anomiid body fossils are rarely found attached to their original substrate, and because the inconspicuous and brittle valves often suffer from destructive taphonomical processes, their attachment traces deserve special attention because these are often the only indication of anomiid presence in many depositional systems. The record of anomiid body fossils and remains of calcified byssi dates back to the Jurassic (Fürsich and Palmer 1982), whereas their etching traces do not appear before the Late Cretaceous (Bromley 2004; this study). The original description of *C. eccentricus* elaborates solely on the etching of the byssus. Here, we show that *C. eccentricus* from the Late Cretaceous of central Europe (France, Germany, Denmark, and Belgium) is more complex. Depending on the shell morphology of its peculiar anomiid tracemaker and the geometry of the substrate, we observe conspicuous imprints on the substrate along the dorsal, lateral, and ventral valve margins. Our interpretation of these new morphological features, in concert with a biometrical analysis based on several hundred traces, permit clues to the poorly known anomiid palaeobiology and palaeoecology, as well as on a potential

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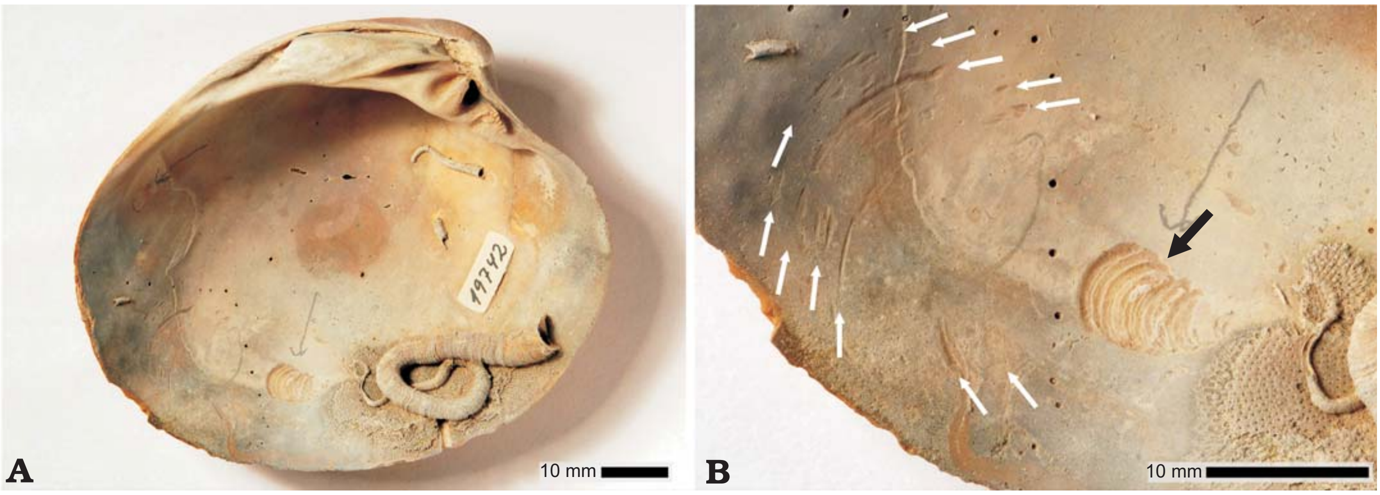


Fig. 1. Holotype (MGUH 19742) of *Centrichnus eccentricus* Bromley and Martinell, 1991, anomiid bivalve attachment trace, from Pleistocene deposits off Palamós, NE Iberian Peninsula, Spain. **A**. Valve of *Arctica islandica* bearing the holotype. **B**. Detail of the holotype; white arrows indicate grooves not included in the original diagnosis, black arrow indicates the main imprint of the byssus.

taxonomic control implied by the presence and high abundance of these new characters in strata deposited in the late Cretaceous chalk sea.

*Institutional abbreviations*.—MfN, Museum für Naturkunde Leibniz Institute for Evolution and Biodiversity Science Berlin, Germany; MGUH, Geologisk Museum Copenhagen, Denmark.

## Material and methods

Detailed examination of macrofossils acting as potential hard substrates for *Centrichnus eccentricus* resulted in the recognition of 468 specimens of *C. eccentricus* from five different sedimentary basins across western and central Europe. The sampled localities cover the Anglo-Paris Basin (Haute-Normandy), the Aachen-Limburg Cretaceous Basin (Lixhe, Belgium), the Lower Saxony Basin (Hannover area, Germany), and the North German and Danish Cretaceous subbasins of the North Sea Basin (Kronsmoor, Jasmund, Møns Klint and Stevns Klint). With the exception of the Hannover area, where marly limestone occurs, the predominant facies in which *C. eccentricus* was found is white chalk (i.e., weakly cemented calcareous nannoplankton ooze). The locality “Jasmund” (Maastrichtian, Rügen Island, Germany) has yielded the richest material (428 specimens). The oldest occurrence is from the Turonian of Haute-Normandy (France), whereas the youngest record stems from the uppermost Maastrichtian of Stevns Klint (Denmark). All sampled localities, their stratigraphy, sample size, substrate type and facies are summarised in Table 1.

The recognition of *Centrichnus* trace fossils is not trivial and requires special observation techniques. Bulk samples of belemnite rostra and other macrofossils have been carefully examined under low angle light using a head lens with a threefold magnification. Each finding has been numbered and the metric characters have been measured to an accuracy of 0.1 mm using a slide calliper. For biometric analyses, only specimens exposing a complete set of characters from the Jasmund locality (n = 367) have been selected. The terms used to describe anomiid morphology and the trace fossil *C. eccentricus* are shown in Fig. 2A–D, and the measured biometric characters are shown in Fig. 2C. Additionally, the type of hard substrate, the growth direction and evidence for predation or competition with other epibionts was quantified. All biometrical analyses were undertaken in MS EXCEL. Photographic documentation was carried out with a NIKON Coolpix 4500 and ring light NIKON SL-1 after coating with ammonium chloride in order to reveal finest details of mi-

Table 1. Localities, stratigraphy, facies and substrate types of examined *Centrichnus eccentricus* attachment traces.

