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A LUCINOID BIVALVE TRACE FOSSIL *SARONICHNUS ABELI* IGEN. ET ISP. NOV. FROM THE MIOCENE MOLASSE DEPOSITS OF LOWER AUSTRIA, AND ITS ENVIRONMENTAL SIGNIFICANCE

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Abstract: A new ichnogenus and ichnospecies *Saronichnus abeli* is described for a protrusive trace fossil produced by the lucinoid bivalve *Thyasira michelottii* from storm-dominated siliciclastics of the Miocene (Lower Badenian) Grund Formation. A chemosymbiotic life strategy under dysaerobic conditions is proposed for this bivalve. The trace fossil expresses an adaptation to oxygen-poor habitats.

Key words: Miocene, Austria, chemosymbiosis, molasse, trace fossils, *Thyasira*.

Introduction

The availability of oxygen is an important factor for the distribution of benthic organisms (Savrda & Bottjer 1991). The distribution of marine trace fossils is frequently reported to indicate oxygen levels in the water column and sediment (e.g. Savrda et al. 1991). Even if their producers are unknown, trace fossil associations and sequences are used to determine depositional history and environmental parameters (e.g. energy, nutrients, oxygen). Sediment-ingesting polychaetes, sipunculids, or even detritus-feeding arthropods have been regarded as potential tracemakers, providing evidence for chemosymbiotic life strategies under dysaerobic conditions (Bromley & Ekdale 1984; Savrda 1992). Chemosymbiosis in fossils is very difficult to prove and the only reliable method is probably the study of ichnofossils, especially if associated with specimens preserved in life position (Savazzi 2001).

Dwelling below the substrate surface is a very common life habit for bivalves. Depending on the physical properties of the environment and substrates, specialized life strategies have been developed by such molluscs. *Lithophaga, Gastrochaena, Gregariella* and *Teredo* produce borings by corrosion or mechanical abrasion in hard or firm substrates such as limestones or wood. The corresponding trace fossils are known as *Gastrochaenolites* or *Teredolites* (Kelly & Bromley 1984; Bromley et al. 1984; Tewari et al. 1998). Almost all such borings are clearly defined permanent structures not obscured by shifting of the valve position, as commonly occurs in soft substrates. More or less stable bivalve burrows are known from the recent *Solemya velum*, which produces Y-shaped structures that shift their position only every few days (compare Frey 1968; Stanley 1970; Levinton & Bambach 1975), and from the fossil state (ichnogenus *Solemyotuba* Seilacher 1990). Clearly defined shapes of bivalve burrows in soft substrates were considered to be relatively rare in the fossil record. Vagile deposit-feeding bivalves such as *Nucula* and *Yoldia* (Bender & Davis 1984), which belong to the Paleotaxodonta, were recognized as producers of the trace fossil *Protovirgularia* (Han & Pickerill 1994; Seilacher & Seilacher 1994; Ekdale & Bromley 2001). Detailed morphological studies enabled the feathered-serpent-shaped *Hillichnus lobosensis* to be identified as a tellinacean trace fossil (Bromley et al. 2003).

The thyasirid bivalve *Thyasira michelottii* (Hörnes, 1875) produced a shaft-like trace fossil in the Miocene of Austria (Zuschin et al. 2001). Here, we present an additional distinct bivalve trace fossil produced by the same species. The unique in situ preservation of the burrowing bivalve *Thyasira michelottii* in the siliciclastics of the Grund Formation (Middle Miocene, Lower Badenian), clearly associated with trace fossil *Saronichnus abeli* Pervesler et Zuschin, allows the life habits of these bivalves and the characteristics of their marine environment to be reconstructed.

Material and methods

Thyasira shells associated with the discussed trace fossil were excavated during the field campaigns in 1998 and 1999 (Zuschin et al. 2001; Zuschin et al. 2004; Roetzel & Pervesler 2004). The slightly cemented trace fossil could be exposed by the use of an air jet, which allowed careful removal of the surrounding sediment. A pistol-shaped valve was used to control the direction and volume of the airflow (Pervesler & Uchman 2004). Clear varnish helped to preserve the trace fossil. This method, mainly developed for loose sands, provides an opportunity to observe three-dimensional aspects of even very delicate structures. *Thyasira* shells in life-position were studied in the sections D, E, G and H (Fig. 1).

