

A symbiotic association of a boring polychaete and an echinoid from the Late Cretaceous of Germany

MAX WISSHAK and CHRISTIAN NEUMANN



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From the Early Maastrichtian white chalk of Rügen Island (N Germany), a specimen of the echinoid *Echinocorys ovata* featuring 27 boring traces of the ichnogenus *Caulostrepsis* is described. Individual traces are shallow to moderately deep U-shaped depressions and show distinct regeneration textures evidencing a *syn-vivo* infestation. All traces are located on the plastron between the peristome and periproct of the host echinoid, indicating an adaptation of the trace maker by choosing the most advantageous position of the specific host. The traces are attributed to the work of boring spionid polychaetes (*Polydora* complex), grounded on the close morphological resemblance with initial borings of Recent polydorids. This is the first evidence for a possible association of a boring polychaete not only with an echinoid but with an echinoderm in general. The symbiotic relationship was commensalistic in nature with the spionid probably taking advantage of organic matter resuspended by the echinoid's locomotion and feeding activity and benefiting from effective shelter. For the host echinoid, the association was moderately harmful. The soft bottom environment of the chalk sea provided very limited hard substrate ecospace for settlers and bioeroders, available only in form of biogenic structures. *Echinocorys* was a dominant component of this benthic community and can be considered as a suitable host for symbiotic interactions because of its size and assumed longevity.

Key words: Trace fossils, Polychaeta, Spionidae, *Caulostrepsis*, *Polydora*, *Echinocorys*, bioerosion, commensalism, Maastrichtian.

Max Wissihak [wissihak@pal.uni-erlangen.de], Institute of Palaeontology, Loewenichstr. 28, D-91054 Erlangen, Germany;

Christian Neumann [christian.neumann@museum.hu-berlin.de], Museum für Naturkunde, Institute of Palaeontology, Humboldt University Berlin, Invalidenstrasse 43, D-10115 Berlin, Germany.

Introduction

Polychaetes range among the most abundant and diverse marine metazoans in Recent benthic communities. Although most of them are free living, many set up symbiotic (*sensu* mutualism + commensalism + parasitism) associations with other invertebrates. For instance, commensal polychaetes are known from associations with more than 500 different host species (Martin and Britayev 1998). Echinoderms are amongst the preferred hosts (more than 200 associations), because they provide effective protection for the polychaete. Surprisingly, none of the known polychaetes infesting echinoderms belong to the widespread group of boring spionids (*Polydora* complex in the family Spionidae) whose fossil and Recent borings are ubiquitous in calcareous and other hard substrates (e.g., Blake and Evans 1973; Bromley and D'Alessandro 1983; Sato-Okoshi 1999). Among the spionids, 35 species are known to have symbiotic relationships with invertebrate taxa (molluscs, sponges, cirripeds, and bryozoans). Owing to the shell damage they cause in commercial bivalve aquacultures, they are often regarded as parasites although they do not directly utilize host resources and should thus

better be considered as commensals (Martin and Britayev 1998). In the following account, fossil evidence for the first occurrence of a *syn-vivo* relationship between a polychaete and an echinoderm is described with the example of polydorid spionid borings—known as ichnotaxon *Caulostrepsis* Clarke, 1908—on the basal side of a Late Cretaceous echinoid.

The holasteroid echinoid *Echinocorys* is a prime candidate for studying symbiotic relationships in the fossil record. This deposit feeder was the dominant macrobenthic taxon in the chalk sea ecosystem for more than 30 million years, before its Mid-Palaeocene extinction. Its relatively large size and longevity promoted an encounter with parasites or commensals. Moreover, recognition of symbiotic associations in fossil echinoids is favoured by the nature of the echinoderm skeleton which is covered by an epithelium and thus enabling it to react directly (by overgrowth, embedment or regeneration) to lesions caused by parasite attacks or commensal attachment. Finally, the excellent preservation in the chalk and its excessive availability in many collections makes *Echinocorys* an excellent target for studying fossil biotic interactions (e.g., Neumann 2003; Donovan and Jagt 2004; Neumann and Wissihak in press).

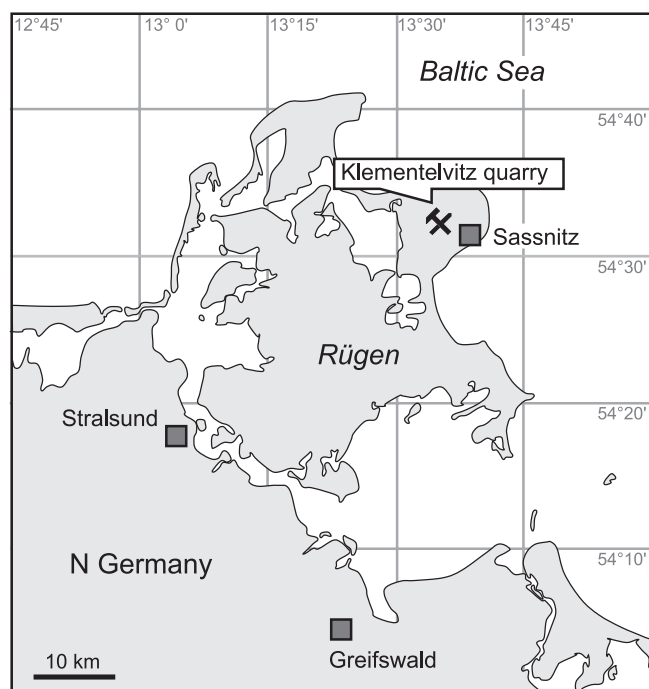


Fig. 1. Map of Rügen Island (N Germany) in the southern Baltic Sea and the location of the chalk pit "Klementelvitiz", where the *Echinocorys* in question was sampled in Early Maastrichtian strata.

Institutional abbreviation.—MB, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany. Collection number MB. E5713. The Recent material figured in the paper is housed at the Institute of Paleobiology, Erlangen, Germany—no collection numbers.

