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The Complex Fungal Microboring Trace Saccomorpha stereodiktyon isp. nov. Reveals Growth Strategy of its Maker

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The Complex Fungal Microboring Trace *Saccomorpha stereodiktyon* isp. nov. Reveals Growth Strategy of its Maker

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A complex microboring trace of fungal affinity is described in shells as a new ichnotaxon *Saccomorpha stereodiktyon* isp. nov. and compared with the earlier established ichnotaxon *Saccomorpha terminalis* Radtke, 1991. The new trace is characterized by a three-dimensional network of tunnels composed of a bifurcate horizontal (parallel to substrate surface) network with an upright (perpendicular to surface) system of tunnels and by the formation of cylindrical to multilobate terminal sporangial swellings. The new trace shares with *Saccomorpha terminalis* Radtke, 1991 the terminal position of sporangial swellings but differs from this ichnotaxon by its complexity in spatial arrangement, segmented construction, and ramification of tunnels. The horizontal parts of the network in the new taxon adhere to the substrate surface and regularly produce thinner tunnels that explore the interior of the substrate, allowing the producer to participate in digestion of organic lamellae incorporated in the shell. Microborings similar to the new trace fossil have been observed in modern bivalve shells of the Atlantic Ocean, North Sea, Adriatic Sea and Red Sea at depths ranging from the intertidal down to 1,550 m. The fossil record of the trace reaches back to the Jurassic and the type material stems from a Lower Oligocene oyster shell. The study shows that complex microboring traces reflect both behaviour and developmental strategy of their makers.

Keywords Development, Bioerosion, Microendoliths, Fungi, Organotrophy, Ichnotaxonomy, Ichnogenus *Saccomorpha*

INTRODUCTION

Fungi and other organotrophic microorganisms are important agents of marine carbonate bioerosion, not only in illuminated shallow seas where they co-occur with phototrophic microboring organisms (e.g. Vogel and Brett, 2009) but also especially in aphotic ocean depths where they are frequent and exclusive inhabitants of carbonate skeletons. In contrast to phototrophic microphytes and microboring invertebrate filter feeders, which primarily seek shelter within their endolithic ecological niche, fungal microborers or euendoliths (Golubic et al., 1981) rely on organic nutrients incorporated (e.g., as organic matrix) in calcareous skeletons by foraminifera, molluscs, and corals (Golubic et al., 2005). Both phototrophic and organotrophic euendoliths play important roles in marine carbonate bioerosion (Tribollet et al., 2011). The identity of euendolithic fungi is often difficult to establish; however, their microboring traces are morphologically quite distinct and show a remarkable diversity as well as a high preservation potential in recent and fossil carbonate substrates; Wisshak, 2012). Considered trace fossils, they are named and classified according to rules of ichnological and zoological nomenclature (Radtke, 1991; Bertling et al., 2006), organized within the currently established four ichnogenera of fungal origin: *Saccomorpha*, *Orthogonum*, *Polyactina* and *Flagrichnus* (Radtke, 1991; Wisshak and Porter, 2006).

We describe here a new endolithic trace fossil of probable fungal origin under the name *Saccomorpha stereodiktyon* isp. nov., and discuss its relation to the microorganism that formed it and to related microbial traces, especially to *Saccomorpha terminalis* Radtke, 1991, which shares the property of terminal positioning of sporangial swellings. The ichnogenus *Saccomorpha* Radtke, 1991, was established with the type ichnospecies *Saccomorpha clava* describing microborings of the thaustrochytrid fungus *Dodgella priscus* Zebrowski, 1937, an organism itself described on the basis of its boring trace in sand grains from a beach in southern Australia (Zebrowski, 1937; Porter and Zebrowski, 1937). Zebrowski also observed the characteristic branching patterns and terminal sporangial

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swellings characteristic of the new ichnospecies and assigned a new genus and species identity to the organism as *Arborella kohli* Zebrowski, 1937. The same organism was observed and identified as oomycete *Phytophthora* by Höhnk (1969), but this designation is problematic since the latter genus contains only terrestrial plant parasites that are ecologically and morphologically quite different.

MATERIALS AND METHODS

Shell Material

Saccomorpha stereodiktyon isp. nov. was observed as a microbial trace in shells of *Delectopecten vitreus* and shell fragments sampled in non-tropical settings such as the Sommerøy-Malangen and Sula Ridge in Norway, Kornat Island, Adriatic Sea in Croatia, and from deep sea sediments of the Red Sea, adding to the already published records from cold-water carbonate settings in Sweden, Australia, Germany and Scotland, as summarized in Table 1. The fossil occurrences are represented by the holotype material in a shell of *Ostrea tigiliana* from the Early Oligocene Stepovak Formation of Alaska, USA. Paratype material is in shells of *Astarte* from the Early Oligocene Ratheim Formation at the Mine shaft Sophia Jakoba 6 (Niederrhein, Germany). Other fossil occurrences were found in the shells of *Camptochlamys alaskensis* in the Late Palaeocene Prince Creek Formation, Alaska. In addition, *S. stereodiktyon* isp. nov. could be reliably identified in fossil shells as old as the Jurassic as represented by a record from the Glasenbachklamm in Austria.

Sample Preparation

Loose shells and shell fragments (<1 cm in diameter) from the various sites, were microscopically surveyed for the presence of microendolithic traces and selected for further study. Selected shells with microborings were subsequently embedded in polymerizing resin applying the embedding-casting technique after Golubic et al. (1970, 1983) or the vacuum cast-embedding technique as described in Wisshak (2012). The casts of borings where exposed by dissolution of the shell carbonate with dilute HCl (5%), and further prepared for scanning electron microscopy (SEM).

