



Large dendrinids meet giant clam: the bioerosion trace fossil *Neodendrina carnelia* igen. et isp. n. in a *Tridacna* shell from Pleistocene–Holocene coral reef deposits, Red Sea, Egypt

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Abstract. The rosette-shaped microboring trace fossil *Neodendrina carnelia* igen. et isp. n. – a large representative of the ichnofamily Dendrinidae – is identified on the inner side of the giant clam *Tridacna maxima* from Pleistocene to Holocene coral reef deposits of the El Quseir district at the Egyptian Red Sea coast. The new dendritic bioerosion trace fossil is diagnosed as a radial rosette comprised of a prostrate system of roofless canals that ramify in a strictly dichotomous fashion forming intermittent branches of uniform width and rounded terminations. The trace appears to be rare, although in the type material it occurs in a cluster of more than a hundred specimens. The location of traces on the interior surface of the shell suggests that boring occurred post-mortem to the host. Its record is presently restricted to shallow marine, euphotic, tropical coral reef settings in the Western Indo-Pacific (Red Sea and Madagascar). The biological identity of the trace maker cannot be resolved yet, but several lines of reasoning allow speculations directed towards a complex attachment scar, perhaps produced by a benthic foraminiferan or a macrophyte.

members of the group still occur in modern oceans, preferentially in temperate to polar waters (Wisshak, 2017). In this study, we describe a new conspicuous dendrinid from a tropic coral reef setting from the Pleistocene–Holocene of the north-eastern Red Sea coast, El Quseir district, Egypt. In a single valve of the giant clam *Tridacna maxima* (Röding, 1798), a large pelecypod common in these settings, hundreds of specimens of this bioerosion trace fossil have been recognized. Their unique habitus and branching pattern merits establishment of a new ichnogenus, addressed as *Neodendrina*, in reference to the type ichnogenus *Dendrina* Quenstedt, 1849 from the Upper Cretaceous, which on first sight exhibits a remarkable similarity but after closer examination reveals a quite distinct architecture.

Geological context

Pleistocene raised coral reefs are a common feature along the Red Sea coast of Egypt, forming terraces at different elevations above the present-day sea level. Between El Quseir and Marsa Alam, three reefal units forming six morphological terraces can be recognized (El-Sorogy, 1997). The reefs form discontinuous strips which run parallel to the shore line, separated by conglomerates, quartz sands and gravels. At the study area, the lithology of the lowermost terrace represents a transition of mixed carbonate–siliciclastic rocks with scleractinians as primary frame builders (Fig. 1a). These Pleistocene reefal limestones are usually referred to as the Samadai Formation (Philobos et al., 1989) and are conformably overlain by Pleistocene raised beaches and coral reefs (Kora et al., 2013, 2014). Their age and diagenesis have been discussed by several workers during the last decades (see Dullo, 1990;

1 Introduction

The Dendrinidae are a diverse ichnofamily of dendritic and rosette-shaped marine microboring trace fossils (Bromley et al., 2007) whose unknown trace makers appear to have flourished particularly during the Devonian and the Late Cretaceous (Wisshak, 2017). While they had been considered largely extinct since the end-Cretaceous mass extinction event, a recent revision of the group revealed that several



Figure 1. The Pleistocene raised coral reef limestones exposed at the type locality of *Neodendrina carmelia* igen. et isp. n. just south of the Carmelia Beach Resort, located between El Quseir and Marsa Alam, exhibiting scleractinian corals as primary reef builders (a) and giant clams *Tridacna* spp. weathering from the carbonate–siliciclastic rocks (b) that mix with Holocene and modern *Tridacna* valves, forming a highly time-averaged assemblage (c).

El Sorogy, 2002, for further references) and have been a classical study area for palaeontological studies (see Kora et al., 2014).

