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PIONEER COLONIZATION EVIDENCED BY *RHIZOCORALLIUM* IN THE MIDDLE TRIASSIC OF POLAND

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Abstract: A large collection of the trace fossil *Rhizocorallium* from the Middle Triassic of the Polish part of the Germanic Basin (Peri-Tethys) is analysed and their ichnotaxonomical classification presented. Special attention is given to the deep form of *Rhizocorallium* with a vertical retrusive spreite, filled with faecal pellets, with detailed documentation of this structure, based on isolated specimens and serial sections. This analysis also reveals ∩-shaped and deep, protrusive structures. A former interpretation of *Rhizocorallium* as a rapidly formed fugichnion is not followed here; instead, an interpretation of the trace fossil as a complex fodinichnion is proposed. Scavengers and their relation to crinoid meadows, as well as predators, are indicated as potential tracemakers of some *Rhizocorallium*. Although *Rhizocorallium* is common throughout the Middle Triassic, unusual forms and the domination of substrates by *Rhizocorallium* in general mostly occur in the transgressive system of the lowermost Muschelkalk, and in regressive, marginal facies of the lower Keuper. Such a distribution of unusual forms of *Rhizocorallium* is interpreted as representing opportunistic, pioneer burrow assemblages that developed during the long-term benthic recovery after the P-T crisis, or in unfavourable conditions generally. Moreover, dynamic conditions with mixed clastic-carbonate sedimentation and rapidly varying salinity promoted smooth transitions from *Rhizocorallium* to *Diplocraterion*. Similar successions of dominant trace-fossil assemblages, of comparable sizes, occur in many sections around the world and demonstrate the record of slow recovery that continued through the Middle Triassic. The illustrated record of evolution of the Middle Triassic *Rhizocorallium* assemblages in Poland documents the last two stages of benthos recovery after the P-T boundary. A similar situation is observed around the world and, in many cases, great abundance of *Rhizocorallium* seems to be an indication of pioneer burrowing in dynamic, unfavourable environments.

Key words: Trace fossils, bioturbation, Muschelkalk, ichnotaxonomy, palaeoecology, post-extinction biota recovery.

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INTRODUCTION

Rhizocorallium is a common ichnogenus of the trace fossils of invertebrates that occurs throughout the Phanerozoic. It is also one of the earliest recognized and most cited trace fossils (Knaust, 2013). Many older papers interpret this trace fossil as a structure, formed by crustaceans or bivalves, but according to Knaust (2013), the most likely producers of marine *Rhizocorallium* are polychaetes. Reviews on this ichnogenus by Fürsich (1974) and Knaust (2013), in addition to many other ichnotaxonomic papers, illustrate and describe diverse forms of *Rhizocorallium* in different areas. Several ichnospecies of *Rhizocorallium* were described by Fürsich (1974), but only two ichnospecies*, R. jenense* Zenker, 1836 and *R. commune* Schmid, 1876, with several ichnosubspecies and variants, are accepted in the recent classification by Knaust (2013). Nevertheless, the junior synonym *R. irregulare* Mayer, 1954 of the latter ichnospecies has been widely used in the literature; recently, some workers (e.g., Feng *et al.*, 2018) suggested several new ichnospecies that seem to be morphological or taphonomic variants of known ichnotaxa.