Microscopy

The presence of microborings was detected by using a dissecting microscope equipped with incident and transmitted light illumination. Boring traces were located, identified, and photo- documented in transparent shells and shell slivers using a compound microscope with transmitted light illumination and multi-focus digital photomicrography with the light microscope Leica M205C and Leica Application Suite LAS-3,7,0 (Leica Microsystems GmbH, Wetzlar, Germany; Camera: DFC425 PC; Software: Leica Application Suite, LAS-3.7.0). The three-dimensional display of microborings was reconstructed by a combination of multi-focus light photomicrographs and SEM images of resin replicas. Measurements of the observed structures were carried out on the basis of photomicrographs and in-scale projections using software of Sigma-Scan Image (Sausalito, CA, USA) and Motic Images Plus (Motic China Group, Xiamen, China).

RESULTS

The Morphological Patterns

Saccomorpha stereodiktyon isp. nov., an euendolithic trace of presumed fungal affinity (discussed below) and its morphology, is described here in reference to fungal morphological characters. It is a complex, well-organized three-dimensional network of repeatedly and regularly branched 1–4 μm wide tunnels, exhibiting elaborate growth and distribution strategy and producing terminally positioned swellings. The network of microborings of considerable density occupied large areas of shells and shell fragments, showing consistently a pattern with two types of regular and repetitive branching in addition to terminal positioning of spherical, elongated, and irregular bumpy swellings (Figs. 1–3). These properties are consistent with the growth of fungal hyphae (Tribollet, 2008) and with formation of fungal reproductive structures such as sporangia (Fig. 1A). In addition, we have observed broken swellings to contain spores. Over time, as the colonization density increases, the boring patterns become less regular, the hyphal tunnels show interference, and sporangial swellings grow elongated, to multilobate and irregular in shape (Fig. 1B). The hyphae-harbouring network of tunnels, which can be observed undisturbed by light microscopy in transparent shells, consists of bifurcating "horizontal" tunnels that spread parallel and close to the substrate (shell) surface, widening abruptly into more or less isodiametric sporangial cavities at their ends (Fig. 1C). The "horizontal" tunnels are composed of one to several distinct segments that are straight and similar in length (20–40 μm; mean ± SD: 29.36 ± 5.15 μm; n = 60); the segments widen gradually in the direction of growth, from about 1.5 μm diameter at their proximal end to form a 3–5 μm wide conical node at the distal end of each segment (Fig. 1D).

The conical nodes are the origins of both "horizontal" (parallel to the substrate surface) bifurcations, which contribute to the lateral spreading of the network (Fig. 1D, h) and "vertical" (perpendicular or inclined to the substrate surface) branches, which explore the interior of the substrate (Fig. 1D, v). Branch-points of upright tunnels occur singly at the distal ends of the intercalary segments, or closely following the horizontal bifurcations, often forming a near trichotomy (Fig. 1E). The upright tunnels are narrower (1.0–1.5 μm wide) and remain mostly unbranched. After reaching a certain level within the shell, the upright tunnels (as observed by light microscopy)

TABLE 1
Distribution of *Saccomorpha stereodiktyon* isp. nov. in shell fragments

Locality	(Palaeo-) water depth	Stratigraphical unit	Substrate	Reference
Ninety Mile Beach, South Victoria, Australia	0 m	Recent	bioclastic sand	Zebrowski (1937, pl. 27, fig. 8) and Porter and Zebrowski (1937, fig. 1c)
Helgoland,	intertidal	Recent	shell fragments	Höhnk (1969, fig. 4b)
Wangerooge,	34 m	Recent	shell fragment	
Løcken, North Sea	31 m	Recent	shell fragments	
British Channel	68 m	Recent	shell fragments	
Steep slope off Scotland	34 m	Recent	shell fragments	
Lady Rock, West Scotland	55 m	Recent	bivalve shell	Glaub (1994, pl. 3, fig. 5; pl. 2, fig. 6)
Port Appin, West Scotland	20 m	Recent	bivalve shell	
Kosterfjord, Sweden	30 m, 85 m	Recent	*Callista chione* (experimental substrate)	Wisshak et al. (2005, figs. 10d–h), Wisshak (2006, figs. 19d–h), and this study
Sommarøy-Malangen, Norway	41–43 m	Recent	*Arctica islandica*	this study
Sula Ridge, Norway	ca.270 m	Recent	*Delectopecten vitreus*	this study
Kornat Island, Adriatic Sea, Croatia	70 m	Recent	shell fragments	this study
Meteor 158, Golf of Aden, Red Sea	1558 m	Recent	shell fragments	this study
West Head, Unga Island, Southwest Alaska, USA	shallow water	Stepovak Formation, Early Oligocene	*Ostrea tigiliana*	Vogel and Marincovich (2004, fig. 4.5), **Holotype**, this study
Mine shaft Sophia Jakoba 6, Niederrhein, Germany	50–80 m	Ratheim Formation, Early Oligocene	*Astarte* sp.	Radtke (1991), **Paratype**, this study
Brendola, Northern Italy	50–80 m	Priabonian, Late Eocene	shell fragment	Radtke (1991) and this study
Ocean Point, Colville	30–50 m	Prince Creek Formation, Thanetian, Late Palaeocene	*Camptochlamys alaskensis*	Vogel and Marinkcovich (2004, fig.4.6) and this study
Glasenbachklamm, Austria	under evaluation	Sinemurian to Pliensbachian, Early Jurassic	shell fragment	this study