Among other fossils (Fig. 1a), the rocks contain numerous large molluscs with giant clams (*Tridacna* spp.) and conchs (*Lambis* and *Strombus* spp.) being the most conspicuous. As the poorly lithified sediments erode, exposed *Tridacna* valves accumulate in large numbers on the surface (Fig. 1b). Here, they mix with subfossil (Holocene) and modern *Tridacna* valves, forming a highly time-averaged assemblage (Fig. 1c). This process was (and still is) promoted by active fishery of giant clams by the native Bedouin population and their ancestors over the course of the last > 125 000 years, producing huge piles of discarded *Tridacna* shells along Red Sea beaches (e.g. Ashworth et al., 2004; Benzoni et al., 2006; Richter et al., 2008).

2 Material and methods

One *Tridacna maxima* valve bearing the new bioerosional traces was sampled at a beach deposit of the Red Sea, Egypt, 25 km south of El Quseir, between Ras Abu Aweid and Mersa Um Gheig. Further, a query in the malacological collection of the Museum für Naturkunde Berlin resulted in the recognition of one additional *Tridacna squamosa* valve from northern Madagascar bearing similar traces.

The two bivalve shells bearing the studied bioerosion traces were digitally photographed with Nikon and Canon

DSLRs, partly after coating with ammonium chloride, and partly applying a Cognysis StackShot Macro Rail for extended focal imaging with the software Helicon Focus Pro. Scanning electron micrographs of the traces were produced with a Tescan VEGA3 XMU applying a backscatter electron detector (BSE) after sputter coating with gold, except for the holotype that was left untreated and was imaged in a low-vacuum setting. In addition, a micro-CT scan of the holotype trace was performed with a GE Phoenix nanotome X-ray tube at 90 kV and 150 μ A, generating 2500 projections with 750 ms per scan and effective voxel size of 4.6 μ m. The cone beam reconstruction was performed using the GE datoslx 2 reconstruction software and the data were visualized in Volume Graphics Studio Max 3.0. For better spatial resolution of the CT scans, the bivalve shell had to be cut into smaller blocks, some of the other ones of which were used for vacuum cast embedding followed by dissolution of the host substrate with hydrochloric acid (for details, see Wisshak, 2012), yielding epoxy cast with the positive infills of the traces that were then visualized with SEM after sputter coating with gold.

Morphometrical measurements were carried out using the measurements tool in the VEGA SEM software, recording the maximum diameter of the trace, the width of the individual galleries (up to five measurements per trace), the branching angle of the dichotomous bifurcations (up to five measurements per trace), the maximum number of subsequent

bifurcations from the centre to the periphery of the trace, and the number of peripheral gallery terminations.

This published work and the nomenclatural acts it contains were registered in ZooBank on 5 October 2017 and have received the LSID number EBD565C7-5042-47A9-8F1A-771ABBDCD1C0: <http://zoobank.org/references/EBD565C7-5042-47A9-8F1A-771ABBDCD1C0>.

3 Systematic ichnology

Dendrinidae Bromley, Wisshak, Glaub & Botquelen, 2007

Neodendrina igen. n.

Type ichnospecies: *Neodendrina carnelia* isp. n.

Etymology: Latinized from ancient Greek νέος (*neos*) and δένδρον (*dendron*), referring to the parent ichnofamily Dendrinidae and its type ichnogenus *Dendrina*, and making reference to the fact that microborings of the new ichnogenus are among the few dendrinids to also occur in modern seas.

Diagnosis: Dendritic bioerosion trace in calcareous skeletal substrates, forming a prostrate system of roofless canals that bifurcate dichotomously.

Remarks: The dichotomous bifurcation pattern of *Neodendrina* igen. n. closely resembles that of the ichnogenus *Abeliella* Mägdefrau, 1937, which is, however, found in a different principal substrate type, namely fossil bone and teeth. Such osteic substrates are considered as a principal substrate type for bioerosion trace fossils at equal rank with xylic and lithic substrates, thus justifying establishment of a separate ichnogenus (Höpner and Bertling, 2017). The dichotomous nature of bifurcations shows some similarity to *Fascichnus bellafurcus* (Radtke et al., 2010), originally established as *Abeliella bellafurca* by the latter authors and transferred to *Fascichnus* by Wisshak (2017), which is much smaller and shows a three-dimensional architecture. Another ichnogenus with some similarity is *Rhopalondendrina* Wisshak, 2017, which differs by the presence of a straight to arcuate entrance tunnel and the development of only a semi-circular plexus of ramifying or anastomosing galleries. *Neodendrina* igen. n. differs from the related ichnogenus *Dendrina* Quenstedt, 1849 by the lack of a tubular inlet tunnel, and by the more regular bifurcation pattern of galleries that are more constant in width. Apart from these distinctions, the main morphological character that distinguishes *Neodendrina* igen. n. from *Dendrina* and most of the other dendrinids is the roofless nature of the open galleries.