Material and methods

The specimen presented herein was a unique finding encountered in the course of an extensive query for parasite traces on the tests of *Echinocorys* during which several thousand echinoids were studied in museum and private collections. The host echinoid in question is an *Echinocorys ovata* (Leske, 1778) collected randomly in the chalk pit "Klementelvitiz" located on the northeast of Rügen Island in Northern Germany (Fig. 1). The quarry exposes a section of the higher Early Maastrichtian (zones of *Belemnella summensis* to *Belemnella fastigata*). The echinoid measures 97 mm in its length axis. The oral surface, two thirds of which is preserved, provides an excellent display of the coronal characters and delicate details of the polychaete borings and their regeneration textures in form of primary and miliary tubercles.

For further detail on the stratigraphy and palaeontological inventory of the Early Maastrichtian white chalk of Rügen, see Frenzel (2000) and Reich and Frenzel (2002).

Digital imaging of the echinoid and the boring traces was undertaken after coating with ammonium chloride. In order to reveal the fine details of the borings, SEM images were taken from latex casts.

Measurements of the length and maximum width of the traces were taken with the aid of precision sliding calipers and the angle of the traces mean axis in relation to the echinoids median axis was determined with a set square under the stereo microscope. For all three quantifications, the mean and standard deviation was calculated. The course and depth of the traces was judged in a semi-quantitative manner applying three classes each, for which the per cent abundances were then determined.

The recent material for comparison stems from calcareous substrates (micritic limestone and mollusc shells) which were deployed for one year in 1 m water depth in the cold-temperate setting of the Kosterfjord (SW Sweden) during the course of a two-year experimental bioerosion study (see Wisshak et al. 2005 for further detail). The substrate surface was photographed under a stereo microscope and SEM images of the borings were taken from epoxy resin casts after gold sputter coating. The *Polydora* specimen was extracted in the laboratory from a bivalve shell fixed in formol.

The boring traces

The *Echinocorys ovata* specimen of interest exhibits a total of 27 fossil boring traces, all of which are positioned on the basal surface. They are exclusively positioned on the plastron plates of interambulacrum 5 between the mouth (peristome) and the anal region (periproct) of the echinoid (Fig. 2, Table 1). The density of the traces is slightly increasing from the peristome towards the periproct. Individual traces are 1.6 to 4.9 mm in length with a mean of 3.4 mm. The maximum width of the traces is in the range of 0.3 to 0.7 mm with a mean value of 0.6 mm. About half of the traces (48%) follow a more or less straight course with respect to the plane of the substrate, while 41% are slightly curved and 11% display a strong curvature. Only one trace (#26) describes a complete U-turn. All traces exhibit prominent regeneration textures in form of primary and secondary tubercles. The penetration of the traces ranges from very shallow depressions (37%) to shallow (26%) and moderately deep (37%) excavations. Maximum depth of the traces is close to 2 mm, which is equivalent to more than half of the test thickness (measured with 3.5 mm in this coronal area). None of the traces completely penetrates the echinoid test. Measurements of the angle of the traces main axis to the echinoids median axis yields parallel to oblique angles in a random distribution with no significant maximum ($41^\circ \pm 28^\circ$).

On a SEM scale, the latex cast prepared from the traces bears shallow U-shaped and rounded intrusions (Fig. 3). The main gallery enters and exits the substrate in a tangential manner and is rapidly inclining towards the point of deepest relief. The orientation of the traces main plane is oblique or inclined in various angles in relation to the substrate surface. Between the limbs of the trace, a moderate axial depression is developed.