Results

The burrowing bivalve *Thyasira michelottii* from the Grund Formation was found together with associated trace fossils (Fig. 3). An inhalent tube from the anterior shell margin pro-

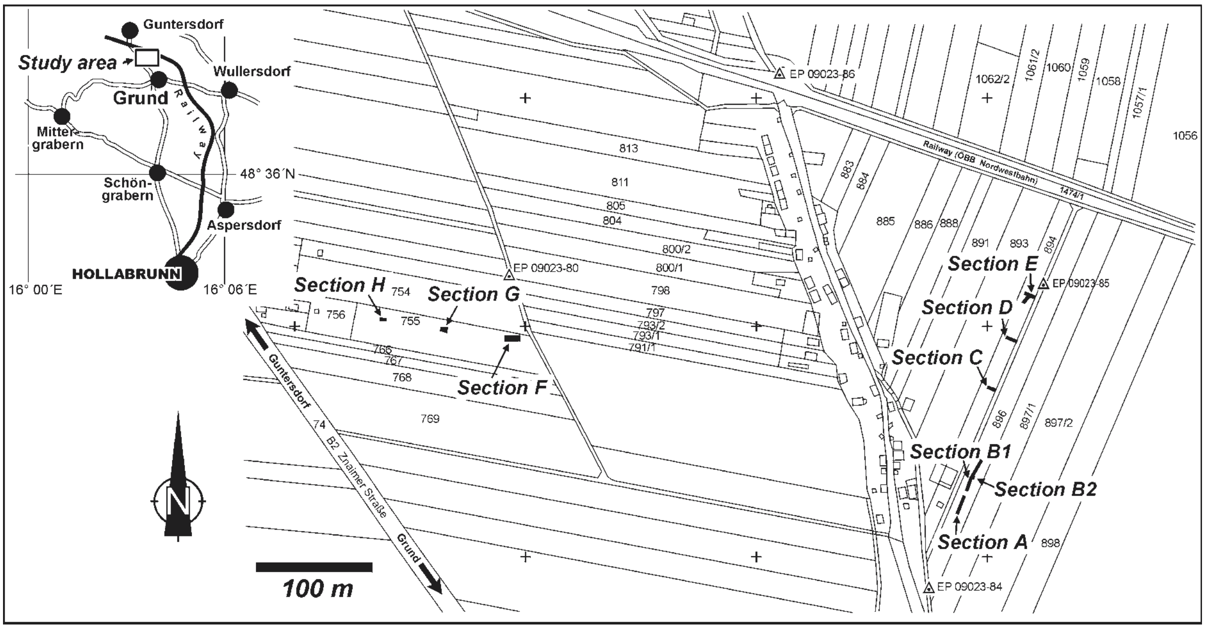

Fig. 1. Type area of the Grund Formation. Sections A, B1, B2, C, D, E excavated in 1998, sections F, G and H in 1999. *Thyasira michelottii* shells in life position together with their trace fossils were found in the sections D, E, G and H.

vided the connection to the former sea floor (Fig. 3.4), and a system of probes below the life position of the bivalves protruded more than 10 cm into the surrounding sediment. The probes show a variety of shapes from broom- to star-like structures (Figs. 3.2–4). In the proximal portion of the trace fossil the probes converge and form a bundle starting from the ventral shell margin (Fig. 2). Distally, the probes are tubular to blade-shaped, up to 3 mm wide, with rounded tips. Their orientation was perpendicular or slightly inclined with respect to the bedding. Horizontal protrusions were never observed. The shifting of these probes started close to the shell margin. Rootlike branchings along the distal portions, as observed in the burrows of the recent *Thyasira flexuosa* (Dando & Southward 1986), were mentioned as being morphologically reminiscent of *Chondrites* (Savrda & Bottjer 1991; Savrda 1992). These features were not observed in the *Thyasira michelottii* burrows.