Neodendrina carnelia isp. n.

Figs. 2–4

Etymology: From Latin *carnelia*, meaning carnelian, red-coloured variety of chalcedony. Referring to “Diving Carnelia”, a former scuba dive centre situated in the direct vicinity of the type locality, and secondarily referring also to the Red Sea.

Diagnosis: Radial rosette nearly circular in outline, ramifying in a strictly dichotomous fashion. Roofless canals with slight swellings but relatively constant in width; terminations rounded. Particularly near the centre of the trace, canals may be very shallow or discontinuous and then appear as a series of pits.

Description: The prostrate circular to oval rosette of the dendrinid microboring is radiating from its centre in a strictly dichotomous pattern, forming open canals of relatively constant width (within a trace and among traces) and featuring rounded terminations (e.g. Figs. 2c–e, 3a–c). From the roughly orthogonal individual points of bifurcation, the canals make a slight turn in direction of the radial expansion of the trace, resulting in an acute angle between two neighbouring branches (Fig. 3a–d). Particularly in the centre of the trace, the canals may be either very shallow (at same width than the deeper ones) or even discontinuous, i.e. no bioerosion having taken place at these points (e.g. Figs. 2c–e, 3h, i, j). In the latter case, the trace appears as an array of short grooves or pits, whereas confined and shallow pits may also be found situated within the shallow canals (Fig. 3h). The presence and degree of these different morphological expressions varies markedly between different specimens, the by far most common morphology being the deep and continuous canals. The surface texture is smooth (Fig. 3e and k). The substrate surface in the direct vicinity of the canals may either be a bit different in colour (Fig. 2b) or morphologically slightly elevated (Fig. 4c). Several traces on the *Tridacna* shell that bears the holotype contain authigenic gypsum crystals, calcite spar, and clay minerals within the boring as well as on the surrounding shell surface (Fig. 3f–g).

Morphometrical measurements obtained from 55 complete specimens on a single *Tridacna* host shell, including the holotype and comprising a range of initial traces to late ichnogenetic stages, show a maximum diameter of the rosette-shaped trace ranging from 1025 to 3770 µm, with a mean of 1931 ± 651 µm ($n = 55$), and individual galleries of relatively constant width ranging from 59 to 153 µm, with a mean of 100 ± 16 µm ($n = 275$). The angle of the dichotomous bifurcations ranges from 43 to 141° with a mean of 90 ± 15 ° ($n = 246$) at the branching points. One to six orders of bifurcations were observed (mean = 3 ± 1 ; $n = 55$), leading to a number of peripheral gallery terminations ranging from 4 to 43 (mean = 13 ± 7 ; $n = 55$).