| Locality | Stratigraphy | Facies | n | Substrate (occurrences) |
|---|---|---|---|---|
| Haute-Normandy (France) | Turonian | chalk | 2 | echinoid (2) |
| Hannover area (Germany) | Campanian | marly limestone | 10 | belemnite (9), oyster (1) |
| Kronsmoor (Germany) | Early Maastrichtian | chalk | 4 | belemnite (4) |
| Lixhe (Belgium) | Campanian–Maastrichtian | chalk | 10 | belemnite (5), echinoid (4), oyster (1) |
| Jasmund, Rügen (Germany) | Early Maastrichtian | chalk | 428 | belemnite (369), oyster (32), brachiopod (16), echinoid (7), inoceramid (4) |
| Møn (Denmark) | Early Maastrichtian | chalk | 13 | belemnite (9), oyster (1), brachiopod (3) |
| Stevns Klint (Denmark) | Late Maastrichtian | chalk | 1 | belemnite (1) |

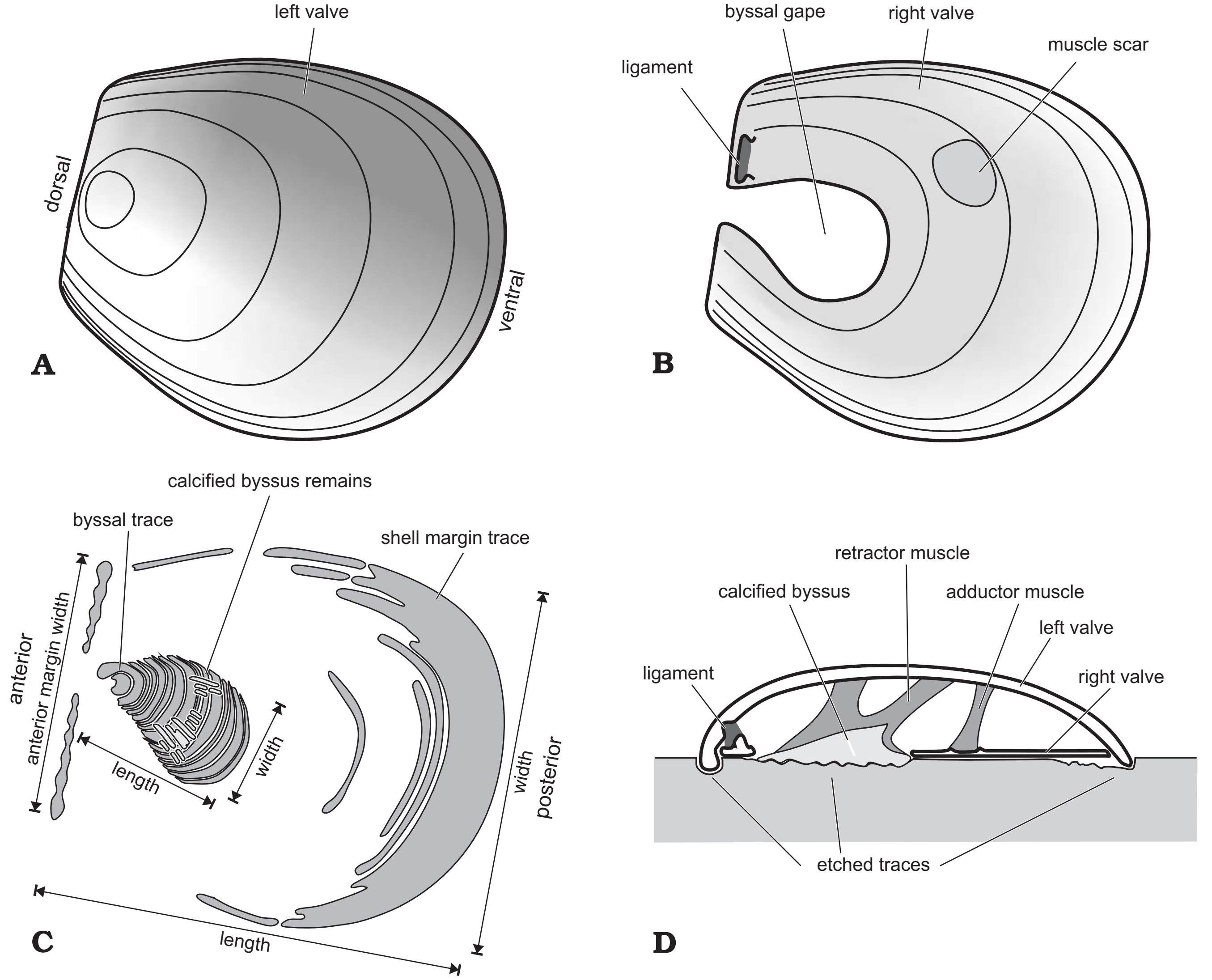


Fig. 2. Sketches illustrating anomiid and trace morphology. **A.** Shell exterior of left valve. **B.** Shell interior of right valve. **C.** Morphological features and measured dimensions of *Centrichnus eccentricus*. **D.** Schematic cross section of a living anomiid attached to the substrate illustrating the position of etching traces (modified after Yamaguchi 1998).

crotopography (see Fig. 3). Samples for scanning electron microscopy (SEM) were sputter-coated with gold and visualised with a TESCAN Vega II.

Apart from the holotype of *Centrichnus eccentricus* (MGUH 19742), which is stored in the collections of the Geologisk Museum Copenhagen (Denmark), all figured specimens (MB.W 3074–3093) are stored in the collections of the Museum für Naturkunde Berlin (MfN), whereas the non-figured specimens remain in the private collections of the authors PG and TR.

# Systematic ichnology

## Ichnogenus *Centrichnus* Bromley and Martinell, 1991

*Type ichnospecies*: *Centrichnus eccentricus,* Pleistocene of Palamós (Spain).

## *Centrichnus eccentricus* Bromley and Martinell, 1991

Figs. 1–7.

1991 *Centrichnus eccentricus* isp. n.; Bromley and Martinell 1991: 248–249, figs. 5, 6.

1999 *Centrichnus eccentricus* Bromley and Martinell; Bromley 1999: 176, figs. 2, 3.

2002 *Centrichnus eccentricus* Bromley and Martinell; Taddei Ruggiero and Annunziata 2002: 48, pl. 2.

2005 *Centrichnus eccentricus* Bromley and Martinell; Wisshak et al. 2005: 108, fig. 14F.

2005 *Centrichnus eccentricus* Bromley and Martinell; Bromley 2005: 903, fig. 8A, B.