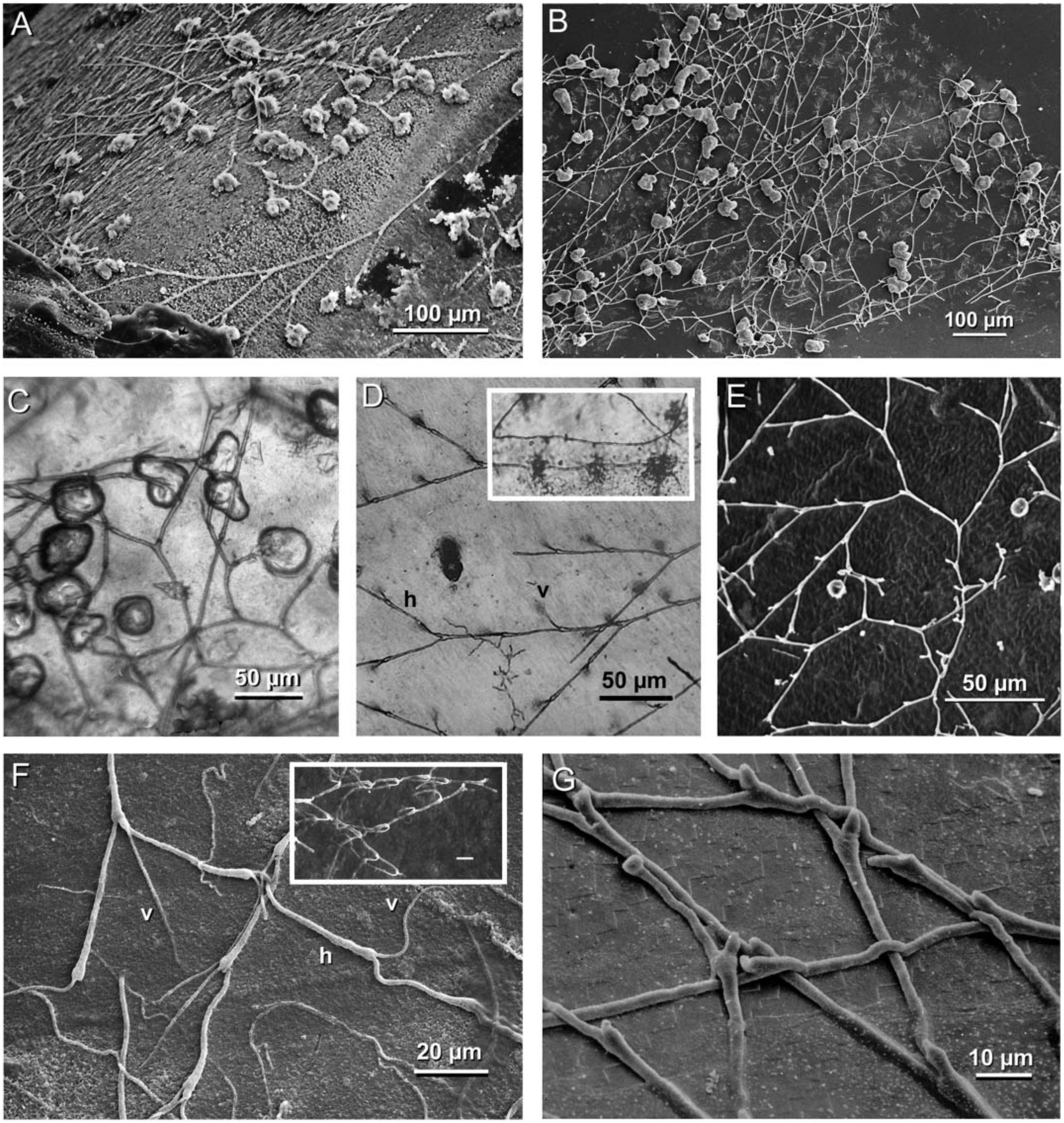

FIG. 1. *Saccomorpha stereodiktyon* isp. nov., a complex trace of fungal affinity. **A.** SEM images of resin-cast microborings arranged over the interior surface of a shell fragment (carbonate removed); Kornat Island, Croatia, 70 m, showing highly organized branched segmented tunnels with terminal sporangial cavities. **B.** Dense interfering colonies with irregularly shaped sporangial cavities in a *Callista chione* shell exposed one year at 85 m water depth; Kosterfjord, Sweden. **C.** Microborings and terminal sporangial cavities in a transparent deep sea shell fragment; Red Sea sediment 1558 m deep (sample Me 158). **D.** Bifurcated segmented tunnels with horizontal (h) and vertical (v) branching. **Insert:** The same shell at different focal plane, showing spotted bioerosion clouds at the level of organic lamella in the shell; Kornat Island, Croatia. **E.** Bifurcation of the horizontal network visualized by SEM of resin-cast borings. **F.** Resin-cast "horizontal" segments of tunnels with collapsed "vertical" tunnels in between; *Arctica islandica* shell from Sommerøy-Malangen, Norway; ca. 43 m. **Insert:** "Vertical" tunnel casts showing unidirectional collapse by drainage of specimens (scale = 20 μm). **G.** Detail image of resin cast of segmented bifurcating tunnels, bearing "buds" of "vertical" branches and showing avoidance at intersections, Kornat Island, Croatia. Images C and D taken by transmitted light microscopy, others by SEM.