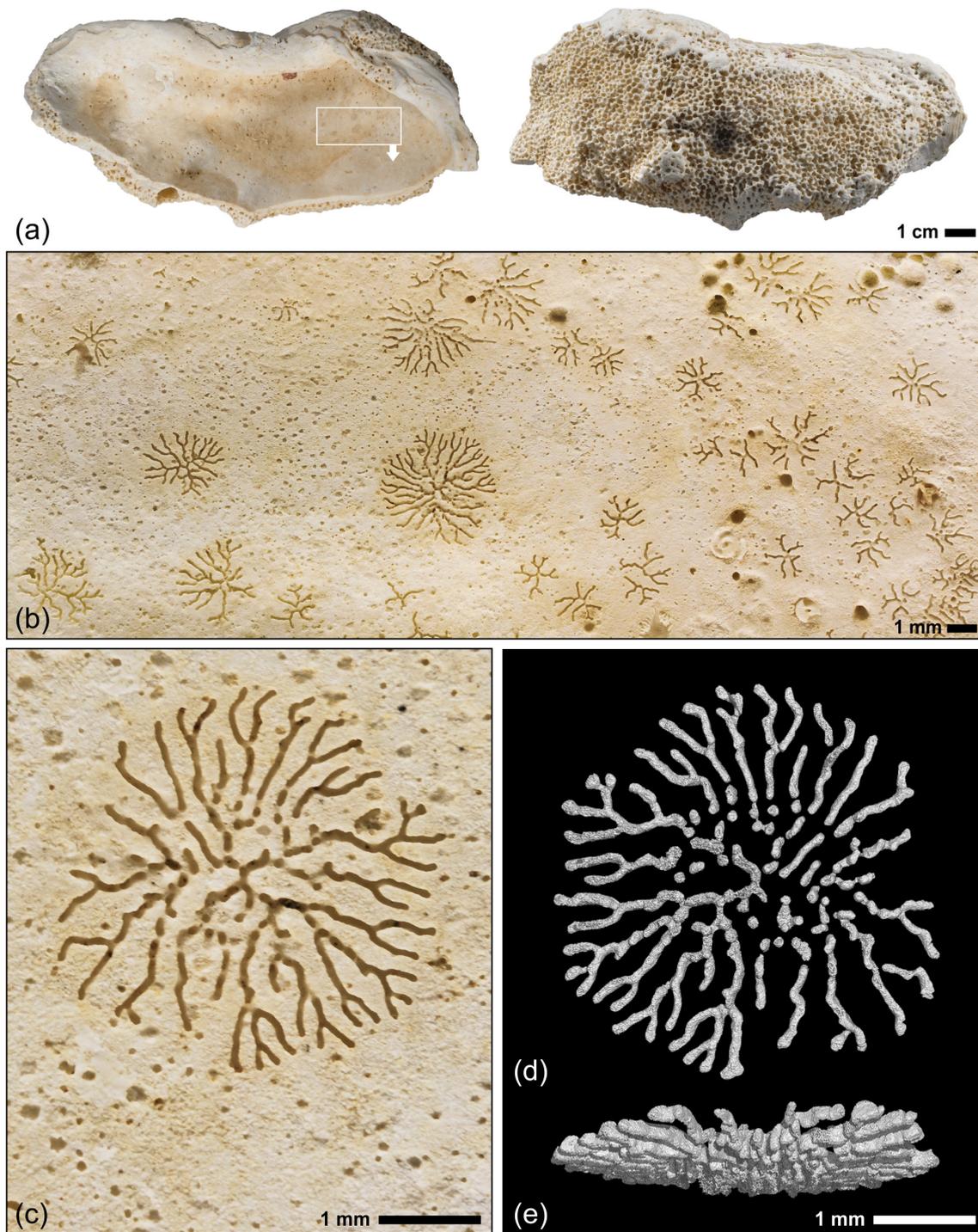


Figure 2. *Neodendrina carnelia* igen. et isp. n. on the inner side of a *Tridacna maxima* bivalve shell from the Pleistocene–Holocene coral reef deposits in the Marsa Alam area, Red Sea, Egypt. **(a)** Inner side of valve (left; prior to sectioning) with hundreds of *N. carnelia* specimens, and outer surface (right) intensely bioeroded by the sponge boring *Entobia* isp. **(b)** Section of the valve (MB.W 5640) with the holotype (centre) and the paratypes (all other specimens) in various ichnogenetic stages. **(c)** Close-up of the holotype trace. **(d–e)** Respective micro-CT scan of the holotype in plan and angular views as seen from inside the substrate.