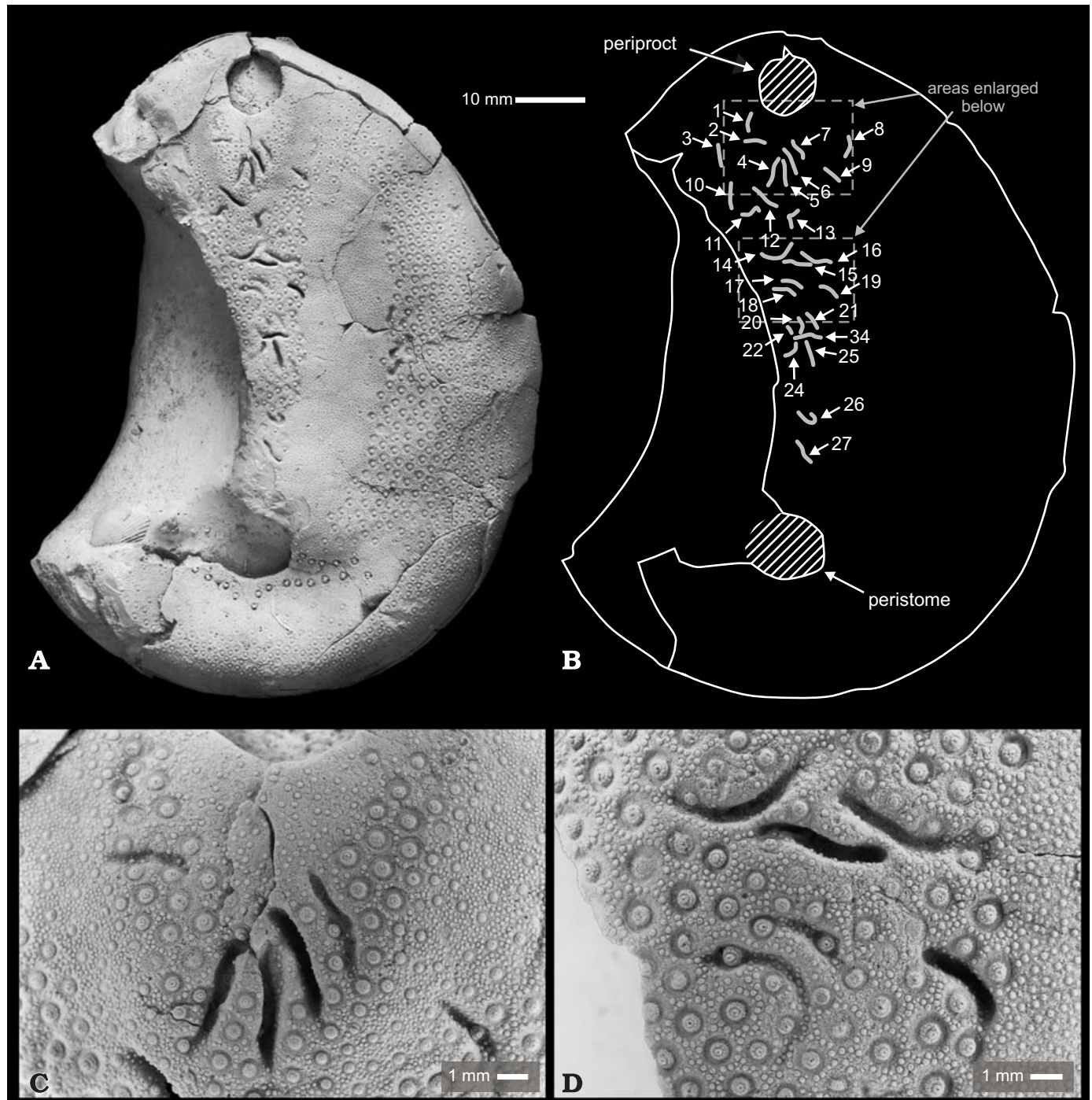


Fig. 2. Oral surface of an *Echinocorys ovata* (Leske, 1778) (# MB.E 5713) featuring *syn-vivo* polychaete boring traces (Early Maastrichtian; “Klementelvitze” quarry, Rügen Island, N Germany). **A.** Overview of the well preserved oral surface with 27 *Caulostrepsis* isp. traces, all of which are located in the interambulacral plates of the plastron. **B.** Schematic sketch of the basal surface indicating the position and number of the traces and the areas enlarged in C and D. **C.** Close-up of several traces in close proximity of the periproct. **D.** Close-up of several traces illustrating their variability in length, boring depth and curvature. Note the prominent regeneration texture exhibited by all traces.

Discussion

Ichnotaxonomy.—Corresponding traces are well known from the Recent as well as the fossil record and are comprised under the ichnogenera *Caulostrepsis* Clarke, 1908 and

Maeandropolydora Voigt, 1965 (see Bromley and D’Alessandro 1983 for a review). *Caulostrepsis* addresses simple U-shaped borings of various kinds whereas *Maeandropolydora* comprises more complex multiple U-shaped and occasionally branching boring systems with often well developed cylindrical galleries. Both ichnotaxa are found in many dif-

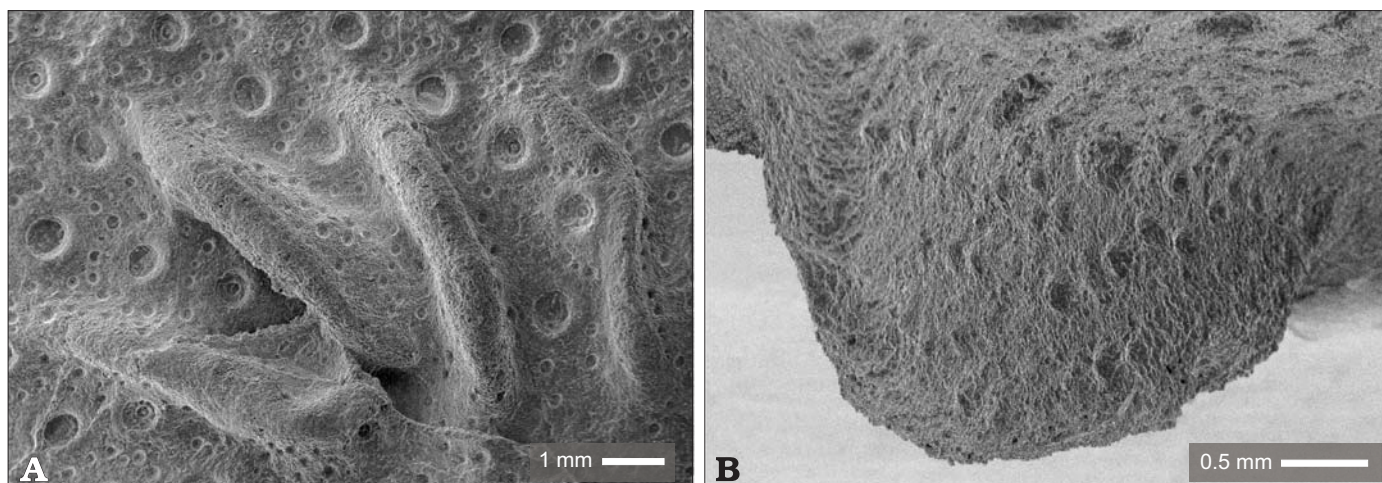


Fig. 3. SEM images of a latex cast prepared from the trace-bearing plastron area of the *Echinocorys ovata* (Leske, 1778) echinoid (Early Maastrichtian; "Klementelwitz" quarry, Rügen Island, N Germany). **A**. Traces # 4–7 oriented sub-parallel to each other in close proximity to the periproct **B**. Lateral view of the moderately deep U-shaped trace # 12 showing a distinct regeneration texture in form of primary and miliary tubercles.

Table 1. Length and width of the individual traces (# indicated in Fig. 2B), qualitative information on their curvature and depth of penetration, and the angle of the traces length axis relative to the echinoids median axis.