2006 *Centrichnus eccentricus* Bromley and Martinell; Bromley and Heinberg 2006: 141–142, fig. 10.

2006 *Centrichnus eccentricus* Bromley and Martinell; Santos and Mayoral 2006: 731, pl. 3: 10.

2006 *Centrichnus eccentricus* Bromley and Martinell; Wisshak 2006: 289, fig. 23E.

2007 *Centrichnus eccentricus* Bromley and Martinell; Beuck et al. 2007: 164, fig. 4a.

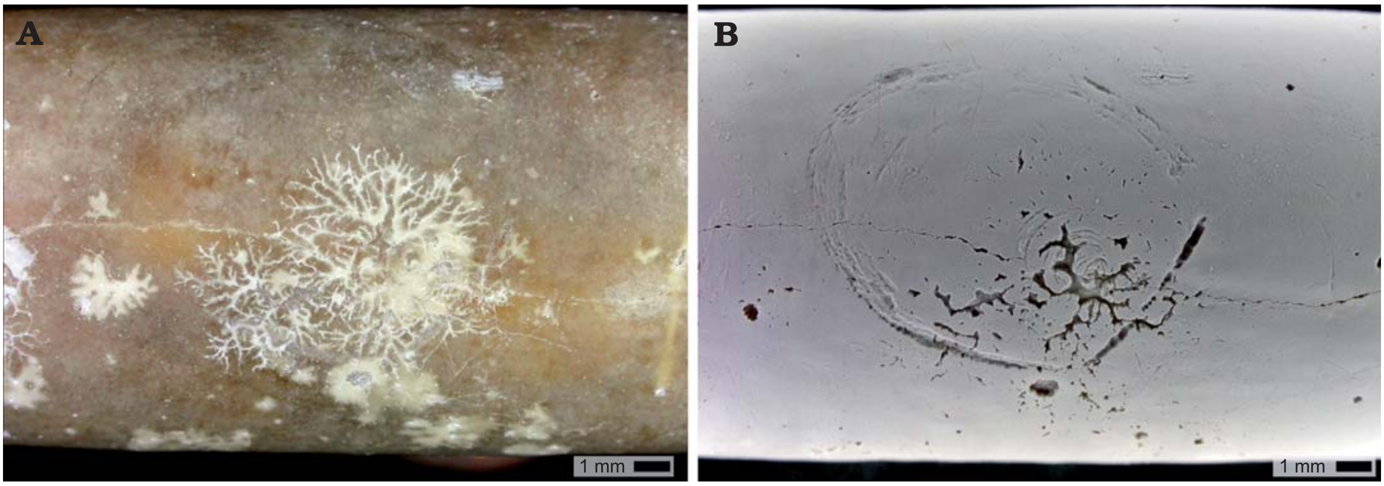


Fig. 3. Belemnite (MB.W3074) from Lower Maastrichtian, Jasmund (Rügen, Germany), exhibiting dendrinid boring traces with superimposed *Centrichnus eccentricus* Bromley and Martinell, 1991 anomiid bivalve attachment trace. In the uncoated belemnite, only the dendrinid boring traces are visible (**A**, colour contrast), with ammonium chloride coating, the *C. eccentricus* trace is clearly visible (**B**, relief contrast).

2007 *Centrichnus* cf. *eccentricus* Bromley and Martinell; Gibert et al. 2007: 792, fig. 9A, B.

2007 *Centrichnus eccentricus* Bromley and Martinell; Olszewska-Nejbert 2007: pl. 32: 4.

2007 *Centrichnus eccentricus* Bromley and Martinell; Taddei Ruggiero and Bitner 2007: 370, fig. 4.

2007 *Centrichnus eccentricus* Bromley and Martinell; Blisset and Pickerill 2007, fig. 2A, B.

2008 *Centrichnus eccentricus* Bromley and Martinell; Wisshak 2008: 216, fig. 2H.

?2008 *Centrichnus* cf. *eccentricus* Bromley and Martinell; Zamora et al. 2008: 21, pl. 3: 8.

2011 *Centrichnus eccentricus* Bromley and Martinell; Wisshak et al. 2011: 508, fig. 9F.

2013 *Centrichnus eccentricus* Bromley and Martinell; Girod and Rösner 2013: 283, fig. 17.

*Emended 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.

*Description*.—The classical *Centrichnus eccentricus* consists of a teardrop-shaped bundle of grooves, curved around a centre that is at or beyond the narrow end of the bundle, and is found on a variety of biogenic hard substrates (Fig. 4A and see below). In 115 specimens of *C. eccentricus* from Jasmund belemnite rostra, the bundle length ranged from 2.8 to 8.9 mm (mean 5.0 ± 1.2 mm) and the width ranged from 1.2 to 4.2 mm (mean 2.9 ± 0.6 mm, see Fig. 4B). One or two further components may be present, the first one of which consists of faint (Fig. 5C) to progressively more deeply carved grooves (Fig. 5B), which frame the teardrop-shaped bundle of grooves and form the lateral and posterior margin of the trace. The second component forms the anterior delineation of the trace and consists of a pair of linear and outwards deepening series of pits which are often fused to elongate grooves. They extend on either side of the longitudinal axis of the trace. The length of the pair of grooves ranges from 2.8 to 8.9 mm (mean 5.1 ± 1.1 mm). The length of the complete trace (Fig. 4B–C) extends from 8.3 to 22.0 mm (mean 13.7 ± 2.9 mm) and its width ranges from 6.2 to 13.8 mm (mean 9.7 ± 1.6 mm). Size frequency analyses of total length shows a normal distribution (Fig. 4C).

*Remarks*.—The original diagnosis and description of *C. eccentricus* is restricted to the byssus imprint, although the holotype (from the Pleistocene off Palamós, NE Iberian Peninsula) and one of the paratypes (from the Lower Campanian of Misburg, Germany) also exhibit groove imprints of the valve margin (Fig. 1). This renders the establishment of a new ichnospecies unfeasible even though the presence of anteriorly positioned imprints cannot be verified in the holotype because the respective area is overgrown by a bryozoan colony (Fig. 1B).