Systematic Ichnology

Chondrites group

Saronichnus igen. nov.

Derivation of name: *Saronichnus* (Greek Σαρων — broom, Ιχνος — footstep, trace).

Type ichnospecies: *Saronichnus abeli* Pervesler et Zuschin (this paper).

Diagnosis: A system of vertical to steeply inclined tubular to blade-shaped simple unbranched probes diverging from broom- or star-like bunches. The probes are up to 100 mm long and about 3 mm wide. The bunch structures start from the posterior ventral edge of bivalve shell. The probes overlap in the upper part of the bunched and form a spreite structure visible in cross-section. The structures are typically cemented.

Discussion: Although the chemosymbiotic trace fossils *Chondrites* and *Saronichnus* may have functional similarities as sulphide wells, and although both are typical elements of the *Zoophycos* ichnofacies, they can clearly be distinguished

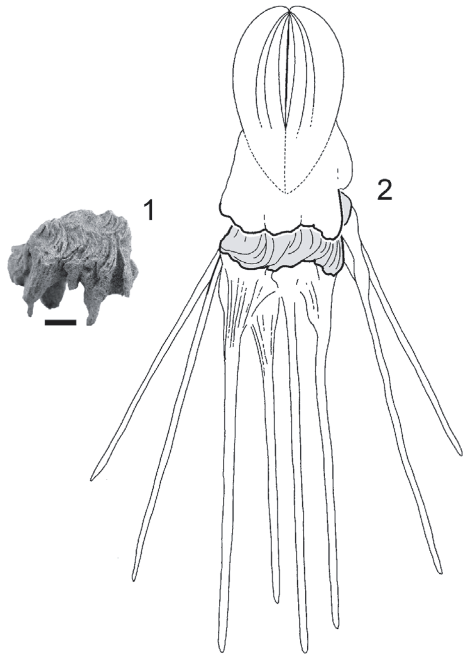

Fig. 2. *Thyasira michelottii* and *Saronichnus abeli* from the Grund Formation. **1** — Horizontal cross-section of *Saronichnus abeli* (paratype IPUW No. 2003-0001-0002). The rootlike structures are composed of falcate backfill-like structures produced during the penetration of the sediment by the extendable foot of the bivalve *Thyasira*. Excavation 1999, section G. Scale bar = 1 cm. **2** — Relation of cross-section shown in figure 2.1 with reconstructed probes and position of the bivalve.