#	length [mm]	max width [mm]	straight	moderately curved	strongly curved	very shallow	shallow	moderately deep	angle from median axis
1	3.3	0.7	X			X			10
2	3.0	0.5	X			X			88
3	2.9	0.5	X			X			15
4	3.4	0.6	X					X	18
5	4.0	0.5	X					X	0
6	3.4	0.4	X					X	22
7	2.7	0.5		X			X		27
8	3.0	0.4	X			X			5
9	4.0	0.3		X			X		48
10	4.5	0.4	X			X			3
11	2.1	0.6		X			X		54
12	4.4	0.6	X					X	48
13	3.4	0.7			X			X	31
14	4.9	0.7		X				X	73
15	4.1	0.6	X					X	80
16	4.8	0.8		X			X		69
17	2.7	0.7		X		X			67
18	3.1	0.6			X	X			80
19	2.8	0.6		X				X	48
20	1.8	0.7		X		X			23
21	2.3	0.6	X			X			18
22	1.6	0.7	X			X			23
23	3.8	0.6		X				X	85
24	4.4	0.5	X					X	10
25	1.7	0.6		X			X		38
26	4.3	0.6			X		X		84
27	4.1	0.6		X			X		39
	3.4 ± 0.9	0.6 ± 0.1	48%	41%	11%	37%	26%	37%	41 ± 28

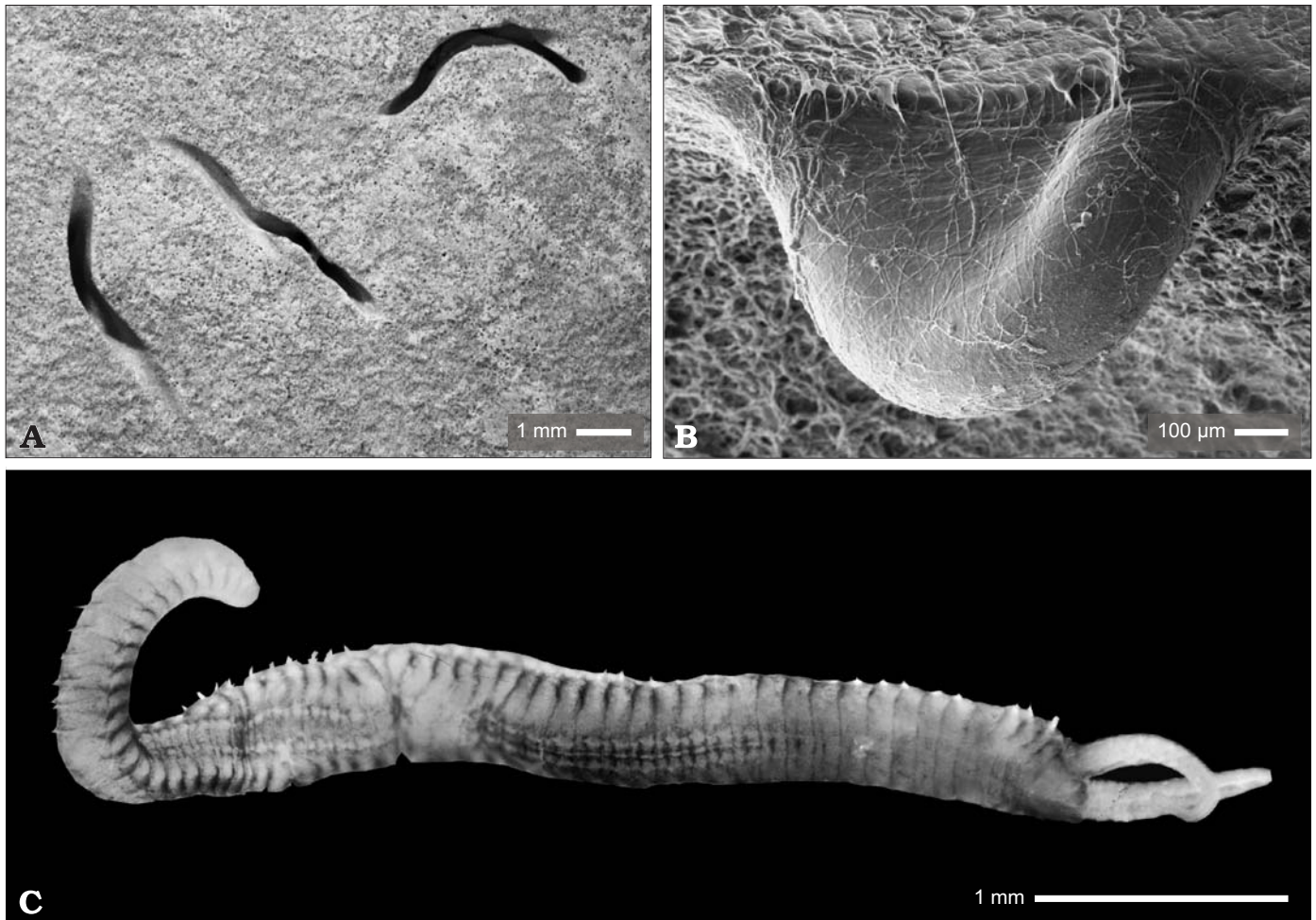


Fig. 4. A. Recent *Polydora* sp. boring traces recorded in an artificial limestone substrate deployed in the Swedish Kosterfjord area during a bioerosion experiment. B. SEM image of an epoxy resin cast of an initial *syn-vivo* *Caulostrepsis* isp. boring taken from a *Littorina littorea* gastropod shell. C. The spionid polychaete *Polydora* sp. isolated from a bivalve shell. (Recent material stored at the Institute of Palaeontology, Erlangen).

ferent calcareous and non-calcareous hard substrates. Their fossil record reaches back to Palaeozoic times (Bromley 2004).