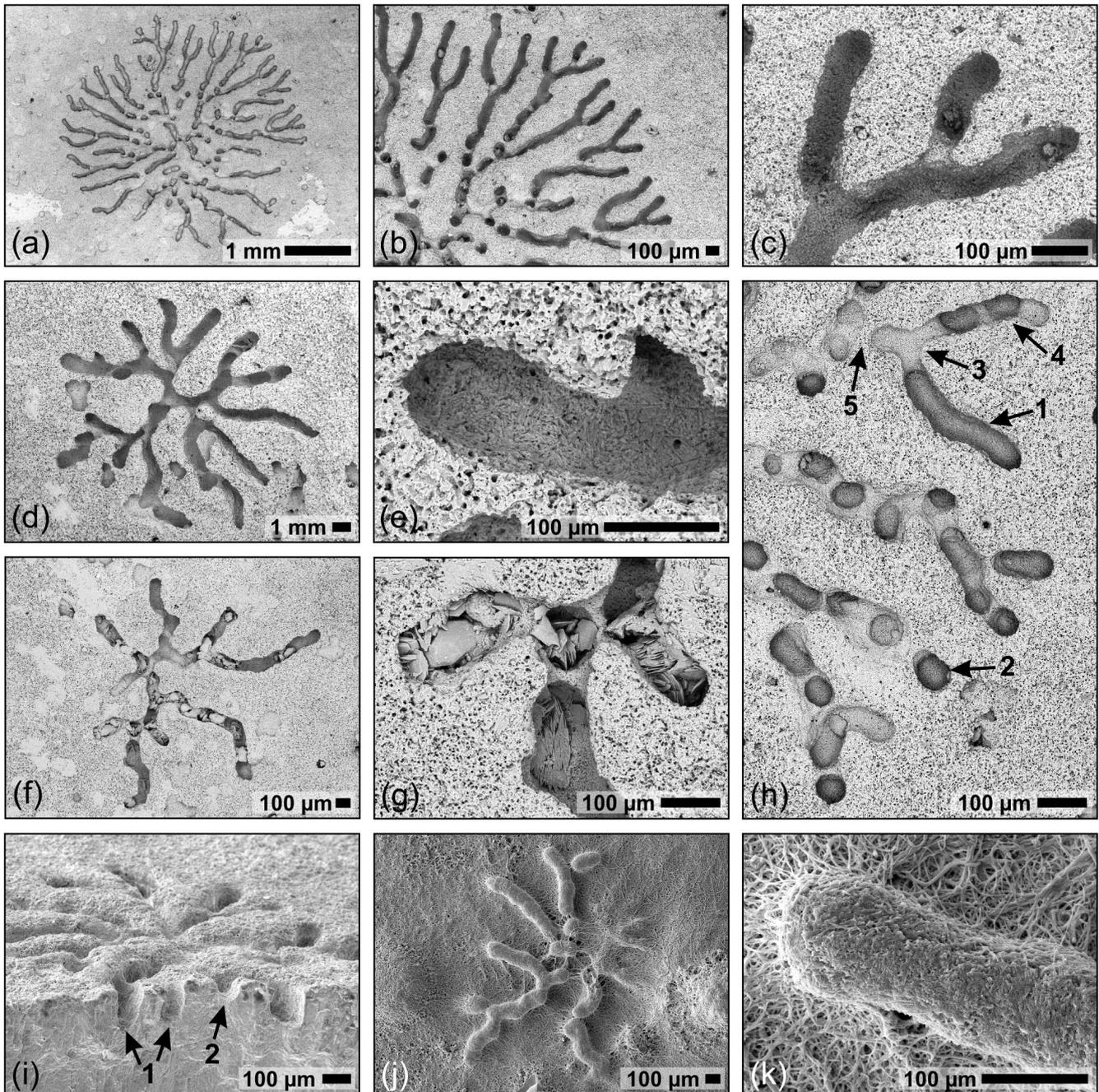


Figure 3. SEM images (BSE detector) of *Neodendrina carnelia* igen. et isp. n. of the inner side of a *Tridacna maxima* bivalve shell from the Pleistocene–Holocene coral reef deposits in the Marsa Alam area, Red Sea, Egypt. **(a–c)** Overview and close-ups of the holotype. **(d–e)** Overview and close-up of an early ichnogenetic stage. **(f–g)** Overview and close-up of a specimen with authigenic gypsum crystals, calcite spar, and clay minerals within the boring as well as on the host's shell surface. **(h)** Different morphologies possibly developed in the trace, comprising deep open canals (1), isolated deep pits (2), shallow open canals (3), pits in shallow canals (4) and discontinuities (5). **(i)** Cross section of a trace showing deep (1) and shallow (2) open canals. **(j–k)** Overview and detail of an epoxy resin cast of a specimen, illustrating the smooth surface texture and the high degree of microbioerosion in the surrounding (partly mechanically removed to gain a view of the dendrinid).