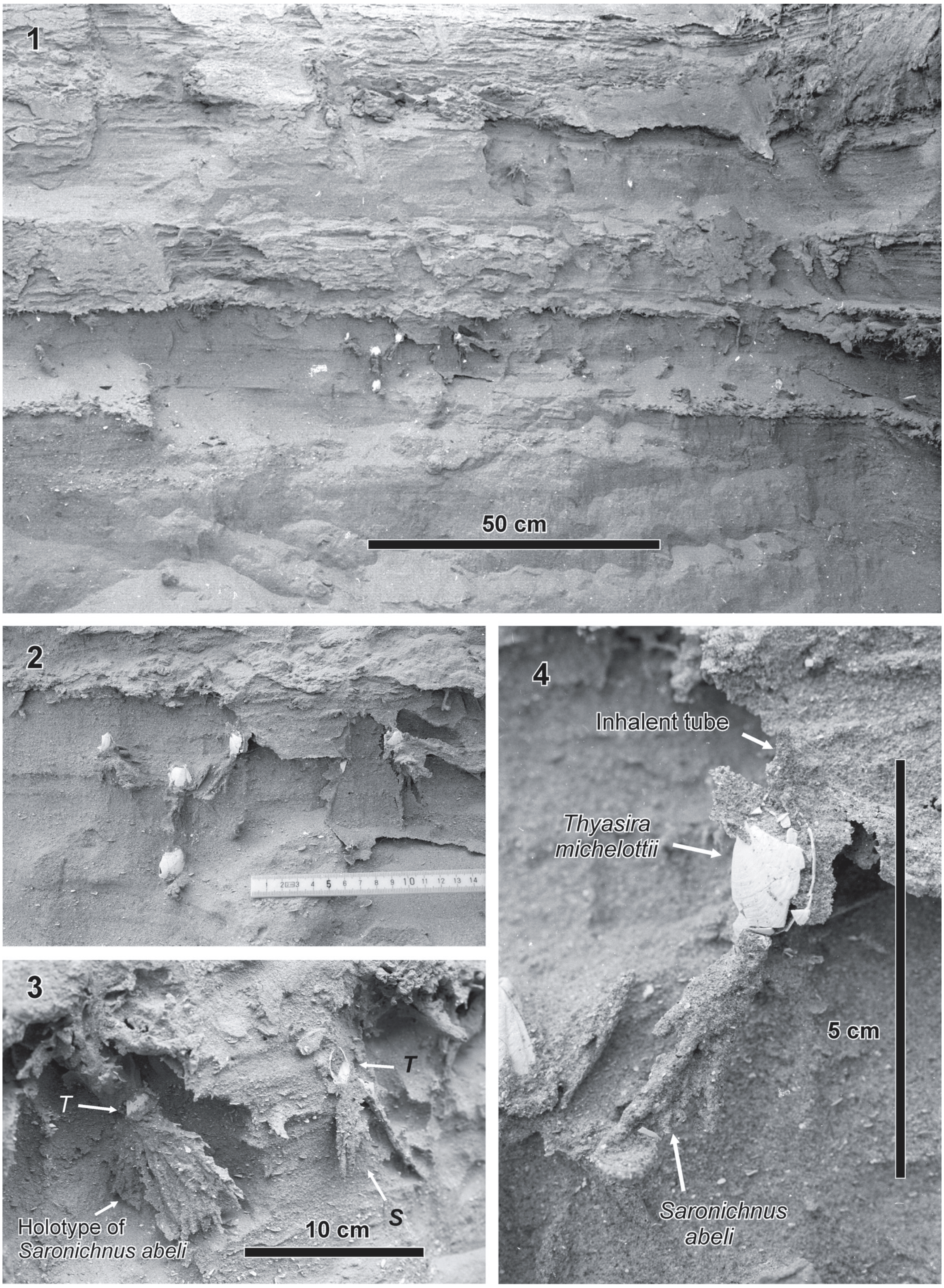

Fig. 3. *Thyasira michelottii* and *Saronichnus abeli* from the Grund Formation. **1** — Overview of an artificial outcrop in the type area of the Grund Formation during the excavation in 1999 (section G). Several individuals of *Thyasira michelottii* in life position, connected to their broom-shaped trace fossils (*Saronichnus abeli*), are associated with a broad variety of other trace fossils typically start from pelitic layers that cover each fining upward sequence. Trace fossils were exposed by using compressed air. Unidentifiable fragments of molluscs are components of the sediment. **2** — In situ *Thyasira michelottii* with *Saronichnus abeli* (detail of Fig. 3.1). **3** — Two in situ individuals of *Thyasira michelottii* (T) with their trace fossil *Saronichnus abeli* (S). Left specimen was defined as the holotype (IPUW No. 2003-0001-0001). Note the large variability of these trace fossils (excavation 1999, section G). **4** — Close-up view of in situ *Thyasira michelottii* with inhalent tube and *Saronichnus abeli* attached to the shell. The single shafts have diameters up to 3 mm and protrude several centimeters into the sediment below the ventral shell margin (detail of Fig. 3.2).

on the basis of their morphology. We therefore do not apply the ichnogenus C*hondrites* to these *Thyasira* burrows, but postulate the new ichnogenus *Saronichnus. Saronichnus* is similar to *Pragichnus fascis* Chlupáč (1987), which was described from the Ordovician of Czech Republic. However, *Pragichnus* displays rather only club-shaped, not blade-shaped, branched probes, which are actively filled. The lower part of the *Pragichnus* probes displays dichotomous branches. The probes were interpreted as sulphide wells produced by an animal using chemosymbiotic bacteria (Mikuláš 1997). *Saronichnus* is also similar to *Syringomorpha* Nathorst, 1886, which is a vertical fan-like structure composed of steep, tightly spaced cylinders (Bartholomäus 1993; Jensen 1997). The upper and lower termination of the latter is not clear. It is not excluded that these two ichnogenera may be synonymized in the future, but *Syringomorpha* requires further studies to recognize its full morphology. *Heimdallia* Bradshaw, 1981 is composed of vertical, superimposed cylinders, but it is a wall-like, long structure in which the terminations of the cylinders remain unknown.