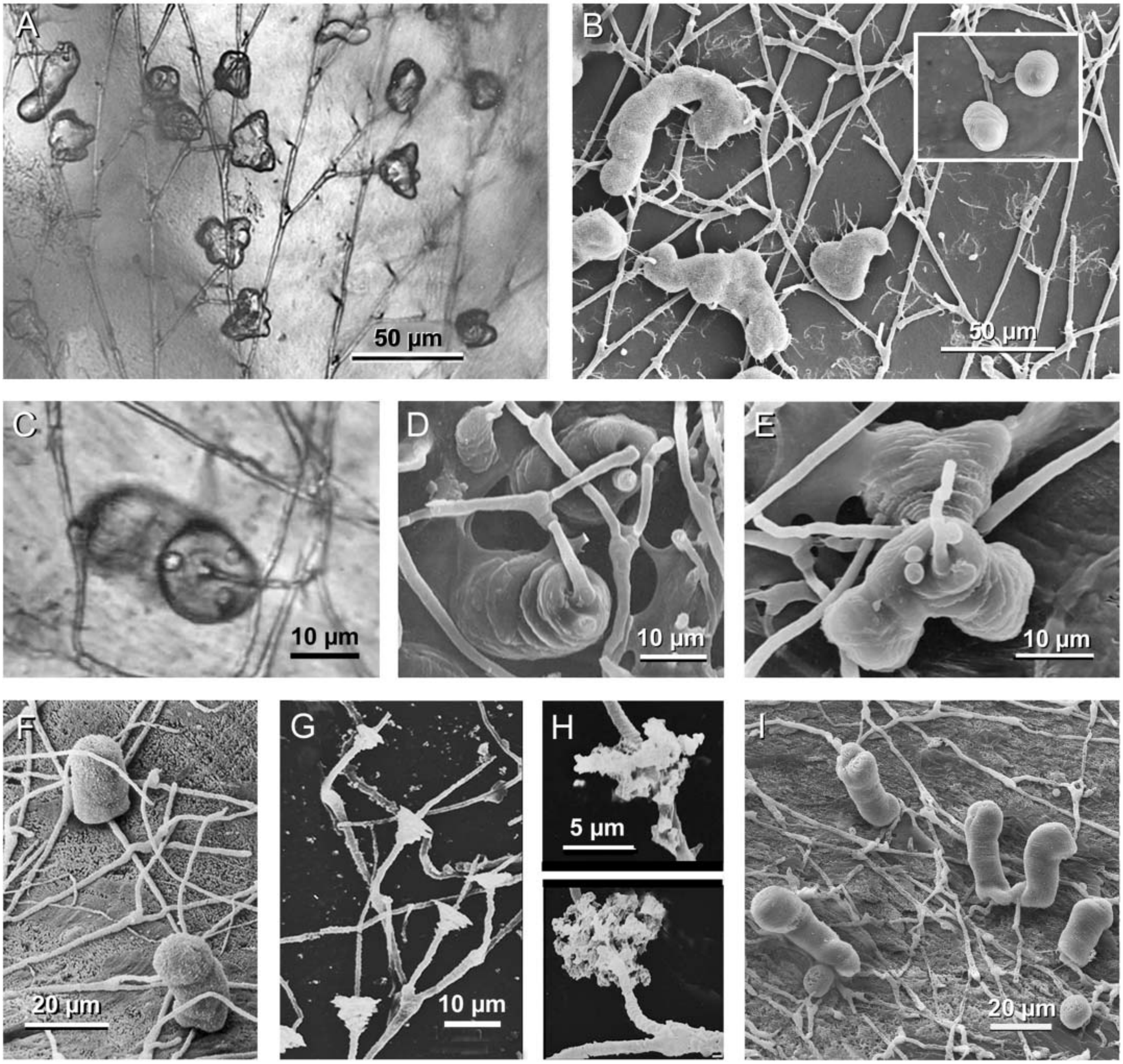

FIG. 2. *Saccomorpha stereodiktyon* isp. nov. reproductive and nutritional adaptations. **A.** "Horizontal" system of tunnels in a shell fragment with irregular sporangial cavities at the ends of side branches. Shell fragment, Kornat Island, Croatia, 70 m. **B.** Resin casts of interfering tunnels and elongated sporangial swellings (detail of Fig.1B). **Insert**: Early developmental stage of spherical terminal sporangial swellings (same magnification). **C.** The floor of a sporangial cavity with centrally attached hyphal tunnel surrounded by three protuberances oriented toward the substrate surface as seen through a transparent shell; Kornat Island, Croatia, 70 m. **D.** Resin cast of two cylindrical sporangial cavities in similar perspective, views from the shell surface inward, same sample as in C. **E.** A cast of an inward diverging sporangial cavity. **F.** Casts of two cylindrical sporangial cavities with interconnecting hyphal tunnels as viewed from the interior toward the surface of the shell of the bivalve *Delectopecten vitreus* from cold-water coral reef Sula Ridge, at 270 m water depth. **G.** A group of vertical tunnels cast in resin showing bioerosional cones diverging upward toward organic lamella in the host shell; a shell fragment at 70 m depth on Kornat Island, Croatia. **H.** Detail of the same sample, showing bioerosional cones in side view (above) and in perspective (below) both at the same scale. **I.** A group of elongated sporangial cavities, one showing a depression at the interior side. Same sample as in Fig. 2F. Images A and C are taken by light microscopy, others by SEM.