*Stratigraphic and geographic range*.—According to Bromley (2004) the fossil record of *C. eccentricus* extends from the Campanian to the Recent from tropical to high-latitude (palaeo-) environments. Today it has a broad bathymetric range from the shallow subtidal to bathyal depths where it has been reported for instance from cold-water coral reefs in a depths down to 1039 metres (Beuck et al. 2007). The present data extend the first occurrence back to the Turonian of Haute-Normandy where two specimens with complete morphology have been observed on the tests of the echinoid *Echinocorys*. The youngest of the specimens studied herein comes from the uppermost Maastrichtian chalk of Stevns Klint (Denmark) where it has been recorded on a belemnite rostrum (*Belemnella kasimirovensis*) just below the Cretaceous–Palaeogene boundary. According to the current fossil record, *C. eccentricus* exposing the complete morphology was dominant in the Late Cretaceous. It has been found in a

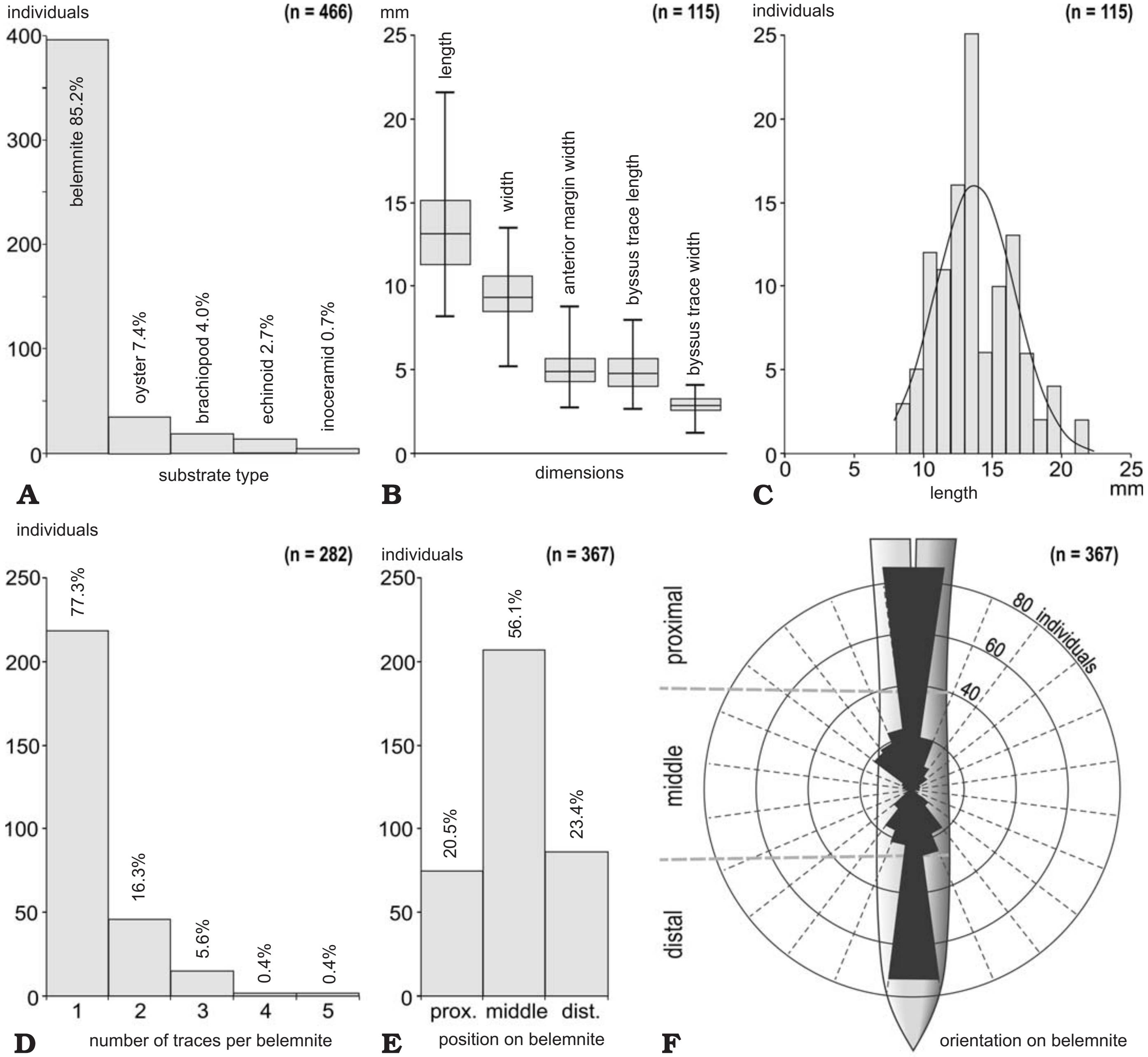


Fig. 4. Statistics and biometry of anomiid bivalve attachment trace *C. eccentricus*. All records (**A**), complete traces on belemnites (**B**–**F**) from the Lower Maastrichtian, Jasmund (Rügen, Germany). **A**. Substrate types utilised for attachment. **B**. Box plot of biometric measurements. **C**. Size frequency distribution of trace length. **D**. Number of traces per belemnite. **E**. Site selectivity on belemnite. **F**. Trace orientation on belemnite.

wide geographical range across western and central Europe, comprising several sedimentary basins. It is most common in the hemipelagic chalk facies but also occurs rarely (10 records) in the more neritic marly limestone of the Lower Saxony Basin (Hannover). The majority of our records are from the Early Maastrichtian white chalk of Jasmund. Although this picture may be biased by a collection artefact (this locality is the one which has been most extensively sampled), a bulk sample from this locality demonstrated that 50 out of 500 belemnites (10%) exposed the trace fossil *C. eccentricus*, a percentage that is probably not observed in the other sampled localities.

# Discussion

## The fossil record and taphonomy

The fossil record of the Anomiidae dates back to the Jurassic (Fürsich and Palmer 1982). Various degrees and modes of byssus mineralisation have been suggested for these early anomiids: *Eonomia* is characterised by the direct, pallial secretion of the shell onto the substrate and the byssus most probably was not calcified at all. Byssal fixation lasted throughout life as indicated by the presence of a byssal foramen in the right valve but apparently attachment occurred without etching of the substrate (Fürsich and Palmer 1982). *Placunopsis inaequalis* had a non-mineralised byssal plug (Todd and Palmer 2002). In "*Placunopsis*" *socialis*, calcification of the byssus seems to have been variable, ranging from non-mineralised to variably calcified (aragonitic) (Todd and Palmer 2002; according to the discussion therein, Triassic members of "*Placunopsis*" are not included in the Anomiidae but are regarded as members of the Plicatulidae). *Juranomia* had a calcified byssus, which probably was calcitic because of its good preservation (Fürsich and Werner 1989). None of the Jurassic anomiids left etching traces in the fossil record.

