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Arachnostega n. ichnog. – burrowing traces in internal moulds of boring bivalves (Late Jurassic, Northern Germany)

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With 3 figures and 1 table

Kurzfassung: Grabgänge an der Oberfläche von Mollusken-Steinkernen werden als *Arachnostega gastrochaenae* n. ichnog. n. ichnosp. beschrieben. Gegenwärtig ist das Ichnogenus nur aus dem norddeutschen Oberjura und der Nordsee bekannt. Die Synökologie der Erzeuger wird eingehend diskutiert: Es handelt sich um vermutlich opportunistische, detritusfressende Polychaeten, die der Coelobiten-Infauna zugerechnet werden müssen. Sie sind nicht in eine ökologische Sukzession eingebunden, da ein Sedimentationsereignis vorausgehen mußte. Auf den skeletalen Rahmen haben sie schwächend gewirkt, doch schnelle Zementation der weichen Internsedimente und Inkrustierer der Oberfläche behindern die Graborganismen. Abschließend werden biostratinomische und fossildiagenetische Aspekte erörtert.

Abstract: Burrowing traces in internal moulds of molluscs are described as *Arachnostega gastrochaenae* n. ichnog. n. ichnosp. Currently, the ichnogenus is only known from the Late Jurassic and Recent of Northern Germany. The synecology of its polychaete producers is discussed in detail: they were probably opportunistic detritus-feeders and have to be regarded as infaunal coelobites. The tracemakers were not part of an ecological succession because their activity was facilitated by a sedimentation event. They weakened the skeletal frame but rapid cementation and encrusters inhibited them. Finally, aspects of biostratinomy and fossil diagenesis are sketched.

Introduction

Most of the trace fossils reported from reef environments belong to the group of borings, i.e. their producers excavated a hard substrate by chemical or mechanical means (e.g. Bromley 1970). The nature of the substrate seems to preclude the preservation of any other type of traces, except for the rarely fossilized biting scratches of fish or sea urchins on its surface. However, the occurrence of internal sediments in reefs is well-documented (e. g. Ginsburg & Schroeder 1973), but so far no trace fossils have been observed in this type of micro-habitat. Due to the soft or firm nature of the substrate, burrows instead of borings can be expected. Burrowing organisms are widespread in most marine facies; their activity either results in diffuse "bioturbation" or in distinct and recognizable traces, depending on the character and stability of the substrate.

Material

During the Late Jurassic, coral patch reefs and thickets grew at several localities in Northern Germany at different times (Bertling 1992). They were formed in various

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environments, mostly in agitated shallow water. Studying the composition and structure of the associations, internal moulds of boring bivalves could be extracted from coral heads repeatedly. At two localities (Fig. 1), the moulds of these bivalves show traces of burrowing organisms described below.

a) Old quarry at Dehlborn (Duckstein), west of Springe – Holtensen (sheet Eldagsen of topographic map 1:25.000; R 3543370, H 5779750). The condition of the outcrop is poor: 4–5 metres of a hard limestone form a steep and almost inaccessible wall. The same material is deposited on dumps in the immediate vicinity. No samples of reasonable size could be obtained from the outcrop itself, but the dumps contain many boulder-sized coral heads. These colonies were broken into chips a few cubic centimetres in size in order to obtain as many boring organisms as possible.

The host rock is a light grey thickly bedded biomicrudite with pronounced oöid content in some layers. Bioclasts comprise coral colonies, mostly fragmented, as well as bivalve shells, and cidaroid spines; other fossil groups are very subordinate. Corals are densely bored by bivalves: *Gastrochaena* is more frequent than *Lithophaga* and other borers at this locality. Most of the borings are empty and abraded, and thus cannot be ascribed to any of the known borers because of the morphologic similarity of the lower parts of their holes (*Gastrochaenolites* ichnosp.).

The limestone has been referred to the "Obere Korallenbank" Member of the Lower Korallenoolith (Late Oxfordian) by Dahlgrün (1923) and Hoyer (1965: 35, 162, pl. 3), but as yet no orthostratigraphic index fossil has been found. This leaves correlations with or discriminations from other coral horizons in Northern Germany rather ill-defined, because the "Obere Korallenbank" is developed only regionally.