The ichnogenus *Rhizocorallium* is typical of shallow-marine environments and its ichnospecies and variants usually reflect some parameters of sedimentation, especially substrate consistency. In fact, this trace fossil, or more precisely its ichnospecies, ichnosubspecies or variants, demarcates the *Cruziana* and *Glossifungites* ichnofacies, depending on the presence or absence of scratches (Seilacher, 2007; Buatois and Mángano, 2011; MacEachern *et al.*, 2012; summarized in Knaust, 2013; Bayet-Goll *et al.*, 2018). Shallow-marine environments usually contain the similar trace fossil, *Diplocraterion* Torell, 1870, which belongs to the same ichnofamily Rhizocoralliidae Richter, 1926, which is rather typical of the *Skolithos* ichnofacies (*sensu* Seilacher, 1967), but usually occurs together with *Rhizocorallium* (e.g., Rodríguez-Tovar and Pérez-Valera, 2008). These two ichnogenera are defined by their different orientations within the sediment, i.e., vertical forms are *Diplocraterion*, whereas horizontal to oblique forms are *Rhizocorallium* (e.g., Rodríguez-Tovar *et al.*, 2007; Rodríguez-Tovar and Pérez-Valera, 2008; Knaust, 2013). In fact, some burrows show a smooth transition between these ichnotaxa. In the last quarter of a century, numerous papers have been published that deal with *Rhizocorallium*, especially its palaeoecological significance which reflects the development of the burrowing benthic community after the Permian/Triassic extinctions around the world (e.g., Twitchett, 1999, 2006; Zonneveld *et al.*, 2001; Pruss and Bottjer, 2004; Mørk and Bromley, 2008; Chen *et al.*, 2011; Feng *et al.*, 2017a, b, 2018; Luo *et al.*, 2020; Stachacz and Matysik, 2020).

Although *Rhizocorallium* is known and described from many places around the world, the best examined and most numerous specimens are in the Triassic of the Germanic Basin, which is the type area for its type ichnospecies, *R. jenense* (see Knaust, 2013, tab. 3). A large collection of *Rhizocorallium* from this basin, mostly in central Germany, was examined by Knaust (2013). Numerous other localities of the Germanic Triassic with *Rhizocorallium* occur in southern Poland (e.g., Szulc, 2000; Kowal-Linka and Bodzioch, 2011; Chrząstek, 2013; Matysik, 2016; Stachacz and Matysik, 2020). Moreover, the Polish Muschelkalk section offers an unusual, deep, retrusive form of *Rhizocorallium*, which previously was described as *Teichichnus* isp. by Szulc (2000) and later recognised as *Rhizocorallium* isp. by Kowal-Linka and Bodzioch (2011). This trace fossil originally was described as *Lithochela problematica* by Gümbel (1861) in the Upper Triassic of the Bavarian Alps and assigned to the ichnosubspecies *Rhizocorallium commune problematica* by Knaust (2013). Similar forms of *Rhizocorallium* have been noted in the Jurassic of England (Fürsich, 1974) and the Jurassic of Portugal (Fürsich, 1981; Schlirf, 2000) and mostly were placed in *R. jenense*.

The paper by Kowal-Linka and Bodzioch (2011) is the only description that illustrated cross-sections of deep *Rhizocorallium,* interpreting it as an escape structure (fugichnion), formed by benthic organisms that were buried rapidly by a thick storm deposit. In contrast, Fürsich, (1974, 1981) and Schlirf (2000) interpreted this structure as a feeding structure. The extensive monograph on *Rhizocorallium* by Knaust (2013), beyond taxonomic classification, only mentioned *Rhizocorallium* with vertical retrusive spreite as being caused by storm deposition.

The present paper illustrates the deep *Rhizocorallium* with a retrusive spreite, including its cross-sections, with details that have never previously been published. Interpretation of this trace fossil as an escape structure, as proposed by Kowal-Linka and Bodzioch (2011), is not followed herein; instead, the burrow is recognised as a polychaete feeding trace, formed within tempestite beds. Moreover, scavenging and possibly predation by the *Rhizocorallium* tracemaker are proposed. Strong development of *Rhizocorallium* assemblages in the early Middle Triassic, observed in the Polish Muschelkalk (Stachacz and Matysik, 2020) and in other parts of the world (e.g., Zonneveld *et al.*, 2001; Luo *et al.*, 2017; Feng *et al.*, 2018), is discussed briefly as one of the stages of benthos recovery. In addition, forms transitional between the ichnogenera *Rhizocorallium* and *Diplocraterion* and their relationship to dynamic, stressful environments of variable salinity also are discussed.