In many of our specimens of *C. eccentricus* from the Upper Cretaceous chalk, fragmentary remains of the calcified byssus are still present (e.g., Figs. 5E, 6D, F, 7B, C). Because aragonite is generally not preserved in the chalk facies, we conclude that the byssus was originally composed of a mixture of calcite and aragonite, and that the aragonitic fraction was dissolved. This corresponds to the bimineralic composition of the byssus in modern anomiids (Pujol et al. 1970; Yamaguchi 1998). However, there is a conspicuous gap in the fossil record of preserved anomiid byssi across the Palaeogene and Neogene where only the byssal etchings are known, suggesting a non-mineralised or purely aragonitic byssus during this time interval. Only in rare cases, the calcitic body fossils of the trace forming anomiids were preserved in situ (Figs. 5F–H, 6C, E), but preservation was too poor to allow a confident taxonomical assessment.

## Palaeobiology and palaeoecology

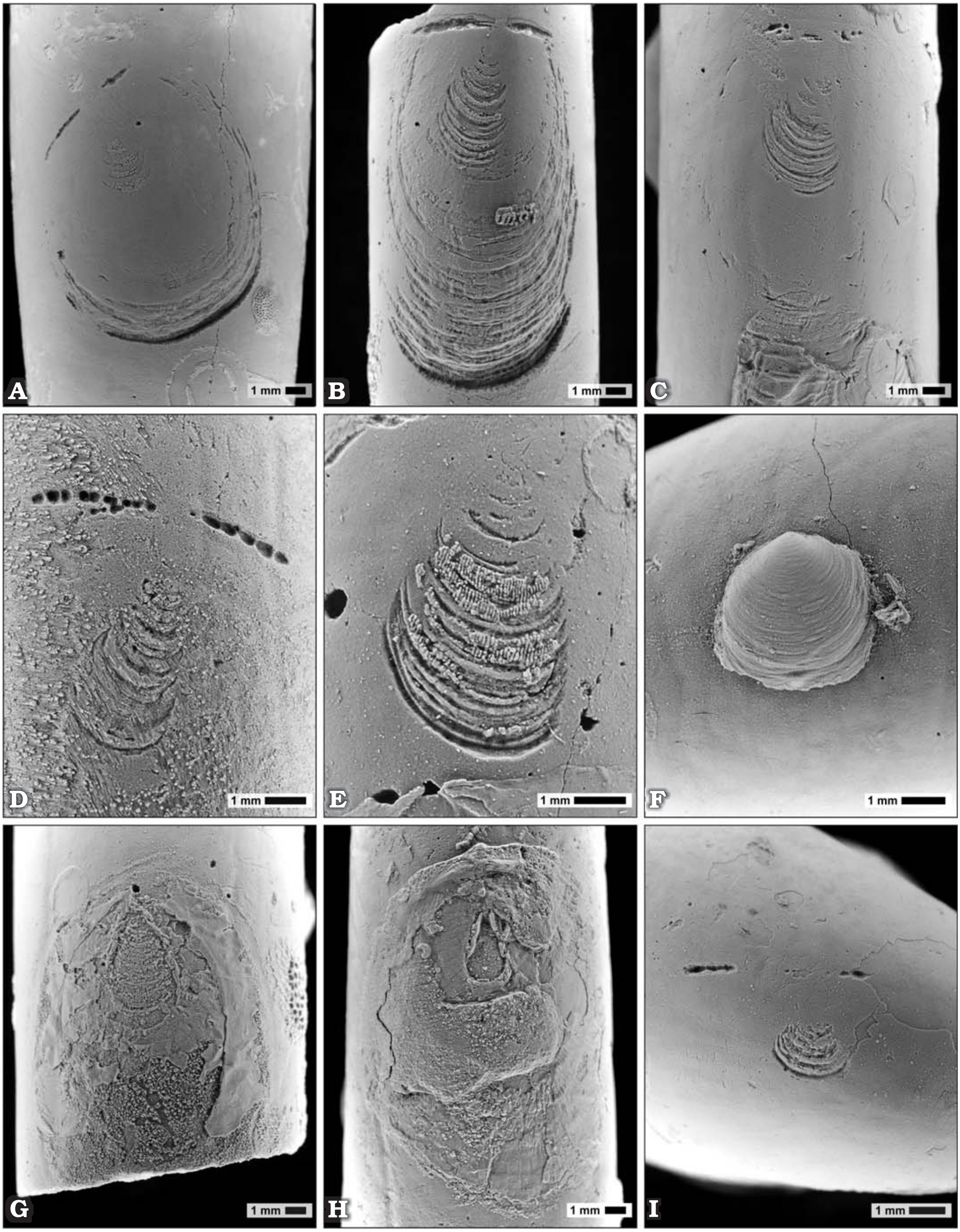
*Growth, shape and substrate/shape relationships*.—In all sampled localities, the trace-making anomiids clearly favoured belemnite rostra as substrate for settlement (Fig. 4A). In the Maastrichtian chalk of Rügen, 85.2% of the traces were found on belemnites (e.g., Figs. 5, 6A), followed by pycnodontid oysters (7.4%; Fig. 6B), terebratulid brachiopods (4.0%; Fig 6C, D), echinoids (2.7%; Fig. 6E), and inoceramids (0.7%; Fig. 6F). It should be noted, however, that our study only considers calcitic biogenic hardparts as potential substrates for anomiids. Because of the prevalent diagenetic loss of aragonite in the chalk facies it is not possible to evaluate the occurrence of anomiids and their traces on purely aragonitic shells, e.g., those of gastropods and ammonites.