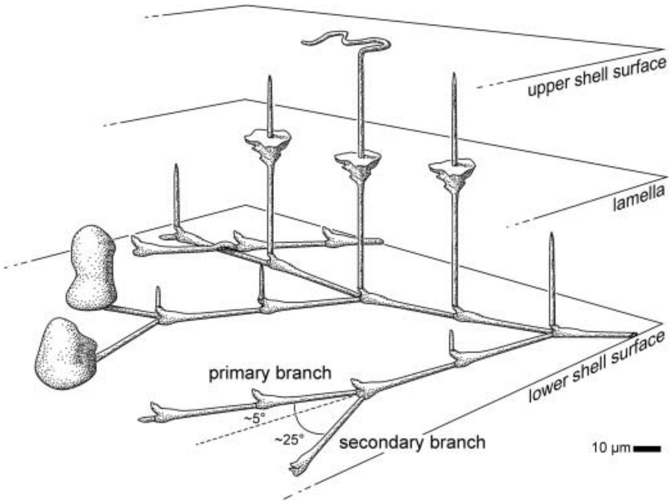

FIG. 3. Schematic presentation of the three-dimensional display of the trace *Saccomorpha stereodiktyon* isp. nov. in relation to the invaded shell and the position of an organic lamella inside. Note the asymmetric angle of bifurcation and distinction between branches and the cone-shaped etch fields on vertical tunnels as they approach organic lamella in the shell.

become surrounded by clouds of a profuse fibrous texture, seen as dark spots, often with a reddish tint (Fig. 1D, insert). Such textures occur consistently at the same level, which coincides with the position of organic lamellae incorporated in the bivalve shell. Further detail of these structures was revealed by SEM imaging (see below).

The "horizontal" network of bifurcating tunnels is often developed along the concave side of a bivalve shell. The resin replicas of the upright tunnels remain preserved when shell fragments are carefully dissolved but they often collapse between the horizontal forks (Fig. 1F), sometimes bending in the same direction when the specimen is drained of fluid following dissolution of the shell (Fig. 1F, insert). The replicas of the more robust horizontal tunnels remain anchored to the interior substrate surface and permit detailed observations by SEM (Fig. 1G): Both horizontal bifurcations and upright branches originate from cone-shaped nodes at distal ends of segments. Upright branches often remain dormant for a while, resembling buds (Fig. 1G), as observed on the periphery of expanding colonies. The mature central parts of the colony exhibit the full three-dimensional display of this trace consisting of bifurcating horizontals and simple, unbranched vertical tunnels.

The bifurcations are not truly dichotomous, because the resulting branches are not symmetrical (Fig. 1A, schematic in Fig. 3). They often depart at an angle of 20–30 degrees, whereby one branch continues with minor declination of 5–10 degrees from the growth axis of the preceding segment, while the other declines by 20–25 degrees; the branch that follows closer the general direction of growth can, thus, be recognized as primary, and the branch that departs at a larger angle as secondary. The general tendency of growth produces a fan, which curves step-wise, following the angles of primary branches, while the fan widens by radiating secondary branches (Fig. 1A, top). Note that the secondary branches are often one-sided; they are usually also the bearers of nodes with vertical branches and they terminate by forming sporangial swellings (Fig. 1A). However, the priority roles of branches may alternate so that the secondary branches take on the characteristics of primary branches soon after the first bifurcation (Fig. 1E). While primary branches guide the expansion of the system, the secondary branches soon terminate growth by taking the role of reproduction. The distinction between primary and secondary branches is less clear when there is an increase of filament density and frequency of interferences among tunnels. The proliferation of tunnels within each colony ceases with the development of terminal sporangial swellings on all branches.

The terminal swellings are irregularly shaped, isodiametric to elongate, often with multiple bumps protruding in different directions (Fig. 2A). The swellings form at the ends of horizontal hyphal tunnels close to the substrate surface and are initially spherical (Fig. 2B, insert); they grow inward to become elongated, up to 30 μm wide and 50 μm long, with an average proportion of 1:2 (Fig. 2B). They assume a cylindrical shape (Fig. 2C) or develop two or more inward radiating growth extensions or bumps (Fig. 2E). Each sporangial swelling is attached to the end of a horizontal branch at the center of its flat or slightly indented bottom. One to several small (2–3 μm in diameter) round protrusions form on the bottom of the sporangial cavities close to the hyphal attachment point. These protrusions extend toward the substrate surface (Figs. 2C–E), probably forming conduits for the release of spores. The sporangial swellings (cylindrical as well as multilobate) are seen standing upright when cast in polymerised resin (Figs. 2F and I).

Trace Development

A colony of *Saccomorpha stereodiktyon* isp. nov. spreads from the initial point of entry into the shell, extending underneath the shell surface and forming a shallow network of bifurcated tunnels up to several mm in diameter. As in many other microbial euendoliths, the differentiation takes place in the opposite direction from that of growth and colony expansion. While the periphery of the colony is dominated by outward radiating segmented and bifurcated "horizontal" tunnels, the upright tunnels start as short stubs (Fig. 1G) and then extend into the interior of the shell, increasing in length from the periphery toward the centre of the colony. As these filaments penetrate deeper into the shell and encounter organic lamellae incorporated there by the mollusc, they produce a "digestion field," an area of high porosity often in the shape of an inverted cone as visualized by SEM (Fig. 2G). This area is seen by light microscopy as clouds of dark, reddish spots (Fig. 1D, insert). The resin replicates this porous area in the form of a clump with spongy texture (Fig. 2H, bottom), which is apparently generated by a combination of carbonate dissolution and selective enzymatic digestion of the organic lamella. Such a biocorroded field surrounds each of the vertical filaments as they approach an organic lamella forming an upward diverging inverted cone with a flat upper surface, that marks the level of the attacked lamella (Figs. 2G and H, top). The tunnels that continue penetrating the shell above the level of the lamella form again a tube with smooth walls and show no evidence of lateral biocorrosion, similar in outline to the tube below the "digestion field." They may encounter further lamellae or other organic compounds deeper inside the shell or, as observed in thinner shells, may reach the opposite surface of the shell, where they continue to wind underneath and parallel to that surface. Morphological differentiation and the resulting three-dimensional display of tunnels and sporangial swellings are reconstructed and schematically presented in Figure 3.