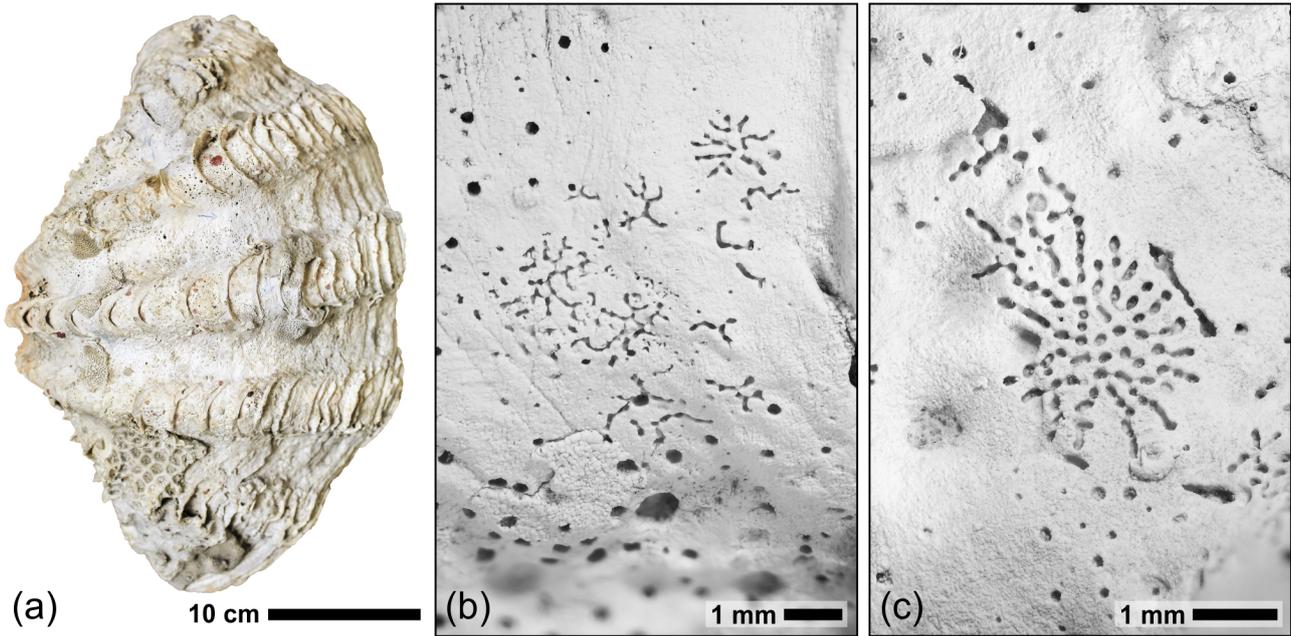


Figure 4. *Neodendrina carnelia* igen. et isp. n. on the outer surface of a large recent *Tridacna squamosa* valve from Nosy-Bé, northern Madagascar (ZMB/Mol 102671). (a) Shell surface with various encrusters as well as bioerosion traces. (b) Close-up of a cluster of *N. carnelia*. (c) A large specimen with distinct pitted arrays developed in most of the branches.

Type material, locality and horizon: The holotype (Figs. 2b–e, 3a–c) is preserved on a piece cut from a *Tridacna maxima* (Röding, 1798) shell, and is housed at the Museum für Naturkunde Berlin, Germany (MB.W 5640). All other specimens preserved on the same slab are defined as paratypes (Fig. 2b). The type locality is 25 km south of El Quseir, between Ras Abu Aweid and Mersa Um Gheig, just south of the former Carnelia Beach Resort (25°54'13" N, 34°24'45" E). The type shell bed is highly time averaged, and hence the exact age remains unresolved, either from the reefal limestones of the Samadai Formation, Pleistocene, or from a late Pleistocene to early Holocene archaeological shell midden, or (least likely) from the recent reef top.