The varying outline of *C. eccentricus* reflects the outline of the anomiid shell and is controlled by the size and shape of the substrate. Where growth of the anomiid shell was not obstructed (e.g., when it settled on the valves of large pycnodonts), the outline is almost circular. Where belemnites act as substrate for up to five traces (Fig. 4D), lateral growth is restricted by the elongate and cylindrical morphology of the rostrum. Here, the growth of the anomiid valve, as indicated by the corresponding trace, shows a clear preference for the central part of the rostrum (Fig. 4E), and follows the longitudinal axis of the belemnite (Fig. 4F). During growth, space becomes more restricted, resulting in a change from a circular (Fig. 5A) towards a more elongate and oval outline (Fig. 5B). However, the anomiid larvae did not always attach themselves in the preferred final growth direction, but were able to change direction in early life stages as indicated by a curved growth axis (Figs. 5A, 7A). The comparison of early and late stages of the traces reveals pronounced allometric growth of the trace-producing anomiids with a more dorso-ventrally elongated shell in late growth stages (Fig. 5F, I).

**Competition**.—From the spatial relationship between *C. eccentricus* and body fossils of other encrusting organisms, it can be inferred that space for settlement was at least occasionally a limiting factor and anomiids competed for space with both, fellow members of the species and other epibionts. Although most belemnite rostra from Rügen only exhibit a single attachment trace of *C. eccentricus* (77.3%), densely spaced multiple infestations also occurred. A maximum of five traces, each produced by an individual anomiid bivalve, were counted on a single belemnite rostrum (Fig. 4D). We observed overgrowth, displacement, and growth obstruction between *C. eccentricus* and cheilostome bryzoans, serpulid polychaetes, other epibiontic bivalves (*Atreta nilssoni*, *Gyropleura ciplyana*), octocorals, and scleractinian corals (*Coelosmila excavata*) (Fig. 6B, D, H, I). Additionally, endolithic organisms such as the producer of the trace fossil *Dendrina* were occasionally overgrown (Fig. 3). Superimposition of *C. eccentricus* on other epibionts, and vice versa, may also represent temporal successions instead of interspecific competition (Fig. 6I). These examples emphasise the importance of biological hard parts as "benthic islands" within soft-bottom communities, providing space, although limited, for recruitment and settlement of a diverse hard-substrate community. Belemnite rostra in particular littered the bottom of the chalk sea in high numbers and matched the needs of anomiid bivalves as a substrate for recruitment and life. Belemnite rostra possess a smooth surface and are composed of dense calcite, thus being suitable for etching, and are heavy enough not to sway around in modest bottom currents.

**Predation**.—Biting traces found on belemnite rostra associated with *C. eccentricus* indicate that anomiids served as diet