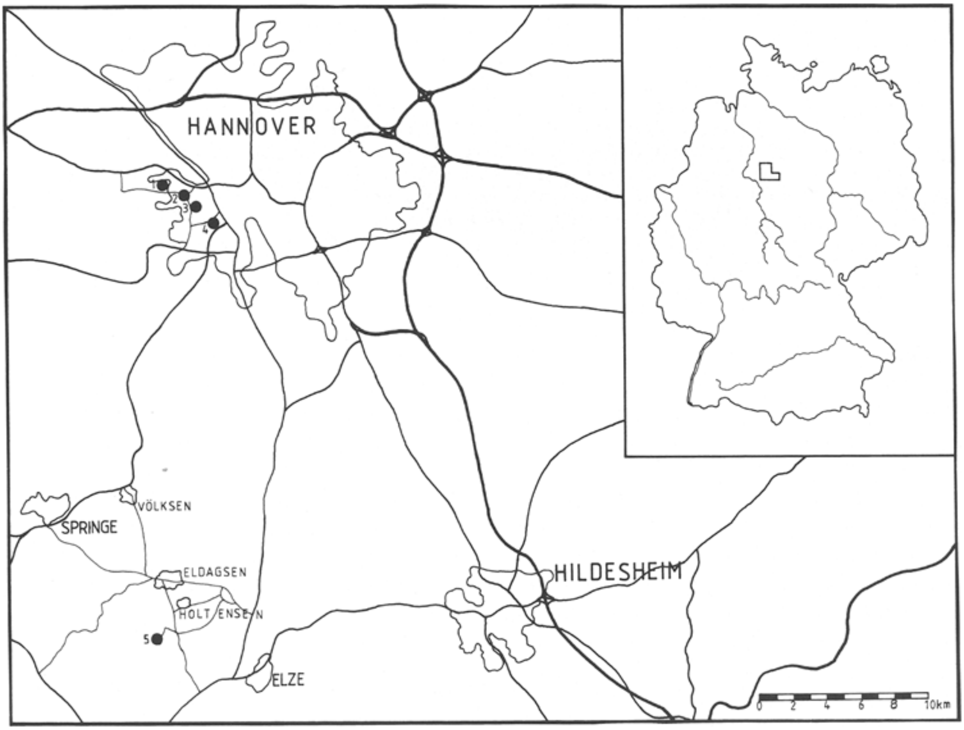

Fig. 1. Location map (Federal Republic of Germany); Localities 1–4: possible places of origin labelled "Hannover"; 1: Mönkeberg, 2: Limmer, 3: Linden railway station, 4: Lindener Berg; 5: Dehlborn.

Abb. 1. Lage der Probenpunkte (Bundesrepublik Deutschland); Lokalitäten 1–4 als mögliche Herkunftsorte »Hannover«; 1: Mönkeberg, 2: Limmer, 3: Bahnhof Linden, 4: Lindener Berg; 5: Dehlborn.

HOYER (1965) advocates a correlation with the "florigemma-Korallenbank" of the more westerly regions on lithological grounds.

b) "Hannover". Isolated internal moulds consisting of a black marly limestone with a high content of rounded quartz grains are labelled "Korallenoolith Hannover" in the collection of the Geological Institute in Göttingen. In this material, *Lithophaga* is the most frequent genus; *Gastrochaena* and *Hiatella* are less important. Despite comprehensive field work, this type of matrix could not be detected in any of the extant outcrops. Therefore, not only the stratigraphic position of the samples but also their provenance remains obscure. Several other coralliferous localities in and around Hannover (numbers 1–4 in Fig. 1) still existed a few decades ago, but material from these former quarries deposited in collections differs from the internal moulds considered here. However, bored corals seem to be restricted to the Lower Korallenoolith in this region (STRUCKMANN 1878), leaving the unknown locality more or less isochronous (Late Oxfordian) with the Dehlborn outcrop.

Taxonomy

Arachnostega n. ichnog.

Derivatio nominis: *arachne* (gr.) = spider and *stega* (gr.) = roof, cave; after the reticulate pattern produced on internal moulds of boring bivalves in their hole (anagram of *Gastrochaena*).