Additional material: More than a hundred microboring specimens remained preserved on the inner shell surface of the same *Tridacna maxima* bivalve shell that bears the holotype (Fig. 2a). In addition, a number of specimens were identified on the outer surface of a large recent *Tridacna squamosa* de Lamarck, 1819 valve (Fig. 4) stored at the Museum für Naturkunde Berlin, Germany (ZMB/Mol 102671), originating from Nosy-Bé, northern Madagascar.

Remarks: Spot checks of morphometrical measurements taken from the additional Madagascar material plot in the range of the specimens from the type material.

4 Further observations and discussion

The *T. maxima* shell that harbours the type material was bioeroded by different types of bioeroders, both syn-vivo and post-mortem. All of the many *N. carnelia* igen. et isp. n. are located on the inner surface of the host valve (Fig. 2a left), thus indicating a post-mortem development (syn-vivo parasitism is very unlikely, considering their occurrence also on the outside of the Madagascar specimen). The outer surface, in contrast, was heavily infested by a bioeroding sponge that produced *Entobia* isp. but did not form connections to the inner surface of the valve (compare Fig. 2a left and right), thus indicating syn-vivo bioerosion. The latter case probably also applies to some specimens of the bivalve macroboring *Gastrochaenolites* isp. (e.g. Fig. 2a lower left) that enter the valve from the outer surface. All other bioerosion traces developed post-mortem on the inner side of the valve, as there are numerous traces of deep endolithic as well as surficial attached foraminiferans (see e.g. Fig. 2b), or the endolithic rhizoidal attachments *Fascichnus grandis* (Radtko, 1991) of the chlorophyte alga genus *Acetabularia* (Radtko et al., 1997). The entire surface of the valve was densely bioeroded by chlorophyte and cyanobacterial microendoliths (see e.g. Fig. 3c, e, g, j–k), taking place both syn-vivo (outer surface) and post-mortem (both surfaces). The overall trace fossil assemblage can be regarded as typical for shallow-marine tropical reef settings.

The exact stratigraphic age of the type material cannot be pinned down with certainty (see above) but is either Pleis-

tocene or Holocene. The trace definitively occurs also in modern seas, as indicated by the material from Madagascar. *Neodendrina carnelia* igen. et isp. n. is a new member of the growing circle of known extant dendrinids, which, according to the revision of the Dendrinidae by Wisshak (2017), already includes six ichnospecies. The biogeographic distribution at present is restricted to the tropical Western Indo-Pacific, represented by the two known records from the Red Sea and Madagascar. With respect to the (palaeo-)environmental setting, both records are from a shallow-marine, euphotic, tropical coral reef.

The biological identity of the trace makers of all dendrinid microborings, including the herein described *N. carnelia* igen. et isp. n., remains largely enigmatic. Published interpretations in this respect are diverse, but the most likely candidates are endolithic naked foraminiferans and microsponges, possibly also hydroids and, in the case of the smallest forms, endolithic fungi or microphytes (for a review, see Wisshak, 2017). As for *N. carnelia* igen. et isp. n., the presence of an epilithic part of the trace maker can be deduced from the partly discontinuous open canals (e.g. Fig. 2b–d), and from the observation that some of the traces appear to show somewhat of a “shadow” surrounding the trace, expressed by a slightly darker colour of the shell surface in the case of the holotype and neighbouring paratypes (Fig. 2b–c). This phenomenon can best be explained by a lower degree of microbioerosion at the place where the dendrinid trace maker was covering the substrate. This line of reasoning is also supported by the presence of a slightly elevated plateau surrounding the largest of the specimens on the Madagascar *Tridacna* (see Fig. 4c). Furthermore, none of the numerous studied specimens showed any signs of a partially preserved or abraded roof, and a very homogenous abrasion that could have resulted in an un-roofing of all of the numerous observed traces on the concave inner side of the host shell is extremely unlikely. Hence, the morphological feature of open canals is here regarded as the original and intact morphology of the new dendrinid. Therefore, the fact that the canals become very shallow (at constant width), or in places even discontinuous (e.g. Fig. 3h), rather suggests continuity of the trace maker’s soft body with an alternation of epilithic and partly endolithic mode of progression.