The present traces are best assigned as *Caulostrepsis* isp., since a confident ichnospecies distinction is not feasible in case of early stages of trace development. In some of the moderately deep and accordingly more mature variations of the present material, it appears that the traces are somewhat narrowing above the point of deepest relief, resulting in an elongated restricted aperture and respective moderate axial depression of the trace. This indicates a relation closest to *Caulostrepsis taeniola* Clarke, 1908 and *Caulostrepsis cretacea* (Voigt, 1971). Progressive (non-preserved) stages of the traces possibly would have developed a more distinct vane and dumbbell shaped aperture diagnostic for the former ichnospecies.

The trace maker.—As for the trace maker of the present material, the close similarity to Recent boring traces produced by polychaete annelids of the family Spionidae with its most important representative *Polydora* Bosc, 1802, al-

lows an interpretation of the traces as the work of boring polydorids with a fair degree of confidence. The morphology of the borings can be compared for instance with mature borings of *Dipolydora commensalis* (Andrews, 1891), which is today only known to infest gastropod shells inhabited by hermit crabs, or initial borings of various other species such as *Polydora ciliata* (Johnston, 1838).

Corresponding traces from a Recent marine environment were recorded in calcareous substrates deployed during the two-year experimental bioerosion study in the Kosterfjord area in SW Sweden (Wisshak et al. 2005). There, very similar traces were encountered already after one year of exposure in micritic limestone plates (Fig. 4A). SEM images of epoxy resin casts of corresponding traces in a *Littorina littorea* gastropod shell from the same locality (Fig. 4B) further underlines the close morphological affinity to the Cretaceous material. From one boring, a spionid polychaete of the genus *Polydora* was extracted in the laboratory (Fig. 4C), yielding direct evidence on the actual trace maker.

Given this close morphological similarity and considering the extensive fossil record of such borings back to the

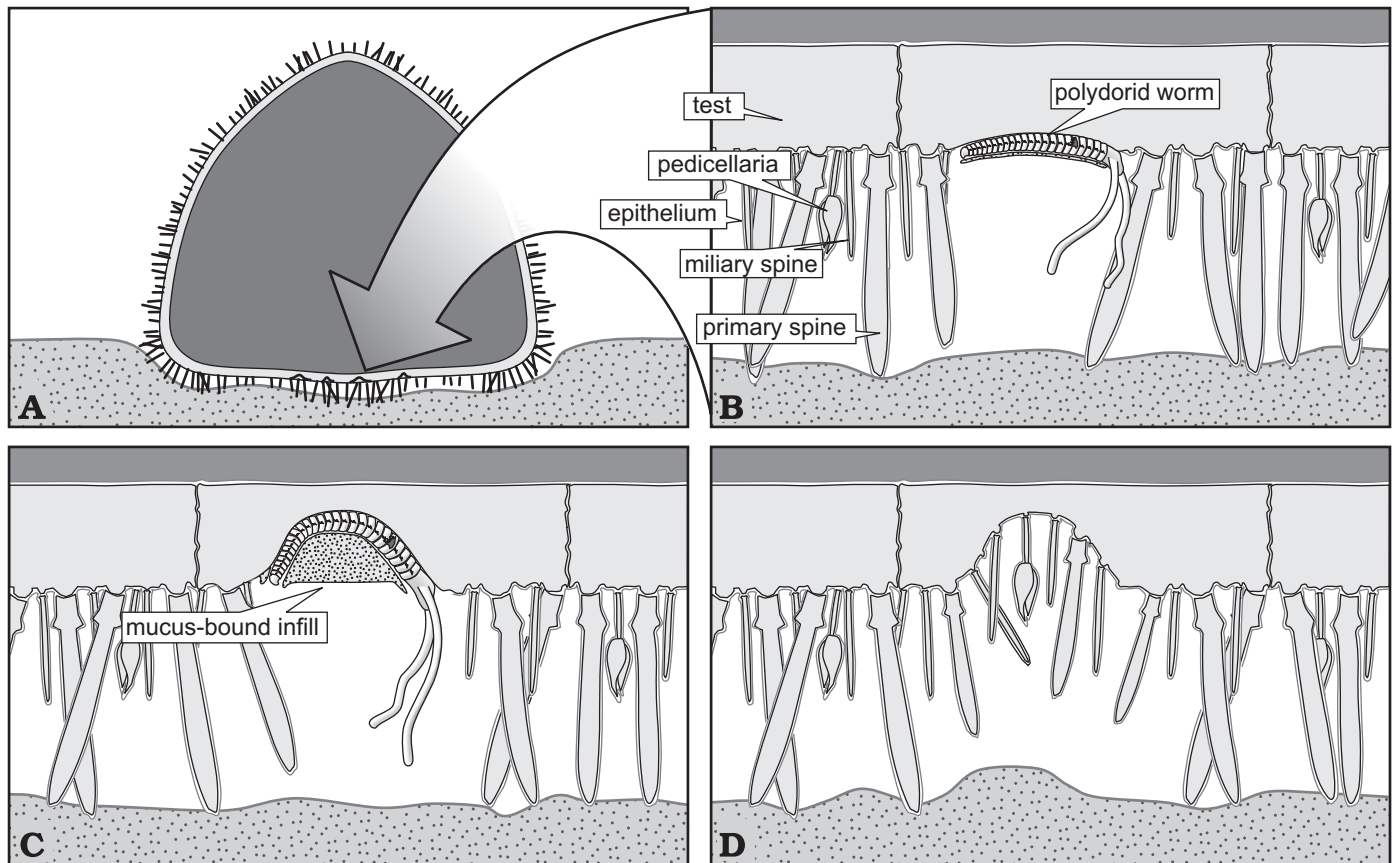


Fig. 5. Schematic sketch of the echinoid / polychaete interaction and the development of a *Caulostrepsis* boring. **A.** Position of the commensal polychaete on the sheltered basal side (plastron) of the echinoid, taking advantage of the hosts ciliary current and sediment resuspension due to locomotion. **B.** A polydorid polychaete producing an initial shallow depression on the test surface. **C.** The polydorid progressively deepens the excavation; the presence of a mucus-bound infill between the limbs as it is known for some Recent polydorids, is hypothetical. **D.** Abandoned trace and regeneration texture developed by the living echinoid skeletal tissue. The mode of penetration is based upon Söderström (1923) and Blake and Evans (1973).