GEOLOGY

General setting

During the Middle Triassic, a large part of present-day Poland, as well as Germany and England, was occupied by the Germanic Basin (Peri-Tethys Basin). This basin was connected to the open Tethys Ocean by narrow depressions: the East Carpathian Gate, the Silesian-Moravian Gate and later in the Pelsonian, the Western Gate (Szulc, 2000). The partial isolation of the basin caused the characteristic facies distribution that reflects progressive northward transgressions from the ocean and diachronism between the different parts of the basin. Generally, normal-marine conditions dominated close to the gates (i.e., the ocean), whilst sedimentation with a terrestrial, more clastic influence took place in central to marginal parts of the basin. The gates opened and closed diachronously from east to west, and generally the centre of the basin migrated to the west, following the Tethyan spreading centre (Szulc 2000). The study area in Upper Silesia (Poland) was located close to the Silesian–Moravian Gate and represents the most open-marine conditions of the Germanic Basin. Marine conditions in Western Europe appeared as three depositional sequences later and the facies, especially those of the uppermost Muschelkalk, distinctly differ. Nevertheless, the depositional development of third-order relative sea-level changes is consistent in both areas (Szulc 2000; Matysik, 2019).

Middle Triassic strata in the Polish part of the basin are developed as a series of diversified marine carbonates. The lowermost Middle Triassic locally comprises the Röt facies, represented by early diagenetic dolomite; next, the entire Muschelkalk consists of diversified carbonates, and the lowermost Keuper is represented by siliciclastic-carbonate deposits. This interval represents a record, which starts with a marine transgression in the Olenekian–Aegean (early Anisian), followed by open-marine conditions in the Bithynian-Fassanian (Anisian–lower Ladinian), and ends with a regression in the Longobardian (late Ladinian; Szulc, 2000; Matysik and Szulc, 2019).

The Lower Gogolin Beds (Aegean) that represent the lowermost Muschelkalk and the Miedary Beds, which lie at the boundaries of the Muschelkalk and Keuper, were analysed. These two lithounits, as described below, respectively represent the earliest stage of the Muschelkalk sea transgression and (in Poland) its closing, regressive stage, when the basin was relocated westward (Szulc, 2000).

Description of exposures

Lower Gogolin Beds

A typical section of the Lower Gogolin Beds crops out in the active quarry at Żyglin (N 50.481846, E 18.964589), but closely comparable lithology of the same age with similar trace-fossil assemblages also was examined in detail at Psary (N50.177545, E19.531288) and several other quarries (Figs 1, 2). The lowest Gogolin Beds belong to the lowermost, transgressive part of the Muschelkalk and are represented by shoreface facies that contain rudstone as well as calcarenite with large-scale cross-bedding, referable to the *Skolithos* ichnofacies (*sensu* Seilacher, 1967). These organodetrital limestones contain very few trace fossils; nevertheless, vertical dwelling burrows (*Skolithos* and *Arenicolites*) and cosmopolitan *Planolites* occur locally (Stachacz and Matysik, 2020).

The upper part of the section forms typical Wellenkalk (wavy limestone) facies of the maximum flooding zone, i.e., marl, micritic limestone, wackestone, peloidal or crinoid calcarenite, which represent the archetypal *Cruziana* ichnofacies (Seilacher, 1967; Fig. 2). These deposits usually are highly bioturbated, but tempestitic beds with hummocky or swaly cross-stratification are clearly visible. The Wellenkalk facies is characterized by an abundance of moderately diverse skeletal and trace fossils. *Rhizocorallium* and *Oravaichnium* ichnofabrics predominate*,* with less common *Thalassinoides, Planolites, Palaeophycus, Ptychoplasma* and *Protovirgularia;* other trace fossils rarely occur (Szulc, 2000; Stachacz and Matysik, 2020).