Type species: *Arachnostega gastrochaenae* n. ichnog. n. ichnosp. (monotypic).

Diagnosis: Irregular elongate and net-like burrows in sediment fills of shells. Visible on the surface of internal moulds. The size of the meshwork may vary from microns to centimetres, depending on the shell-bearing and the burrowing biota involved.

Occurrence: Late Jurassic (Late Oxfordian) and Recent.

Comparison: Other ichnogenera for burrows relate to geometrically ordered or level structures and/or show a distinct internal texture. *Arachnostega* may be considered the trace

Table 1. Differences between morphologically similar borings, *Entobia* and *Dictyoporus*, and *Arachnostega* n. ichnog.; data for borings after BROMLEY & D'ALESSANDRO (1984) and MÄGDEFRAU (1937).

Tab. 1. Unterschiede zwischen morphologisch ähnlichen Bohrspuren (*Entobia* und *Dictyoporus*) und *Arachnostega* n. ichnog.; Daten der Bohrspuren nach BROMLEY & D'ALESSANDRO (1984) und MÄGDEFRAU (1937).

	Entobia	*Dictyoporus*	*Arachnostega*
nature	boring	boring	burrow
substrate			
– type	(not restricted)	belemnite rostra	internal sediment in mollusc shells (others?)
– structure	hard, crystalline	hard crystalline	firm, fine-grained
– chemistry	calcareous	calcareous	slightly calcareous, rich in clay minerals
morphology			
– "ontogenetic" change	present	absent	absent
– early diameter	ca. 500μ	ca. 50μ	ca. 50μ
– "ontogenetic" increase in diameter	by factor 10–30	absent	by factor 5–10
– constrictions	present	absent	absent
– best visibility	beneath surface	at surface	at surface
producer	boring sponges	?	polychaetes (crustaceans?)

of an organism which could have produced other traces without the spatial limitations of an internal mould. However, the establishment of a separate ichnogenus is neccessary, because organisms requiring soft substrate can be documented within hard substrate associations only by this way.

Superficially, morphological similarities exist to two borings, *Dictyoporus* and *Entobia*. Their different genesis as well as other features such as substrate, position, "ontogeny" and morphological details (absence of chambers) comprise reliable criteria to separate these traces from *Arachnostega* (Table 1).

Arachnostega gastrochaenae n. ichnosp.

Fig. 2 a – f

Derivatio nominis: The ichnospecies was first recorded from internal moulds of *Gastrochaena*.

Locus typicus: "Hannover" (label in collection).

Stratum typicum: "Korallenoolith" (label in collection), presumably Lower Korallenoolith, Late Oxfordian, Late Jurassic.

Material: 17 burrowed internal moulds of *Gastrochaena, Lithophaga and Hiatella.*

Holotype: The type specimen is No. 974–14 in the collection of the Geologisch-Paläontologisches Institut der Georg-August-Universität, Göttingen, Germany. An internal mould of the boring bivalve *Lithophaga inclusa* (Phillips) of 15 mm length contains different "ontogenetic" stages of *Arachnostega* which cut each other. It cannot be decided whether the specimen resulted from the burrowing action of one or more individuals. Thus identification of a holotype in the type specimen is problematical. However, the co-occurrence of different "ontogenetic stages" is typical of this ichnospecies.

Paratypes: B4A-2-4 (5 specimens of *Gastrochaena* from Dehlborn; Geologisch-Paläontologisches Institut und Museum der Westfälischen Wilhelms-Universität, Münster), 974–9 (2 specimens of *Gastrochaena* from "Hannover"), 974–13 (specimens of *Lithophaga* from "Hannover"), 974–16 (1 specimen of *Hiatella* from "Hannover"; Geologisch-Paläontologisches Institut der Georg-August-Universität, Göttingen).

Diagnosis: Ramified burrows on the surface of internal moulds with an oval cross-section which increases slowly in diameter by a factor of 5 to 10, approximately. At ramifications, the bent main burrow is not reduced in size. Lateral burrows mostly have a smaller diameter. Polygonal areas on the surface of internal moulds may be produced by the unification of ramified burrows.