Fig. 5. Morphology of *Centrichnus eccentricus* Bromley and Martinell, 1991, anomiid bivalve attachment trace on belemnite substrates from the Lower Maastrichtian, Jasmund, Rügen, Germany (except D, F, I). **A**. Subcircular outline of a complete specimen (MB.W3075). **B**. Strongly elongate and deeply etched complete specimen (MB.W3076). **C**. Faintly etched complete specimen (MB.W3077). **D**. Series of etched pits forming anterior margin of trace (MB.W3078; Campanian, Misburg, Germany) **E**. Byssus attachment trace of preserved remains of calcified byssus (MB.W3079). **F**. Juvenile anomiid bivalve body fossil (MB.W3080; Maastrichtian, Kronsmoor, Germany). **G**. Right valve of anomiid bivalve partly preserved in situ on attachment trace visible through the byssus gape (MB.W3081). **H**. Left and partly preserved right valve of trace producing anomiid (MB.W3082). **I**. Immature trace illustrating allometric growth of anterior margin vs. byssus attachment (MB.W3083; Maastrichtian, Haccourt, Belgium). →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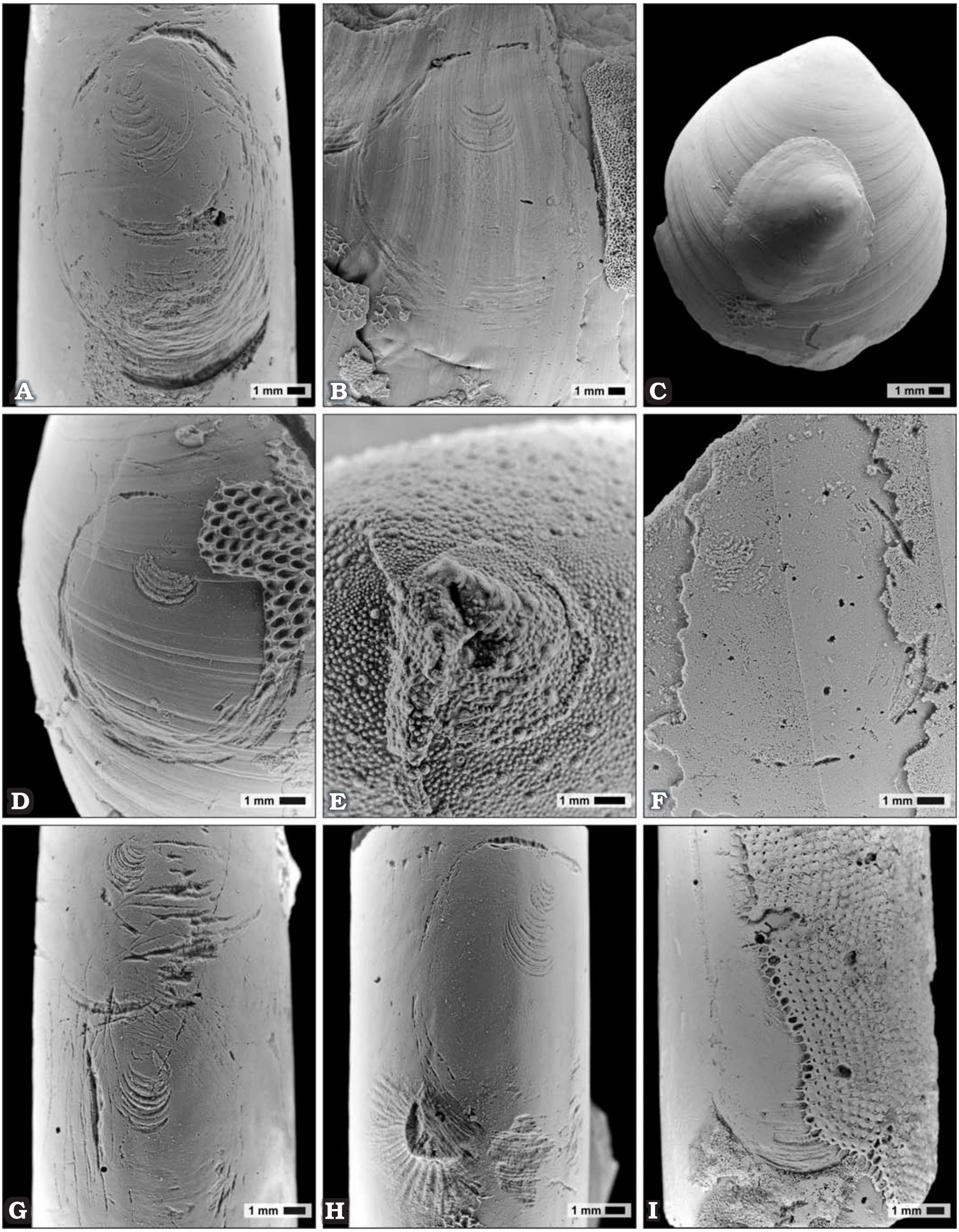
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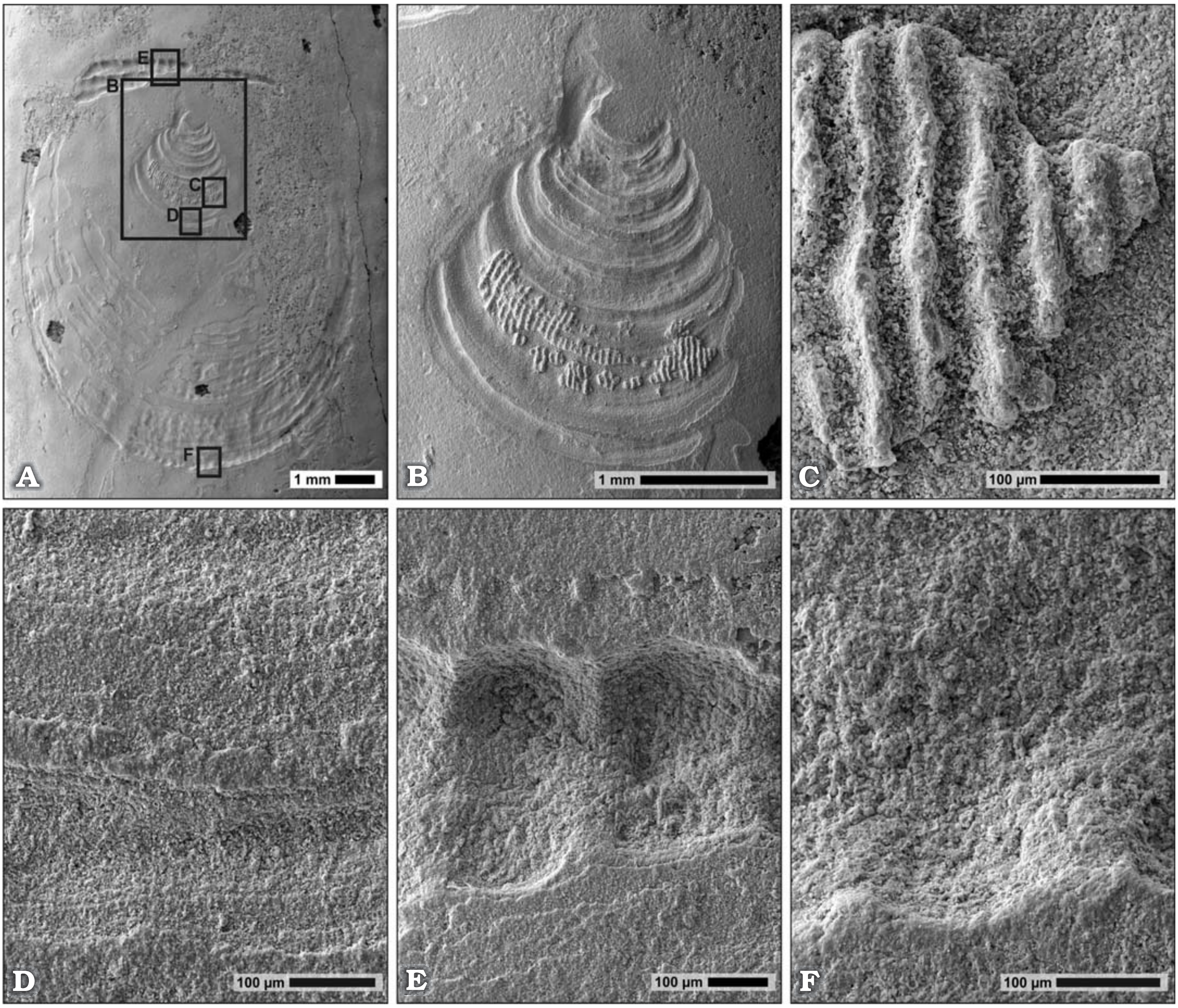

Fig. 7. SEM images illustrating details of *Centrichnus eccentricus* Bromley and Martinell, 1991, anomiid bivalve attachment trace on a belemnite from the Lower Maastrichtian, Jasmund, Rügen, Germany (MB.W3084). **A**. Complete morphology overview. **B**. Byssal attachment trace with preserved remains of calcified byssus. Close-up of calcified byssus (**C**), byssus attachment grooves (**D**), pits forming the anterior margin (**E**), posterior marginal groove (**F**).

for durophagous predators, most probably teleostean fishes. The shape and arrangement of the biting traces (Fig. 6G) indicate that a predator possessing sharp and pointed teeth has torn apart the bivalve from the substrate. Martin and Fox (2007) reported a durophagous mosasaur (*Globidens*) with a preserved gut content consisting mainly of anomiid shells. As a possible response to predation pressure, chalk anomiids may have evolved the deeply etched suture along the outline of the shell, providing firm attachment to the substrate as an effective defence mechanism against shell-crushing enemies