With respect to indicative morphological characters that could help identifying the trace maker, *N. carnelia* igen. et isp. n. has admittedly little to offer. The absence of anastomoses and particularly the strictly dichotomous bifurcation pattern are highly convergent characters that are developed in algae, fungi, cyanobacteria, and other potential trace makers (see discussion in Radtke et al., 2010). This suite of euendolithic microborers can, however, most likely be excluded on grounds of the comparatively large size of the dendrinid in question. Together with the above proposed epilithic component, this raises the question of whether *N. carnelia* igen. et isp. n. could reflect a complex attachment scar of a larger trace maker rather than the

work of an euendolithic microborer. Matching epiliths could perhaps be expected either among the benthic foraminiferans or in the form of either a rhizoidal structure or etching of a hapteron of a macrophyte (for a review, see Bromley and Heinberg, 2006). As for benthic foraminiferans, many species are known to produce attachment scars or endolithic microborings (for a recent review, see Walker et al., 2017), and at least one modern dendrinid microboring was interpreted as the work of a foraminiferan. This is *Nododendrina europaea* (Fischer, 1875), formerly *Semidendrina pulchra* Bromley et al., 2007 (for the revision, see Wisshak, 2017), which presumably is produced by the foraminiferan *Globodendrina monile* Plewes et al., 1993. As for macrophytes, various representatives of the large unicellular green algae of the genus *Acetabularia* form rhizoidal bioerosion traces (Radtke et al., 1997) that are addressed as *Fascichnus grandis* (Radtke, 1991). As outlined above, these traces also co-occur with *N. carnelia* igen. et isp. n. on the very same *Tridacna* shell, and just like the new dendrinid, these traces do bifurcate and have a smooth surface texture, but they are much larger than morphologically similar cyanobacterial microborings. Unlike *N. carnelia* igen. et isp. n. they are rather deeply penetrating, but this fact alone does not justify ruling out the possibility that *N. carnelia* igen. et isp. n. might be the work of a large chlorophyte alga within or similar to the genus *Acetabularia*. Among the rhodophytes, many of the phaeophycean kelp and seaweeds attach themselves to hard substrates by means of a holdfast or gripping hapteron. According to Oliveira et al. (1989) the rhizoid’s adhesive material is composed of a glycoprotein or an acid-polysaccharide/protein complex. Some representatives have been suspected or reported to etch carbonate substrates (e.g. Emery, 1963; Barnes and Topinka, 1969; Warme, 1975; Radwanski, 1977), but a detailed ichnological investigation and ichnotaxonomical treatment of these attachment etchings is pending. In general, both chlorophytes and rhodophytes may exhibit a dichotomous branching pattern of their endolithic or epilithic thalli (e.g. Sitte et al., 2002).

Last but not least, clues for the trace maker identity could be derived from the observed abundance patterns of *N. carnelia* igen. et isp. n., which appears to be fairly rare. This is suggested by the fact that this conspicuous and large dendrinid has not been previously recognized, and considering that visual inspection of hundreds, if not thousands, of further *Tridacna* valves at the type locality did not yield a single additional record. In contrast, where it occurs, it appears clustered in a remarkably high number of specimens on a single host shell, as indicated by the *T. maxima* that bears the holotype in a cluster together with hundreds of other specimens. Such clustering would be in line with both a foraminiferan and a macrophyte trace maker, and is also typical for several other dendrinid ichnotaxa, such as the aforementioned *S. pulchra* or ichnospecies of the Cretaceous ichnogenus *Dendrina*. However, despite the number of the above observations, the favoured options in respect to the trace maker’s

biological identity remain highly speculative until evidence from body fossils or organic remains in extant specimens of *N. carnelia* igen. et isp. n. can be identified.

Data availability. The samples are deposited in museum collections (as specified in the Systematic Ichnology section), and all necessary data can be found in the text.

Competing interests. Christian Neumann and editor Florian Witzmann work at the same institution but do not collaborate scientifically, and the paper was accepted on the basis of reviews from two outside reviewers. The authors declare no other competing interests.

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