The section reveals several horizons of hardgrounds that contain borings and encrustations of the *Trypanites* ichnofacies (*sensu* Frey and Seilacher, 1980). Such horizons are developed as an uneven surface of micritic limestone, or as irregular, lithified intraclasts, eroded from the seafloor (flat-pebble conglomerate). In both cases, numerous *Placunopsis* encrustations and the boring *Trypanites* occur. Moreover, numerous firmgrounds with *Balanoglossites* and scratch traces (mostly on *Rhizocorallium*) occur. Locally, the Gogolin Beds contain horizons of characteristic wavy-bedded, micritic, usually marly mudstone without lamination as well as body and trace fossils. This limestone facies is interpreted as resulting from the soft deformation of platy-bedded intervals (Stachacz and Matysik, 2020).

The intervals of the Wellenkalk facies of the Lower Gogolin Beds (Sequence Anisian1) and Upper Gogolin Beds (Sequence Anisian2) are separated by lagoonal facies of the Zellenkalk (Szulc, 2000). The latter facies is developed as an early diagenetic dolomite that contains no body or trace fossils.

Miedary Beds, Miedary (N50.4536, E18.7702)

The inactive clay pit at Miedary, approximately 6 km west of Tarnowskie Góry town (Fig. 1), consists of olive-grey, brownish to greenish and reddish silt with intercalations of beige to yellow dolomite and grey sandstone (Fig. 2) that as a facies represents the lowermost Keuper (Kotlicki, 1974a, b). According to Sulej *et al.* (2011), the Miedary section lies above the uppermost Muschelkalk, represented by the Boruszowice Beds, although the relationship of these two