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← Fig. 6. Substrate types and biotic interactions between *Centrichnus eccentricus* Bromley and Martinell, 1991, producing anomiid bivalves and predators and competing epibionts in the Lower Maastrichtian, Jasmund, Rügen, Germany (except C, E). **A**. Trace on belemnite, the obliquely orientated anterior margin indicates change of growth direction in an immature state (MB.W3085). **B**. Two closely spaced traces on the oyster *Pycnodonte vesicularis* Lamarck, 1806 competing for space with a calcareous sponge (MB.W3086). **C**. Anomiid body fossil on the terebratulid brachiopod *Carneithyris subcardinalis* (Sahni, 1925) (MB.W3087; Maastrichtian, Kronsmoor, Germany). **D**. Trace on terebratulid brachiopod overgrown by a cheilostome bryozoan colony (MB.W3088). **E**. Body fossil of a juvenile anomiid attached to the test of the holasteroid echinoid *Cardiaster granulosus* Goldfuss, 1816 bio-immuring the echinoid's tuberculation (MB.W3089; Maastrichtian, Lixhe, Belgium). **F**. Faint trace and calcified byssus remains on inoceramid valve (MB.W3090). **G**. Two *C. eccentricus* traces on belemnite and predatory biting traces, probably produced by a teleostean fish (MB.W3091). **H**. Holdfast organ of scleractinian coral *Parasmilia centralis* (Mantell, 1822) abraded by anomiid tracemaker (MB.W3092). **I**. Trace indicates anomiid bivalve successfully suppressing growth of calcareous sponge. Note subsequent post-mortem overgrowth by a cheilostome bryozoan (MB.W3093).

such as crustaceans and small teleosts (see also below). Because of its synchrony with an intensification of predation pressure in marine environments in the Late Cretaceous (Vermeij 1987), we interpret this phenomenon to be an anti-predatory response of anomiid bivalves.

**Etching of the substrate and its function**.—The characteristic morphological features of *C. eccentricus* bear implications for the behaviour of the anomiid bivalves that produced the studied traces and the effectiveness of the attachment mechanism. Primarily, attachment involves etching of the substrate surface and subsequent cementation by a calcified byssus (Bromley and Martinell 1991; Bromley 1999). In addition, the substrate is also etched along the outline of the anomiid bivalve, as indicated by the successive positions of troughs in the substrate that correspond to the growing shell margin. These chemical etchings in a carbonate substrate were possibly produced by secretions from glands along the mantle edge of the bivalve (cf. Morton et al. 2011). The etchings along the anterior margin of the trace were probably induced by the supradorsal extensions of the mantle lobes that are characteristic of anomiid bivalves (Yonge 1977). Another organ of anomiids known to be capable of carbonate dissolution is the foot. Projections of its soft tissue, which is responsible for byssus formation, produce holes in the calcified byssus through which adhesives are supplied to the bottom of the byssal apparatus (Yamaguchi 1998). However, because these holes are formed by the proximal part of the foot and the foot of adult anomiids is reduced (Yamaguchi 1998), it is much more likely that the observed etchings along the distal valve margins were generated by the mantle margins. The smooth micromorphology, apparent from SEM examination (Fig. 7), supports a chemical etching process but additional mechanical abrasion along the shell margins is conceivable.

The substrate etchings along the shell margins provide a tight fit and stability of the upper (left) valve when pulled firmly onto the substrate by the byssal retractor muscle. In combination with further muscles (see Yonge 1977), the interlocking of the shell margin with etchings in the substrate conveys increased shear resistance when the valves are closed. Thus, enhanced stability is provided to withstand torsion induced by hydrodynamic force or predators. The impression of a planar shell into a cylindrical rather than a planar substrate results in deeper cutting and thus, even more effective shear resistance, providing a potential explanation of belemnites being the preferred substrate.

**Did Cretaceous anomiids possess a "pseudo-hinge"?**—The anterior linear to slightly arcuate arrangement of small pits or grooves in the substrate (Fig. 5B, D, I; Fig. 7A, E) is somewhat reminiscent of the sockets of a taxodont bivalve hinge. The anomiids have lost a marginal hinge (Yonge 1977), but is it feasible that the function of a hinge is accomplished by the interlocking of the dorsal shell margin of the upper valve and the substrate, thus forming a "pseudo-hinge". This scenario seems unlikely because it requires that shell projections at the dorsal shell margin of the left (upper) valve articulate with corresponding pits in the substrate. Evaluating the existence of such hypothetical pseudo-teeth was not possible with the few poorly preserved anomiid body fossils found in situ in the present material. Anyway, it is difficult to conceive how the calcium carbonate of the substrate is dissolved selectively and calcite is segregated as exactly corresponding projections of the dorsal shell margin. Also, the position of the rotation axis of the opening valves is defined by the position of the ligament on a stalked crurum (Fig. 2D). A shift to a new rotation axis, i.e., the pits and grooves forming the anterior part of the trace, is impractical for mechanical reasons (Fig. 2D).

# Conclusions

- The ichnospecies *Centrichnus eccentricus* is an attachment trace produced by anomiid bivalves. Based on 468 specimens from the Late Cretaceous of central Europe, new morphological characters have been identified, resulting in an emended diagnosis of the ichnotaxon.
- The stratigraphical range is extended to the oldest occurrence of *C. eccentricus* now recorded in the Turonian stage of the Late Cretaceous.
- In the Late Cretaceous, *C. eccentricus* exhibiting the full set of characters dominate, whereas in the Paleogene and Neogene, *C. eccentricus* largely consists of the byssus imprint only. This suggests different anomiid tracemakers for Cretaceous and Cenozoic times. Preserved remains of the calcified byssi suggest a bimineralic (i.e., calcitic and aragonitic) composition of anomiid byssi in the Cretaceous, analogue to extant taxa, whereas Paleogene and Neogene anomiids most likely possessed non-mineralized and/or purely aragonitic byssi.
- In all *C. eccentricus* traces, a byssus attachment structure is etched into the substrate. In Cretaceous traces, the substrate is also etched along the outline of the anomiid bivalve, probably by glands along the mantle edge, providing a tight fit and stability of the upper valve and increased shear resistance when the valves were closed.
- In the studied localities, anomiid bivalves utilized a variety of calcitic biogenic hard substrates for settlement with a clear preference for belemnites.
- Rare observation of predation traces associated with *C. eccentricus* indicate that Cretaceous anomiids seldom served as diet of shell crushing vertebrate predators. The attached epibiotic life style may thus have been an effective escape strategy from predation, adding to the increased shell stability.
- Observed growth obstructions and mutual overgrowth are expressions of competition for settlement space between anomiids and other epibionts, suggesting that substrate availability was a controlling factor in the chalk sea and emphasizing the role of "benthic islands" in marine soft-bottom communities.

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