Description: The burrows are best visible on the surface of internal moulds and may either be empty or filled by sparite. The diameter is 30µ to 50µ in the earliest visible stages and gradually increases up to 150µ. Because the traces are not confined to the surface of internal moulds they sometimes appear to be constricted or even terminated, depending on the angle of descent from the surface.

The frequency of ramifications decreases with an increase of the diameter. At junctions, the main burrow is somewhat widened at first but afterwards quickly returns to the former

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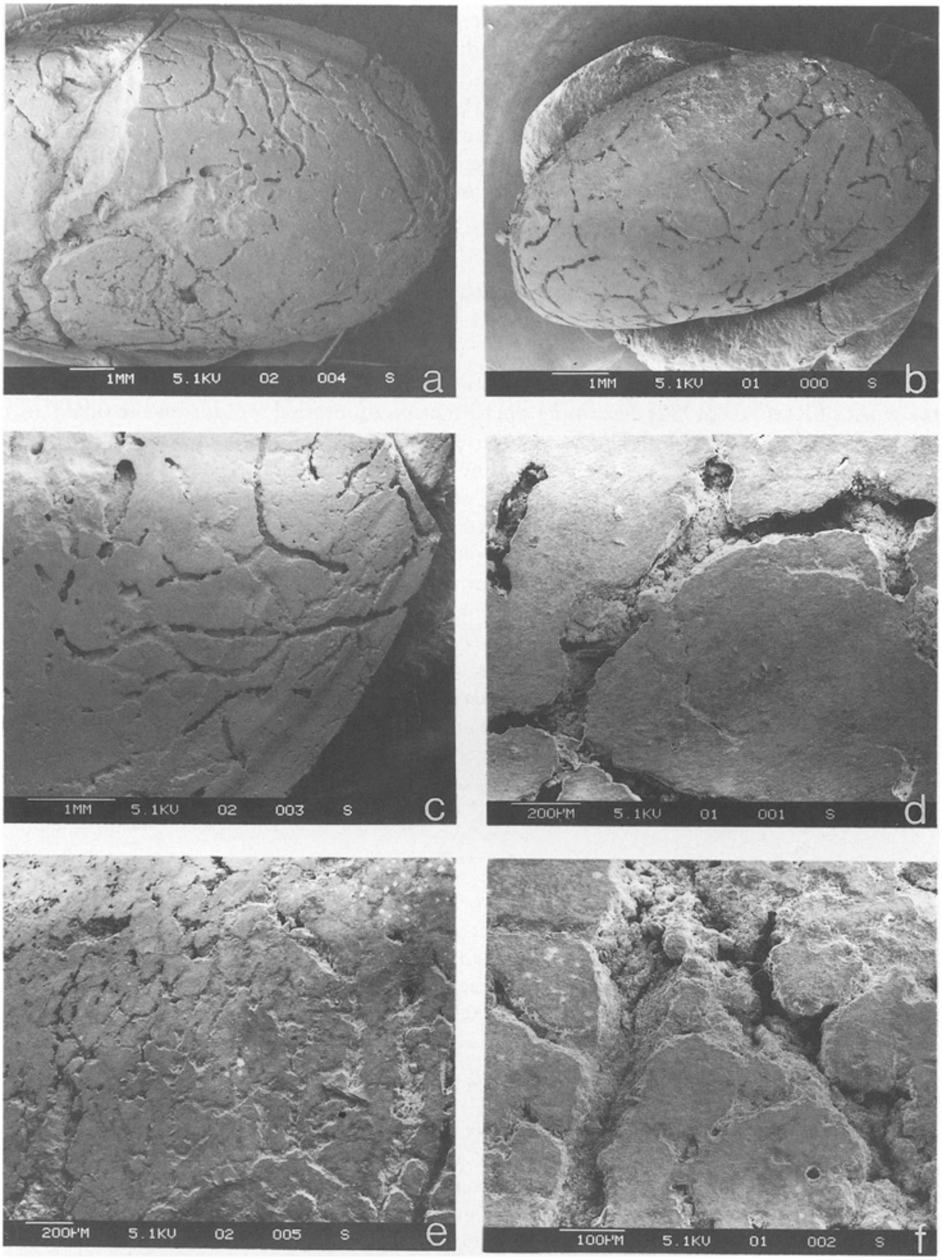
Fig. 2. SEM micrographs of *Arachnostega gastrochaenae* n. ichnog. n. ichnosp.; a, c, e: holotype 974–14, b, d, f: paratype 974–13 (Geological Institute, Göttingen). a: holotype in internal mould of *Lithophaga;* c: detail of holotype showing thick burrows partly broken open; e: detail of holotype showing small reticulate burrow system; b: paratype in internal mould of *Lithophaga;* d: detail of paratype showing frequent ramifications; f: detail of paratype showing anastomosing burrows.