Palaeozoic, we feel reasonably confident in attributing the Cretaceous traces encountered in the *Echinocorys* test to the work of a polydorid spionid. Consequently, this is the first record of a *syn-vivo* association of a boring polychaete not only with an echinoid but with an echinoderm in general.

The trace formation.—The mode of penetration of polydorid worms has been controversial since the late 19th century when the first theories emerged (Lankester 1868). Both, boring by mechanical means utilising specialised heavy spines of the 5th setiger as well as chemical penetration with the aid of acetic acid secretion have been suggested (see review in Blake and Evans 1973). It is now established that the boring mechanism most likely bears a combination of chemical and mechanical components (Van der Pers 1978). The relative dominance of either mode of trace formation is probably considerably dependant on the species involved and on the substrate properties.

The trace making worm followed a lateral mode of penetration as opposed to an axial boring mechanism (*sensu* Bromley and D'Alessandro 1983). Once the polychaete larvae had overcome the echinoids defence mechanism and undergone metamorphosis on the basal plastron area (Fig. 5A),

the worm was oriented parallel to the substrate and formed a shallow groove (Fig. 5B). Thereby the worm did not adopt a preferred orientation (indicated by the random distribution in orientation lacking a significant maximum). The polydorid worm then progressively deepened the boring, resulting in a U-shaped excavation (Fig. 5C). Whether the worm was protected by an agglutinated tube during the initial phase or the presence of a mucus-bound lining of the tunnel and infill between the limbs such as formed by some Recent polydorids (e.g., Söderström 1923; Blake and Evans 1973) can not be deduced from the present material. After the trace maker ceased or left the boring, the echinoids regeneration mechanism commenced and new primary as well as miliary spines were developed (Fig. 5D).

The nature of the symbiotic relationship.—Polydorids are capable of feeding either on seston (suspension feeding) or on detritus (deposit feeding). Many species switch between these two modes according to the local conditions for instance in terms of current velocity or particle flux (Wildish and Kristmanson 1997; Hentschel 2004). With a position on the basal surface of the present *Echinocorys* host, principally both modes were applicable. The polychaete probably took

advantage of organic matter resuspended by the echinoids locomotion and feeding activity. The increasing density of borings towards the periproct may be explained by additional coprophagous feeding or by benefiting from the ciliary current provided by the fasciole-like structure surrounding the periproct (Stephenson 1963). A concentration of polydorids in areas close to the potential source of food is also well documented from Recent associations as for instance in case of *Dypolydora* and its host bivalve *Gomphina* in Japan (Sato-Okoshi 1999).

The restriction of the traces to the interambulacral region of the plastron between the peristome and periproct witnesses a highly selective behaviour of the trace maker or its respective larvae, choosing the most advantageous position on the host. In contrast to the periplastral plates, the interambulacral area of the plastron has a dense cover of primary spines, providing superior interspace between spines as well as between the test and the underlying sediment (Fig. 5). However, no traces were observed in the laterobasal interambulacral regions despite similar tuberculation and spine canopy. A position on the basal surface grounded in optimised protection, is regarded as typical for echinoderm commensals in general and especially for other (non-boring) polychaetes (Martin and Britayev 1998).

While the polychaetes utilised the echinoid as a mobile host, benefiting from shelter and food availability, we need to evaluate the effect of the polydorid infestation in turn on its *Echinocorys* host. Both were deposit feeders, resulting in some degree of competition for nutrients. The borings contribute to a weakening of the echinoid test in analogy to boring polydorids that reduce shell strength of bivalves and consequently cause indirect mortality by facilitating predation (Bergmann et al. 1982). Also, by offering an entry for microbes to the soft tissues, the tube-dwelling may affect the echinoid's susceptibility to secondary infection. Moreover, the worms may have had a harmful impact on the host physiology because of a potential deviation of host energy towards worm-induced repair of test damage. Although this particular case was not lethal (as evidenced by the advanced regeneration structures), we see no advantage but only evidence for somewhat harmful effects on the host. In conclusion, it is indicated that the symbiotic relationship was neither parasitic nor mutualistic, classifying the polydorids as inquilistic commensals.

Whether this relationship was an aimed or rather fortuitous one is difficult to assess as there is evidence for either interpretation: A fortuitous association can be suspected, grounded on the pronounced rarity of these boring traces. In fact, only one among approximately 8000 *Echinocorys* tests examined by the authors show such traces. On the other hand, intensity and distribution of polydorid polychaete infestation may vary strongly even on a small scale depending on the local environmental circumstances (e.g., Almeida et al. 1998). However, further evidence for *Echinocorys* being a false host can be seen in the fact, that the present borings only reached an initial to moderately mature state, implying

unsuitable conditions even though the polychaetes were able to initially overwhelm the echinoids defence mechanisms at least for a short period of time. It can, however, not be ruled out that the traces are actually mature and were produced by a polydorid which is developing only shallow borings and lives within a mucus-bound sand tube or a canal generated within the host soft-tissue. Moreover, a fortuitous infestation is unlikely when taking the pronounced selective behaviour of the trace maker or its respective larvae into account, who chose the most advantageous position on the host (see above). This is strongly suggesting some degree of adaptation to the specific host. Also, the relatively high number of traces implies gregarious recruitment, which in turn provides further arguments for a symbiotic association because this behavioural pattern requires host recognition as for instance driven by specific chemical cues. Alternatively, the aggregate distribution could be explained by asexual reproduction via schizogamy following even a single-larvae infestation—a behavioural pattern known for instance for Recent *Polydorella* (Radashevsky 1996; Martin and Britayev 1998).