Saronichnus abeli isp. nov.
Figs. 2, 3.1–4

Derivation of name: *abeli* [Abel, Othenio * 20. 6. 1875 Vienna, † 4. 7. 1946 Mondsee (Upper Austria), was one of the founders of paleontology as an independent science. He worked on understanding how extinct animals interacted with their environment].

Types: Holotype IPUW No. 2003-0001-0001 (Fig. 3.3), paratype IPUW No. 2003-0001-0002 (Fig. 2). Together with 5 further specimens of *Saronichnus abeli* they are housed in the Department of Paleontology of the University of Vienna, Austria.

Diagnosis: As for the ichnogenus.

Description: As for the ichnogenus.

Discussion

Life habit of Thyasira michelottii

The posterio-ventral probes are thought to record the search of the burrowing, worm-shaped foot for pockets of sulphidic material in an otherwise low-sulphide environment, similarly to the recent bivalve *Lucinoma aequizonata* (Cary et al. 1989). Chemosymbiotic strategies may be responsible for the similarity between recent *Thyasira* burrows and *Saronichnus abeli* trace fossils. In chemoautotrophic symbioses, bacteria that use sulphides for their metabolism serve as food for the bivalve, which in turn creates a protected environment for the bacteria (Felbeck 1985). Among the superfamily Lucinoidea, special anatomical and morphological features such as thick gills, reduced palps, short simple gut, and an elongated burrowing foot are interpreted as an adaptation to oxygen- and nutrient-poor habitats (Allen 1958). The broom-like burrow systems are formed when the clams use their extendable foot to obtain hydrogen sulphide from interstitial water in the underlying sediments (Turner 1985). The length and number of burrows are related to the concentration of hydrogen sulphide in the sediment (Dufour & Felbeck 2003). For a detailed discussion of the life habit see Zuschin et al. (2001).

Environment

The Grund Formation is characterized by a rapid alternation of allochthonous psammitic and autochthonous pelitic sedimentation, with a distinct decrease in water energy from the base to the top. The sandy layers, especially in the lower part of the section, commonly show channel structures. They consist predominantly of thick skeletal concentrations; common features include sharp erosive bases, graded bedding and a densely packed bioclast-supported fabric (Roetzel & Pervesler 2004; Zuschin et al. 2004). They are therefore interpreted as high-energy, short-term events and most likely represent proximal tempestites, similar to the Jurassic deposits of India (Fürsich & Oschmann 1993). *Thyasira michelottii* occurs in life position in close association with the pelitic layers. The life position is confirmed by valve articulation and preservation of the inhalant and posterio-ventral *Saronichnus* probes. The abundance of *T. michelottii*, as well as its monospecific occurrence, indicate that the chemical and physical conditions of the sediment preferred by this thyasirid species were unsuitable for other molluscs.

The post-event pelitic layers are background sediments that accumulated mostly between storm events. These poorly bioturbated pelitic layers represent periods of colonization (colonization window *sensu* Pollard et al. 1993). The trace fossils occurring in sandy layers are related to colonization surfaces in the overlying pelitic layers. All the burrows represented by the trace fossils had connections to the sea floor. Primary sedimentary structures are well preserved, and the trace fossils disturb them only to a limited extent. The connection of the burrows to the sea floor and the limited bioturbation suggest poor oxygen conditions within the sediments, but not in the water column above the sea floor. The impermeable pelitic layers sealed the coarse event layers rich in organic matter and prevented the exchange of oxygen between the sediment and the water column. This resulted in a low-oxygen content in the coarse sediments and the colonization by a low-diversity post-event climax community. The community produced long-occupied burrows that document complex living strategies (e.g. chemosymbiosis, gardening).

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