Abb. 2. REM-Aufnahmen von *Arachnostega gastrochaenae* n. ichnog. n. ichnosp.; a, c, e: Holotyp 974–14, b, d, f: Paratyp 974–13 (Geologisches Institut, Göttingen). a: Holotyp im Steinkern einer *Lithophaga;* c: Detail des Holotyps mit teilweise aufgebrochenen dicken Gängen; e: Detail des Holotyps mit dünnem netzartigen Gangsystem; b: Paratyp im Steinkern einer *Lithophaga;* d: Detail des Paratyps mit häufigen Verzweigungen; f: Detail des Paratyps mit anastomosierenden Gängen.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200µM 5.1KV 02 005 S
e
100µM 5.1KV 01 002 S
f

size. There are no sharp corners within the burrow for this reason. The angle of ramification is not fixed, and even anastomoses occur.

Discussion: The ichnogenus *Arachnostega* is currently monospecific. Further ichnospecies should not be based on different dimensions alone, but should show different patterns of increase in size or of ramification.

Similar traces have been reported from Recent tidal flat deposits of the North Sea by Reineck (1980). Despite photographic documentation, it remains uncertain whether these modern analoga may be included in the same ichnospecies as the Jurassic specimens. More material is needed to estimate the variability of the forms considered.

Biology of the burrowers

Systematic position

The most important clue for the systematic position of the producers of *Arachnostega* is the work of Reineck (1980) describing the formation of internal moulds on the tidal flats of the modern North Sea. Mud-filled and exposed articulated valves of the burrowing bivalve *Mya (Arenomya)* contain bent and ramified burrow systems in a firm substrate. Disarticulation of the valves reveals a surface pattern on the moulds which exactly matches that of Jurassic *Arachnostega.* Reineck (1980) found living polychaetes *(Nereis, Heteromastus)* in the burrows which suggests their responsibility for the traces. The amphipod *Corophium* was also present but this is only a tube-dwelling genus. Independently of Reineck's results, the form of the burrows strongly supports the theory of elongate producers.

Although the environments of fossil *Arachnostega* and its Recent counterpart are somewhat different, the overall conditions (i.e. shallow marine) and the topology of the traces (i.e. the surface of internal moulds of bivalves) are strikingly similar. In addition, errant polychaetes are well-known as important members of the cryptofauna in modern reefs (see compilation by Hutchings [1983]). Polychaetes also occur as burrowers in internal sediments of Bahama reefs (Ginsburg & Schroeder 1973) but no description of their traces is given.

Mode of life

It can be concluded from the small diameter of the initial parts of the burrows that larvae of the producer and not adult animals settled after exposition of the substrate. At least in some cases, infestation occurred repeatedly, leading to intensive bioturbation. It is not clear whether the burrowers were able to leave their confined micro-habitat again. The obvious concentration of the burrows on the surface of the internal moulds points to repeated attempts of the tracemakers to extend their radius of activity. Hindered by the bivalve shells, they had to re-use previous burrows or crawl back into the main burrow from "exploratory shafts". These activities led to an anastomosing or ramifying course of the burrows. The polygonal nets characteristic of the ichnogenus can also be explained by recurring use of tunnels by one or more individuals.