***Echinocorys*—a suitable host for boring polydorid polychaetes?**—Considering its comparatively large size, we can assume *Echinocorys* to be a long-living and slow-growing echinoid typical for a K-strategist in a relatively nutrient-deficient environment. Hence, *Echinocorys* is a suitable host for symbiotic interactions since it is prone to larval settlement or adult migration for a comparatively long period of time besides the fact that it provides superior potential living space if compared to small hosts. In contrast to the echinoid, polydorids exhibit a much shorter lifespan. For instance, the lifespan of *Polydora* in the temperate French Atlantic coast comprises only between 1 and 2 years (Ruellet 2004).

However, boring in a living echinoid test requires special skills for overwhelming the host's defence system. Generally, the epithelium covering all parts of the skeleton as well as pedicellariae and chemical cues serve to prevent parasite attacks and larval settlement of biofouling organisms (Janguoux 1990). The response of polydorid worms to dissolved chemical cues—such as those potentially released as defence mechanism by the host echinoid—is poorly understood as yet, but initial experiments indicate significant phagostimulatory or phagodepressing effects on some species (Ferner and Jumars 1999). In any way, the large number of other known symbiotic associations of echinoderms with (non-boring) polychaetes witnesses that infestation is principally achievable (Martin and Britayev 1998).

The floor of the chalk sea, consisting of hemipelagic calcareous nanoplankton ooze (mainly coccolithophorides and their remains) was characterised by oligotrophic bottom conditions and comparatively low megabenthos abundance (Jarvis et al. 2002). For bioeroders and settlers, the sea floor provided very limited hard ground ecospace which was available only in form of secondary biogenic remains and specifically calcareous skeletons. The deposit feeding *Echinocorys* often was the dominant component of these benthic communities

(Néraudeau and Villier 1997) and its dead tests were frequently subjected to biofouling and bioerosion as evidenced also on the very same echinoid test by the presence of encrusting serpulid worms. Although spionid polychaetes are generally known to bore also in dead substrates, the present trace maker chose an alive host instead of taking advantage of the more easy access to the many dead *Echinocorys* tests littering around on the seafloor. This fact provides further evidence for a symbiotic strategy of the trace maker.

Conclusions

The *Echinocorys ovata* specimen of interest features 27 randomly oriented fossil boring traces of the ichnogenus *Caulostrepsis*, positioned on the plastron between the peristome and periproct of the host echinoid. Individual traces are shallow to moderately deep U-shaped borings with a mean length of 3.4 mm at a mean width of 0.6 mm, and show distinct regeneration textures evidencing a *syn-vivo* infestation.

Based upon the close morphological resemblance with initial boring traces of Recent polydorid polychaetes of the family Spionidae, the present traces can be interpreted as a work of these boring polychaetes with confidence. Hence, this is the first record of a *syn-vivo* association of a boring polychaete with an echinoderm.

Once the polydorid larvae had overcome the echinoids defence mechanism and undergone metamorphosis, the worm followed a lateral mode of penetration and formed a shallow groove. The polydorid subsequently deepened the boring, resulting in a U-shaped excavation. The presence of an agglutinated tube or mucus-bound infill between the limbs remains hypothetical. After the trace maker ceased or left the boring, the echinoids regeneration mechanism commenced.

The nature of the symbiotic relationship can be addressed as commensalism. The facultative either suspension or deposit feeding polydorid probably took advantage of organic matter resuspended by the echinoids locomotion and feeding activity and additionally benefited from effective shelter. For the host echinoid in turn, the association was moderately harmful (competition for nutrients; weakening of the test; enhanced susceptibility to secondary infection; distress).

A fortuitous association could be seen grounded on the pronounced rarity of these boring traces and the fact, that they only reached an initial to moderately mature state. They may, however, actually be mature when produced by a spionid which is only developing shallow borings. On the other hand, strong evidence for a true symbiotic relationship and an adaptation to the specific host is given by the pronounced selective behaviour of the trace maker or its respective larvae, choosing the most advantageous position on the hosts plastron area.

For bioeroders and settlers, the oligotrophic soft bottom environment of the chalk sea provided very limited hard ground ecospace, available only in form of dead and alive biogenic structures. *Echinocorys* was the dominant compo-

nent of the macrobenthic community and can be considered as a suitable host for symbiotic interactions because of its size and assumed longevity. Even though boring in a living echinoid test requires special skills for overwhelming its defence system, it was settled by the polydorid instead of taking advantage of the more easy access to dead tests, providing further evidence for a symbiotic strategy.

Note

Shortly after submission of this manuscript, our quest for traces of symbiotic interactions involving *Echinocorys* yielded one additional specimen (collection Matschke, Sassnitz) featuring polydorid traces closely resembling the ones described herein. The new finding is another *Echinocorys ovata* and was collected from the same locality and stratigraphic level as the specimen mentioned in our study. Comparably, this *Echinocorys* test exposes eighteen *syn-vivo* polydorid borings on its oral surface which are all located on the plastron and the laterobasal area. The less densely tuberculated periplastral areas (ambulacra I and V) were not infested. Hence, there is further evidence that this symbiotic couple was not all that rare after all and further specimens are likely to be recognised with the current knowledge in mind.