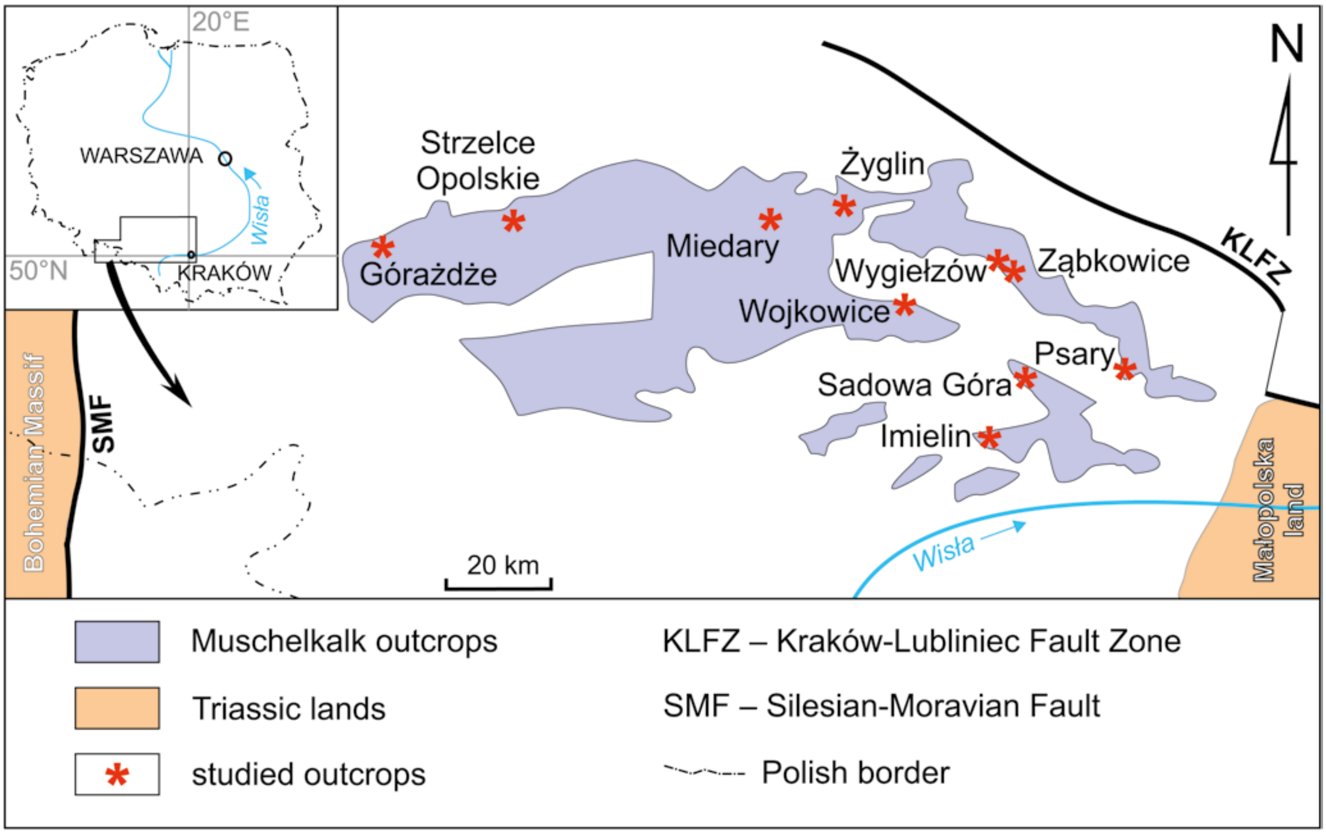

Fig. 1. Location maps. Geology after Szulc (2000).