The substrate could only be used in the geologically short interval between infilling of the bivalve boring with sediment and cementation of the fill. Thus the burrowers must have been opportunistic to a certain degree, i.e. the probability for a larva to find a suitable substrate was rather low. The results of Reineck (1980) point into the same direction: Only specimens of *Mya* which had been exhumed after filled with mud showed an infestation with polychaetes. Unexposed specimens in the sediment were not colonized. This proves that the larvae of burrowers did not actively search for the correct substrate but rather passively "took what they could get". This behaviour is typical of *r*-strategists. (Perhaps the internal sediments were even richer in nutritional particles for the deposit-feeder than its surrounding because of the decayed bivalve.)

However, this conclusion has to be relativized, because the polychaetes found in the Recent counterparts of *Arachnostega* are not confined to this very special substrate. Both genera burrow in unrestricted habitats of the tidal flats as well, and this can also be assumed of the Jurassic tracemakers. In unrestricted habitats, only a blurred bioturbation will result but confined by the surrounding bivalve shell, the preservation potential of the burrows as distinct traces increases.

Synecology

Due to the poor representation of *Arachnostega* in the studied fauna, no quantitative synecological data are available as yet. Its importance for the skeletal frame and interactions with other members of the reef community may be estimated despite this lack of knowledge.

The position of the producers of *Arachnostega* within the skeletal frame is ambiguous. They certainly belong to the coelobite clan which comprises organisms inhabiting reef cavities of any size (GINSBURG & SCHROEDER 1973). Burrowers in internal sediments are included in this definition (GINSBURG 1983). The tracemakers should not be regarded as cryptofauna just because of their hidden habitat which was created by borers (see HUTCHINGS 1983): All other cryptofaunal elements encrust or move about the surface of the reef cavities and are thus dependant on a hard substrate. This is clearly not the case with *Arachnostega*.

The designation as infauna would be more appropriate for the tracemakers despite their host corals being typical members of the epifauna. This contradiction also reflects the peculiar situation to record detritus-feeding elements from the mostly suspension-feeding fauna of the inner reef complex. In this respect, it is important to be able to identify a unique trace fossil as *Arachnostega* representing soft-substrate detritus-feeders.

Its producers are not part of the ecological succession of a reef body. For designation of a faunal change as ecological succession, biological agents must directly interact in an evolutionary process. In this case, the substrate was biologically altered by the action of boring bivalves, but this change alone did not facilitate the establishment of the *Arachnostega* tracemakers. A non-biological process, the sedimentary fill of the boreholes, was neccessary thus terminating the previously extant succession. It is doubtful whether the burrowing action could initiate yet another succession, e.g. facilitating cryptofauna via removal of internal sediments (Fig. 3).

The role of *Arachnostega* may be considered functionally as well (Fig. 3). All the processes in the skeletal frame of a reef are either weakening or strengthening this framework. Reef-building organisms and encrusters act consolidating as does sedimentary fill. On the other hand, borers destroy the rigid structure, and *Arachnostega* perforates firm internal sediment. This must essentially be interpreted as a weakening action.

An important aspect of synecological considerations are heterospecific interactions. *Arachnostega's* producers obviously did not interfere with organisms of similar mode of life, i.e. no other infaunal burrowers are known from the localities studied. In the Recent, possible interactions between the amphipod *Corophium* and the errant polychaetes of the *Arachnostega* burrows have not been studied either. Members of the cryptofauna of modern reefs are mostly deposit-feeders living on coral mucus (HUTCHINGS 1983). Because of this and also because of the different habitats, competition with sediment-feeders is virtually