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References

- Almeida, M.J., Machado, J., Moura, G. Azevedo, M., and Coimbra, J. 1998. Temporal and local variations in biochemical composition of *Crassostrea gigas* shells. *Journal of Sea Research* 40: 233–249.
- Andrews, E.A. 1891. A commensal annelid. *American Naturalist* 24: 25–35.
- Bergmann, K.M., Elnor, R.W., and Risk, M.J. 1982. The influence of *Polydora websteri* borings on the strength of the shell of the sea scallop *Placopecten magellanicus*. *Canadian Journal of Zoology* 60: 2551–2556.
- Blake, J.A. and Evans, J.W. 1973. *Polydora* and related genera as borers in mollusk shells and other calcareous substrates. *Veliger* 15: 235–249.
- Bosc, L.A.G. 1802. *Histoire naturelle des vers, contenant leur description et*

- leurs mœurs, avec figures dessinées d'après nature. 258 pp. Deterville, Paris.
- Bromley, R.G. 2004. A stratigraphy of marine bioerosion. In: D. McIlroy (ed.), The application of ichnology to palaeoenvironmental and stratigraphic analysis. *Geological Society of London, Special Publications* 228: 455–481.
- Bromley, R.G. and D' Alessandro, A. 1983. Bioerosion in the Pleistocene of Southern Italy: Ichnogenera *Caulostrepsis* and *Maeandropolydora*. *Rivista Italiana di Paleontologia e Stratigrafia* 89: 283–309.
- Clarke, J.M. 1908. The beginnings of dependant life. *Bulletin of the New York State Museum* 121: 146–196.
- Donovan, S.K. and Jagt, J.W.M. 2004. Site selectivity of pits in the Chalk (Upper Cretaceous) echinoid *Echinocorys* Leske from France. *Bulletin of the Mizunami Fossil Museum* 31: 21–24.
- Ferner, M.C. and Jumars, P.A. 1999. Response of deposit-feeding spionid polychaetes to dissolved chemical cues. *Journal of Experimental Marine Biology and Ecology* 236: 89–106.
- Frenzel, P. 2000. Die benthischen Foraminiferen der Rügener Schreibeckreide (Unter-Maastricht, NE-Deutschland). *Neue Paläontologische Abhandlungen* 3: 1–361.
- Hentschel, B.T. 2004. Sediment resuspension and boundary layer flow dramatically increase the growth rates of interface-feeding spionid polychaetes. *Journal of Marine Systems* 49: 209–224.
- Jangoux, M. 1990. Diseases of Echinodermata. In: O. Kinne (ed.), *Diseases of Marine Animals III*, 439–567. Biologische Anstalt Helgoland, Hamburg.
- Jarvis, I., Mabrouk, A., Moody, R.T.J., and Cabrera, S. de 2002. Late Cretaceous (Campanian) carbon isotope events, sea-level changes and correlation of Tethyan and Boreal realms. *Palaeogeography Palaeoclimatology Palaeoecology* 188: 215–248.
- Johnston, G. 1838–1865. *A Catalogue of the British Non-parasitical Worms in the Collection of the British Museum*. 365 pp. British Museum, London.
- Lankester, E.R. 1868. On lithodomous annelids. *Annals and Magazine of Natural History* 4: 233–238.
- Leske, N.G. 1778. *Jacobi Theodori Klein Naturalis dispositio Echinodermatum, edita et descriptionibus novisque inventis et synonymis auctorum aucta*. xxii + 278 pp. G.E. Beer, Lipsiae.
- Martin, D. and Britayev, T.A. 1998. Symbiotic polychaetes: a review. *Oceanography and Marine Biology, Annual Reviews* 36: 217–340.
- Néraudeau, D. and Villier, L. 1997. Enregistrement des fluctuations environnementales par les échinides irréguliers de la Craie campanienne de Charente-maritime (SO France). *Annales de la Société Géologique du Nord* 5: 175–179.
- Neumann, C. 2003. Shell-breaking predation on Cretaceous sea urchins: Spatial and temporal patterns. *Geological Society of America, South Central Meeting Abstracts with Programs* 35 (2): Abstract No. 50367.
- Neumann, C. and Wisshak, M. (in press). A foraminiferal parasite on the sea urchin *Echinocorys*: Ichnological evidence from the Late Cretaceous (Early Maastrichtian, Northern Germany). *Ichnos*.
- Radashevsky, V.I. 1996. Morphology, ecology and asexual reproduction of a new *Polydorella* species (Polychaeta: Spionidae) from the South China Sea. *Bulletin of Marine Science* 58: 684–693.
- Reich, M. and Frenzel, P. 2002. Die Fauna und Flora der Rügener Schreibeckreide (Maastrichtium, Ostsee). *Archiv für Geschichtskunde* 3 (2–4): 73–284.
- Ruellet, T. 2004. *Infestation des coquilles d'huîtres Crassostrea gigas par les polydore en Basse-Normandie: recommandations et mise au point d'un traitement pour éliminer cette nuisance*. 536 pp. Unpublished Ph.D. thesis, Université de Caen/Basse-Normandie.
- Sato-Okoshi, W. 1999. Polydorid species (Polychaeta: Spionidae) in Japan, with descriptions of morphology, ecology and burrow structure. 1. Boring species. *Journal of the Marine Biological Association of the United Kingdom* 79: 831–848.
- Stephenson, D.G. 1963. The spines and diffuse fascioles of the Cretaceous echinoid *Echinocorys scutata* Leske. *Palaeontology* 6: 458–470.
- Söderström, A. 1923. Über das Bohren der *Polydora ciliata*. *Zoologische Bidrag från Uppsala* 8: 319–326.
- Van der Pers, J.N.C. 1978. Bioerosion by *Polydora* (Polychaeta, Sedentaria, vermes) off Helgoland, Germany. *Geologie en Mijnbouw* 57: 465–478.
- Voigt, E. 1965. Über parasitische Polychaeten in Kreide-Austern sowie einige andere in Muschelschalen bohrende Würmer. *Paläontologische Zeitschrift* 39: 193–211.
- Voigt, E. 1971. Fremdsulpturen an Steinkernen von Polychaeten-Bohrgängen aus der Maastrichter Tuffkreide. *Paläontologische Zeitschrift* 45: 144–153.
- Wildish, D. and Kristmanson, D. 1997. *Benthic Suspension Feeders and Flow*. 409 pp. Cambridge University Press, Cambridge.
- Wisshak, M., Gektidis, M., Freiwald, A., and Lundälv, T. 2005. Bioerosion along a bathymetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): an experimental study. *Facies* 51: 93–117.