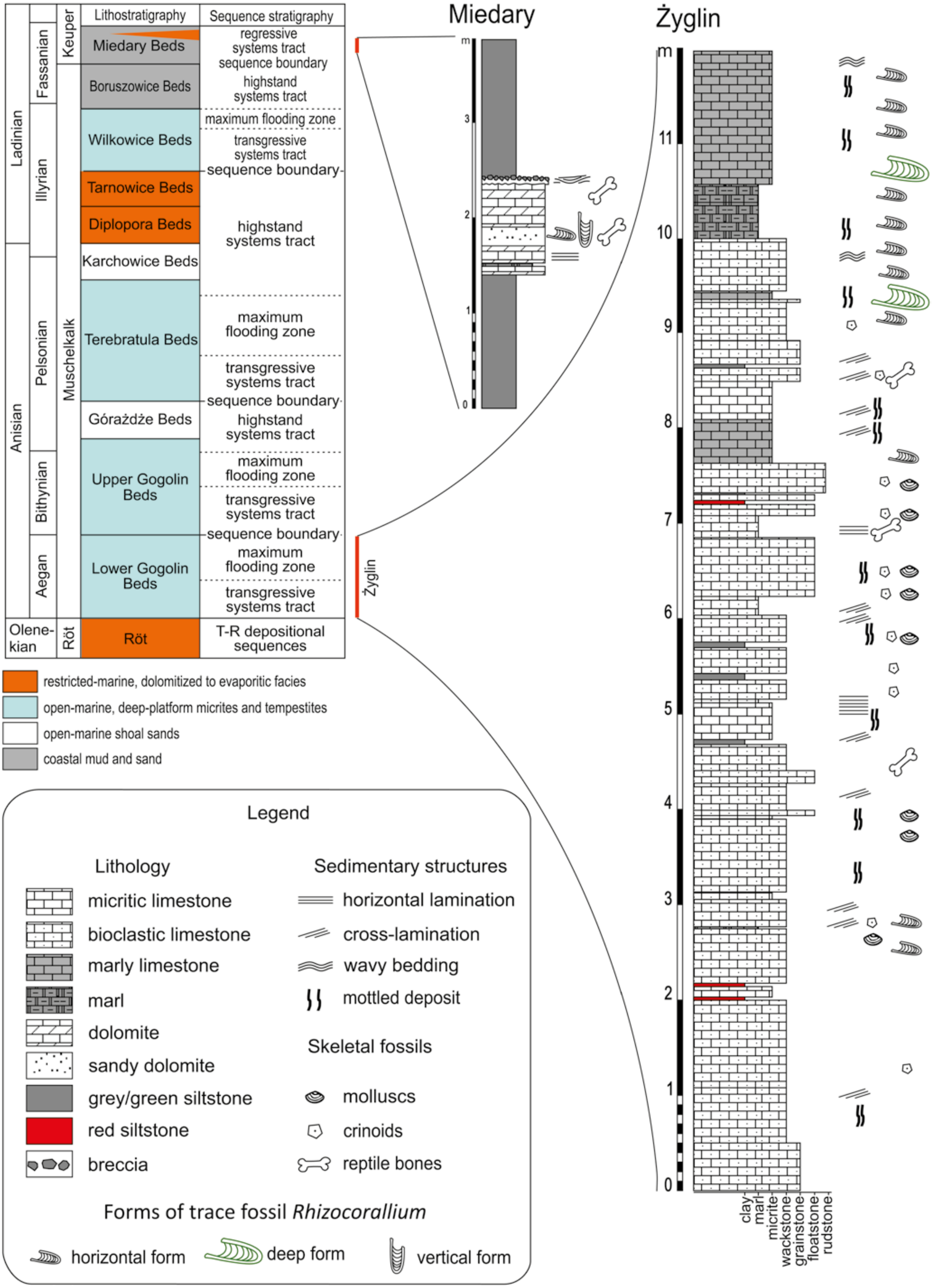

Fig. 2. Stratigraphic position and logs of the sections studied.

divisions is unclear and its lithology is similar to that of the Boruszowice Beds (cf. Assmann, 1944; Kotlicki, 1974a). The age of the studied rocks is still under debate, but palynomorphs point to the Ladinian (Sulej *et al.*, 2011) and the closest exposures (at Laryszów, 1 km to the east) reveal lower Ladinian strata of the *Ceratites spinosus* Zone of the Fassanian (Kotlicki, 1974b; Salamon *et al.*, 2003).

Sandy dolomite intercalations in the upper part of the section are mostly layered, although Sulej *et al.* (2011) mentioned partly bioturbated beds with trace fossils, assigned to *Diplocraterion, Monocraterion*, ?*Planolites* ?*Palaeophycus* and cf. *Diplichnites*. Moreover, abundant fish and other marine vertebrate remains occur in different parts of the section (Sulej *et al.*, 2011; Pawlak *et al.*, 2022). At least one bed of sandy dolomite contains numerous *Rhizocorallium* of diverse orientations. The uppermost dolomitic bed contains cross-laminated (?hummocky) quartz sandstone and breccia, composed of angular, 2–15 mm clasts of siltstone.

MATERIALS AND METHODS

A large collection of trace fossils, mostly *Rhizocorallium,* was collected from several active and abandoned quarries, clay pits and small exposures, scattered in the Kraków-Silesia and Opole areas (Fig. 1). The trace fossils, found in the walls of the quarries and loose blocks, have been analysed in detail. The most interesting beds, containing the deep form of *Rhizocorallium* were vertically slabbed sequentially at distances of 2–30 mm and polished for detailed observation. As well, one completely preserved deep burrow was dissolved in 10% acetic acid (CH_3COOH) for analysis of noncalcareous remains. The details of the polished slabs and microscopic remains were analysed using a Nikon SMZ1000 binocular, coupled with a Nikon camera. All samples are housed at the Institute of Geological Sciences, Jagiellonian University in Krakow.