Fossil Record

The formal description of the new trace follows the custom of trace description and ichnological nomenclature by being based on fossil type material. The holotype we selected that shows the characteristics of the new ichnotaxon was found in an oyster shell recovered from the Stepovak Formation, Early Oligocene of Alaska, USA. The same characteristics are also illustrated in the trace specimen selected as paratype from the Ratheim Formation, Early Oligocene in Niederrhein, Germany. Other fossil occurrences were found and identified in Late Eocene (Priabonian) at Brendola, Northern Italy and Late Palaeocene Prince Creek Formation in Alaska. The specific mode of branching of the new ichnospecies permitted a reliable identification of this ichnotaxon in shell fragments of Jurassic age (Table 1). Earlier occurrences of similar forms as old as the Ordovician were found to be different; they remain within the earlier described ichnospecies *S. terminalis*. We have reassessed the published record of modern and fossil traces characterized by terminal swellings and clarified the synonymy in the systematic ichnology section below.

Relation to *Saccomorpha terminalis* Radtke, 1991

Terminal position of sporangial swellings is a conspicuous property, which was first used in describing and naming a microbial euendolithic trace of presumed fungal affinity: *Saccomorpha terminalis* Radtke, 1991. The formation of terminal swelling in a variety of traces was noticed by Radtke (1991, p. 97), who compared their other properties. The present study confirmed that *S. stereodiktyon* isp. nov. is a morphologically well-defined ichnotaxon with elaborate differentiation in form and function that is distinct from *S. terminalis,* whereas the terminal position of sporangial swelling alone occurs in different unrelated taxa apparently by convergent evolution. The distinctive features are summarized in the systematic ichnology below.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Saccomorpha* Radtke, 1991

Ichnospecies *Saccomorpha stereodiktyon* isp. nov.

Figs. 1–4

Synonymy:

1937 *Arborella kohli* Zebrowski: p. 562, pl. 27, fig. 8 (= biospecies)

1937 "An arborescent species"—Porter and Zebrowski: pp. 254–257, fig. 1c

1969 *Phytophthora* sp.—Höhnk: p. 135, fig. 4b (= biospecies)

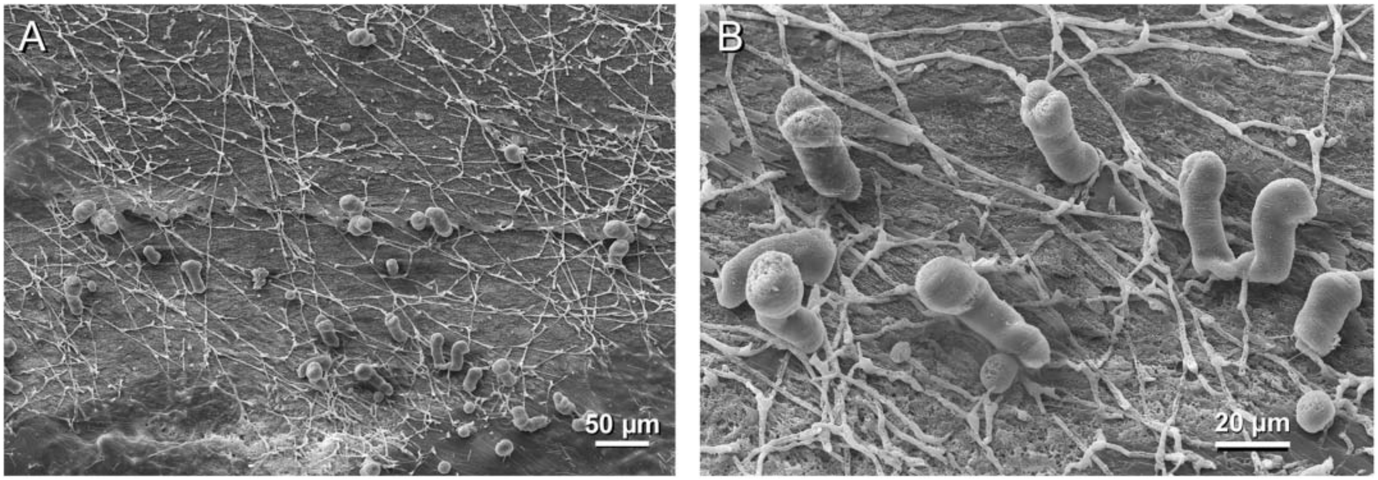

FIG. 4. *Saccomorpha stereodiktyon* isp. nov., holotype from a fossil oyster shell (*Ostrea tigiliana*) of Early Oligocene, Stepovak Formation of SW Alaska. **A.** View of the network of cast microborings with terminal swellings inside the shell. **B.** Detail showing several inward expanding sporangial swellings. SEM of epoxy resin casts.