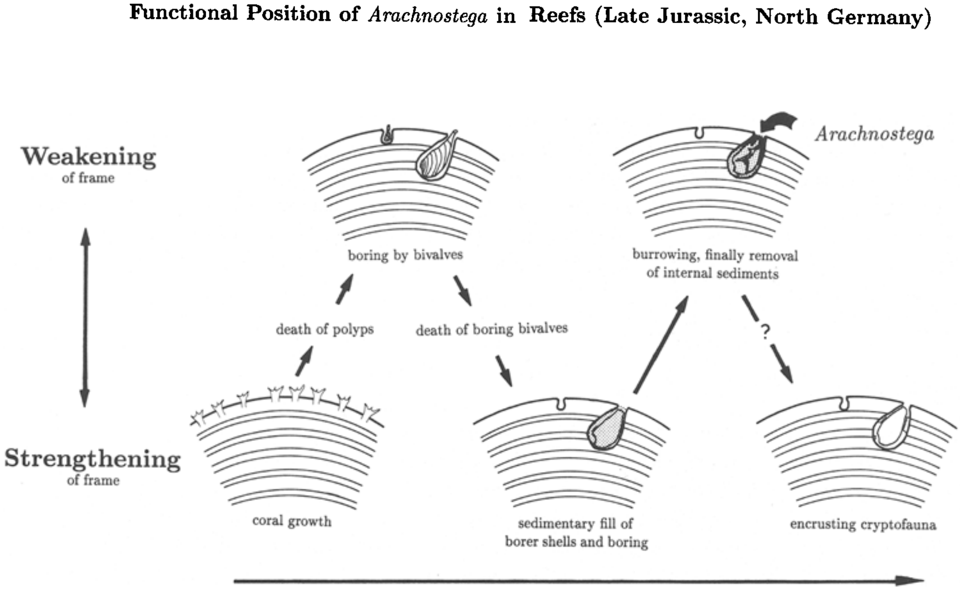

Fig. 3. Temporal development as indicated by the lower, horizontal arrow of the skeletal frame of a reef towards establishment of *Arachnostega;* note functional interplay of strengthening and weakening processes.

Abb. 3. Zeitliche Entwicklung (angegeben durch den unteren, horizontalen Pfeil) des skeletalen Rahmens eines Riffes hin zur Etablierung von *Arachnostega;* man beachte den funktionalen Wechsel stärkender und schwächender Prozesse.

excluded. Two processes, however, have a negative impact on the vital functions of the producers of *Arachnostega:* Firstly, rapid cementation turning the firm into a hard substrate which cannot any longer be burrowed. Lithification is happening very fast in modern reef environments and takes place even less than 1 cm below the surface (SCHROEDER & ZANKL 1974). Secondly, the encrustation of the coral surface by other organisms may lead to limited water exchange with the burrows inside the boring and may even seal them off completely. An avoidance mechanism of the tracemakers cannot be deduced from the fossil record.

Preservation and facies implications

Arachnostega can only be produced in a firm substrate; in soft mud, the burrow would collapse immediately after passage of the animal. With cementation taking place comparatively shortly after burrowing, the preservation potential of the traces is high. They may be left empty, as is the case at the locality "Hannover". Later during diagenesis, they may secondarily be filled with sparite, e.g. at the locality "Dehlborn". Thus, the presence of *Arachnostega* ichnofossils mainly depends on the primary nature of the substrate and the diagenetic history. Commonly *Arachnostega* will be enhanced diagenetically, whereas diagenetic extinction is less likely. For this reason, its absence depends on primary facies conditions.

Up to now, the trace is only known from shallow marine environments. This does not imply restricton to turbulent water since this is not the case in the Recent example from the North Sea. However, a certain degree of water movement is necessary in order to provide enough oxygen for the rather secluded fauna in internal sediments. Since only few occurrences are known so far, it is too early to discuss facies limitations. Principally, *Arachnostega* may be expected in deeper marine facies as well as in freshwater environments, although there preservational conditions are not favourable.

Conclusions

Arachnostega is a burrowing trace visible on the surface of internal moulds of bivalves. Currently, it is only known in boring bivalves from the Late Jurassic and in infaunal bivalves from the modern North Sea.

From comparison with the Recent counterparts, errant polychaetes (and perhaps crustaceans) are responsible for the trace. The diameter and the course of the burrows suggest an accidental and opportunistic larval infestation in recently sediment-filled bivalve borings. The producers of the trace were probably not restricted to this very special substrate but there had a greater preservation potential. They do not belong to the cryptofauna of the reef because of their burrowing habit, but may be considered detritus-feeding infaunal coelobites; a unique constellation for fossil reef environments. *Arachnostega* cannot be grouped as part of the ecological succession within reefs because of the neccessarily interfering sedimentation event. This matches the larval behaviour, because *r*-strategists normally only occur at the very beginning of a succession. Calcareous nature and high stability of the substrate are essential for the recognition of this trace fossil.

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