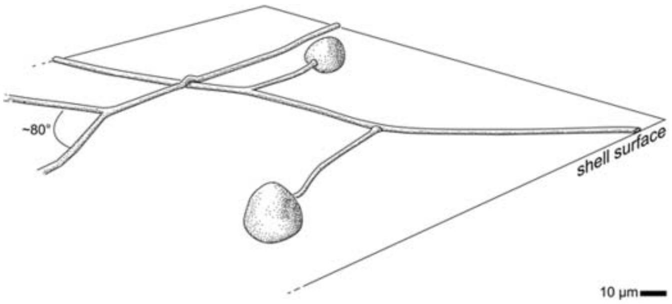

FIG. 5. Schematic presentation of *Saccomorpha terminalis* Radtke, 1991, showing primarily two-dimensional extension but also producing terminal sporangial swellings. Note the wide angle of tunnel branching.

1991 *Saccomorpha terminalis* Radtke: tab. 29: Bo7/36, Bo7/116, Bo7/147 (= isp. nov.)

1994 "Unbestimmte rezente Bohrspur"—Glaub: pp. 83–84, pl. 2, fig. 6, pl. 3, fig. 5

2004 "Sack-shaped form"—Vogel and Marincovich: pp. 13–16, fig. 4.5

2004 "Thumb-branches form"—Vogel and Marincovich: p. 14, fig. 4.6

2005 *Saccomorpha terminalis*—Wisshak, et al.: pp. 106–108, figs. 10D–H (non Radtke, 1991)

2006 *Saccomorpha terminalis*—Wisshak: pp. 68–69, figs. 19D–H (non Radtke, 1991)

Etymology: From stereos (Greek: στερεός) = solid, occupying space and from (Greek: δίκτυον) = net.

Holotype: Sample Bo 16/10 of Vogel and Marincovich, 2004: fig. 4.5, SMF 111 (Senckenberg Forschungsinstitut, Frankfurt a.M.).

Paratype: Sample Bo 7/147 of Radtke, 1991, Hückelhofen, Mine shaft Sophia Jakoba 6 (Niederrhein), Germany, Ratheim Formation, Early Oligocene.

Locus typicus: West Head, Unga Island, SW Alaska, USA.

Stratum typicum: Stepovak Formation, Early Oligocene.

Diagnosis: Complex system of borings composed of (a) bifurcated and segmented tunnels underneath and parallel to the substrate surface (shells), producing (b) numerous simple upright branches penetrating the interior of the shell, and (c) terminal swellings. The segments of the horizontal network are straight, gradually widening in direction of growth and forming distal conical nodes, where horizontal and vertical branches originate. Swellings are spherical later becoming elongated toward the interior of the shell or growing irregular protrusions. Smaller protrusions at the bottom of the swellings form separate connections to the substrate surface. The casts of deeply penetrating upright tunnels carry an upward diverging widening where they pass the organic lamellae of the bored shell and may extend to the opposite surface of the substrate.

Remarks: Because of similarity in positioning of terminal sporangial swellings, the trace has been in the past confused with *Saccomorpha terminalis* Radtke, 1991. *S. stereodiktyon* is a well characterized ichnospecies quite distinct from *S. terminalis,* while the latter retains its validity as summarized below.

Ichnospecies *Saccomorpha terminalis* Radtke, 1991
Fig. 5

Synonymy:

? 1990 "Lampion-Form"—Schmidt: p. 114, pl. 15, fig. 7

1991 *Saccomorpha terminalis* Radtke: pp. 97–98 [partim], pl. 14, figs. 4+6 (Bo7/75 + Bo7/27), non pl. 5 (Bo7/8) (= *Ichnoreticulina elegans?*), non tab. 29: Bo7/116 + Bo7/147 (= *S. stereodiktyon*)

? 1992 *Saccomorpha terminalis*—Schmidt: pp. 78–79, pl. 8, figs. 4 and 5

non 1994 *Saccomorpha terminalis*—Glaub: pp. 83–84, fig. 29, pl. 3, fig. 4 (= ?)

1996 "Fungoid-Form B"—Hofmann: p. 57, pl. 3, figs. 1 and 2

non 2005 *Saccomorpha terminalis*—Wisshak, et al.: pp. 106–108, figs. 10D–H (= *S.*stereodiktyon)

non 2006 *Saccomorpha terminalis* – Wisshak: pp. 68–69, figs. 19D–H (= *S. stereodiktyon*).

Remarks*:* In the original description Radtke (1991) defined *Saccomorpha terminalis* as a network of fine, branching galleries with thick, oval to spherical, terminal cavities. She further characterised the trace as thin tunnels 2–3.5 μm in diameter (up to 6 μm), with dichotomous branchings at blunt angles of 120–130°, with widening up to 7 μm at the branch-points. Individual tunnels avoid other traces, and may exhibit repeating arches ("jumping"). Spherical to irregularly shaped cavities (sporangia) measuring 7–36 μm are connected to tunnels in terminal position. Based on new observations and new state of knowledge, one of the paratypes (Radtke, 1991, pl. 14, fig. 5) is now regarded as probably terminal swellings belonging to *Ichnoreticulina elegans* and is thus questioned. The holotype (Radtke, 1991: pl. 14, fig. 4) as well as the other paratype (Radtke, 1991, pl. 14, fig. 6) are most representative of diagnostic features of this ichnotaxon. Variants of tunnel organization and terminal sporangial swellings require further investigation. A schematic sketch of the architecture of *S. terminalis* (Fig. 5) is presented for comparison with the more complex three-dimensional colony pattern of *S. stereodiktyon* isp. nov. (Fig. 3).

DISCUSSION

The new ichnofossil describes an elaborate system of microboring traces with consistent arrangement of segmented tunnels, rhythmic occurrence of branching, differentiation, and dual orientation (horizontal and vertical) of branches in addition to formation of terminally positioned sporangial swellings. This trace is produced by a heterotrophic (organotrophic) organism as indicated by its distribution in skeletal carbonates down to aphotic water depths. A corresponding cladochytrid fungus has been described and illustrated from beach sand in Australia by George Zebrowski under the name *Arborella kohli* (Zebrowski, 1937, pl. 27, fig. 8). The new ichnofossil has been placed in the ichnogenus *Saccomorpha* Radtke, 1991, which unifies complex traces composed of narrow hyphal tunnels and sack-like sporangial swellings.

Due to the terminal position of sporangial swellings, this trace was previously included in the ichnotaxon *Saccomorpha terminalis* Radtke, 1991 (see list of synonyms). However, it has now been shown that *S. stereodiktyon* isp. nov. is distinguished by a pattern of several specific characteristics, which grant a separate ichnospecies status. It has also been observed that the terminal position of sporangial swelling occurs in a number of different and often unrelated organisms, such as the chlorophyte *Ostreobium quekettii* and its trace *Ichnoreticulina elegans* (e.g., Radtke, 1993; Radtke and Golubic, 2005). However, the validity of *S. terminalis* is not affected by the description of the new ichnospecies, instead this contribution recognized subtle but consistent morphological differences between those traces that share terminal sporangial swellings. The distinction characterizing the new ichnospecies as different from *S. terminalis* is evident in tunnel segmentation, branching pattern and in the two-tier organization of horizontal and vertical tunnels. The unique asymmetric bifurcation of segmented filaments and rhythmic distribution of upright branches are the most characteristic properties of *S. stereodiktyon* isp. nov. In contrast, the established *S. terminalis* Radtke, 1991, as illustrated by the holotype (Radtke, 1991, pl. 14, figs. 4 and 6) forms straight to curved but unsegmented tunnels of variable diameters.

The fossil Early Tertiary specimens of the new trace *S. stereodiktyon* isp. nov. are almost indistinguishable from their modern counterparts (compare Fig. 4 with Figs. 1 and 2) regarding the specific mode of branching and shape and growth direction of terminal swellings. Our findings confirm earlier observations that the shape of microborings in carbonates are tightly controlled by the shape of their makers and, given the stability of the substrate (limestone, shells), microborings have a high preservation potential (e.g., Wisshak, et al., 2008) producing what may be considered "instant fossilization" (Radtke et al., 2011).

An important factor in the distribution of organotrophic euendolithic microorganisms refers to the composition, amounts and structuring of the organic matter incorporated in shells and other skeletal carbonates. The participation of organic matter in biocalcification and mineral organization of skeletal carbonates has been widely acknowledged (e.g., Keith et al., 1993; Kobayashi and Samata, 2006), emphasizing an impressive diversity of proteins participating in skeletal construction, although these organic compounds are present in very low concentration mostly not exceeding 5% (Zhang and Zhang, 2006). The amount, consistency, and distribution of organic matter in shells vary depending on the species of the mollusc. This diversity may be reflected in substrate preference or specificity of organotrophic microborers as reflected in their distribution and feeding strategies, which requires further investigation.

Unlike phototrophic euendoliths, microboring fungi are not confined by intraskeletal organic lamellae (Golubic et al., 1975, fig. 12.8) but instead are rather attracted to them, as demonstrated by fungal boring of the nacreous layer in the Polynesian black pearl oyster *Pinctada margaretifera* var. *cumingii* (Mao Che et al., 1996, fig. 2a) that left traces marked by dark pigmentation. The dark brown pigment associated with fungal activity is most probably mycosporine, a common secondary product of fungi (Volkman and Gorbushina, 2006; Sinha et al., 2007). This pigment is also released by fungi penetrating coral skeletons, especially when they attack the euendolithic alga *Ostreobium quekettii;* the pigment became aligned with the faces of aragonite crystals (Priess et al., 2000, figs. 3b and c).

The present study of microbial traces demonstrates the interaction between hyphae inside the upright tunnels and the structural organic lamellae in the bored shell, visualized by dark pigmented specks (Fig. 1D, insert) and by SEM images, showing the upward diverging fields of biocorrosion as the hyphae approached the organic lamellae (Figs. 2G and H). This finding illustrates the importance of the organic matter embedded in skeletal carbonate as a source of carbon and energy for fungi and other organotrophs, which extensively exploit this resource while bioeroding the skeletal remains even after the death of the animal.

The study of complex microbial boring traces offers an opportunity to follow the developmental process of the euendolithic organism over time, starting from the moment of its initial penetration into the substrate and, whenever possible, to the completion of its life cycle. In some cases, the size of the borehole may provide developmental information. Many microbial euendoliths reproduce by tiny propagules (spores, baeocytes) that may also initiate their endolithic life. The propagule may enter the substrate by excavating a small hole, whereas larger galleries form later as the organism grows while penetrating into the substrate's interior. The euendolith may maintain repeated contacts with the surface, to secure exchange of nutrients and metabolic products or to form openings for propagule release. The progression in development of euendolithic microorganisms can be reconstructed by comparing colonies of different sizes (i.e., ages). It can also be studied on single populations that differentiate as they grow in form and function. Such a growth strategy includes an aggressive exploratory stage observable at the periphery of a growing colony, while later, more mature developmental stages are observable toward the colony center. Such a growth pattern was observed on traces *Ichnoreticulina elegans* produced by a siphonale chlorophyte (Radtke, 1993; Radtke and Golubic, 2005) and *Rhopalia clavigera,* produced by a segmented chlorophyte (Golubic and Radtke, 2008). It is presently shown in the development of the fungal trace *S. stereodiktyon* isp. nov.

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