TRACE FOSSIL DESCRIPTIONS

Horizontal to subhorizontal, shallow form – *Rhizocorallium commune "irregulare"* (Mayer, 1954)

Single burrows or crowded accumulations of *Rhizocorallium commune "irregulare"* (see Knaust, 2013 for classification) are the predominant trace fossils in the lower Muschelkalk. This trace fossil usually produces an almost monospecific assemblage (*Rhizocorallium* ichnofabric; Stachacz and Matysik, 2020). The burrows are represented by diverse, horizontal to subhorizontal forms, composed of a marginal tube and spreiten between its limbs (Fig. 3). Simple U-shaped (Fig. 3A) and curved to spiral tongue-shaped burrows, 30–170 mm wide and 50–400 mm long (Fig. 3B–D; cf. Stachacz and Matysik, 2020, supplementary data) occur between them. Most of the burrows have faecal pellets within the spreite between the marginal tube (Fig. 3F). The faecal pellets are ellipsoidal, about 0.5 mm wide and 1.5 mm long and represent *Coprulus oblongus* Mayer, 1952 (Knaust, 2013). Some burrows display scratch traces on the surface of the marginal tube (Fig. 3D, E). Scratch traces, relatively short, parallel to each other and loosely arranged, are arranged in predominantly small sets (Figs 3F, 4B). However, some burrows show closely spaced criss-crossing scratches (Figs 3E, 4C) that are typical of inclined *R. jenense* (Knaust, 2013) and could be considered as belonging to this ichnospecies (cf. Stachacz and Matysik, 2020). The horizontal to subhorizontal form of *Rhizocorallium commune* is very common in most sections of the Lower Muschelkalk of Poland, especially in the Lower Gogolin Beds, and rarely in the Terebratula Beds at Górażdże and Strzelce Opolskie (see Stachacz and Matysik, 2020 for details).

Deep form – *Rhizocorallium commune problematica* (Gümbel, 1861)

Alongside the horizontal, shallow *Rhizocorallium*, diversified, deep forms are locally abundant. They are represented mostly by three-dimensional, troughed-shaped burrows with smooth or occasionally scratched marginal tubes (Fig. 4A, B). Rarely, scratched spiral forms also occur (Fig. 4C). The deep form of *Rhizocorallium* usually occurs within the tempestitic, micritic limestone bed, associated with a crinoidal tempestite (Fig. 4D, E). No apertures have been observed in any of these cases. Although the burrows occur within the tempestitic beds, occasionally with relics of cross-lamination, the sediment surrounding the burrows is always homogenized (Figs 5, 6A, D).

Cross-sections of the burrows display vertical to oblique, predominantly U-shaped, teichichnial, wall-like structures, formed by retrusive (dominant) or protrusive spreite limbs and a marginal tube (Figs 4E, 5, 6A, 7). In addition to the vertically U-shaped form, asymmetrical burrows with an underdeveloped retrusive limb, as opposed to a disproportionately deep second limb, also occur (Figs 5A, B, 6A, 7B; cf. Kowal-Linka and Bodzioch, 2011). The entire structure is commonly up to 160 mm long and 80 mm wide, up to 80 mm deep, and with a marginal tube 10–45 mm wide, depending on the burrow size. Some burrows have a different architecture and form an inverted U as ∩-shaped structures without a spreite between the limbs of the marginal tube (Figs 5C, E, 7C), or have a strongly developed horizontal part (area between the limbs of the marginal tube) that forms *Zoophycos*-like structures with occasional secondary tunnels or probes (Fig. 5D). Vertical, steeply inclined to subhorizontal protrusive limbs or tongues, up to 140 mm long, that penetrate into the sediment, are also observed (Fig. 5A, B). Some burrows, especially ∩-shaped ones (in vertical section) show secondary branches, forming a simple tube or chamber-like structures (Fig. 5D). One deep, retrusive spreite, ∩-shaped (in vertical section) burrow is cut by a smaller, shallow, horizontal burrow of 'normal' *Rhizocorallium commune* (Fig. 5E, left). However, the relationship between these two burrows is unclear, because in the opposite section, the smaller one seems to be connected with the larger limbs (Fig. 5E, right).

The spreite limbs and the areas between them, as well as the marginal tubes are filled with faecal pellets (*Coprulus oblongus* Mayer, 1952), as in *R. commune irregulare*

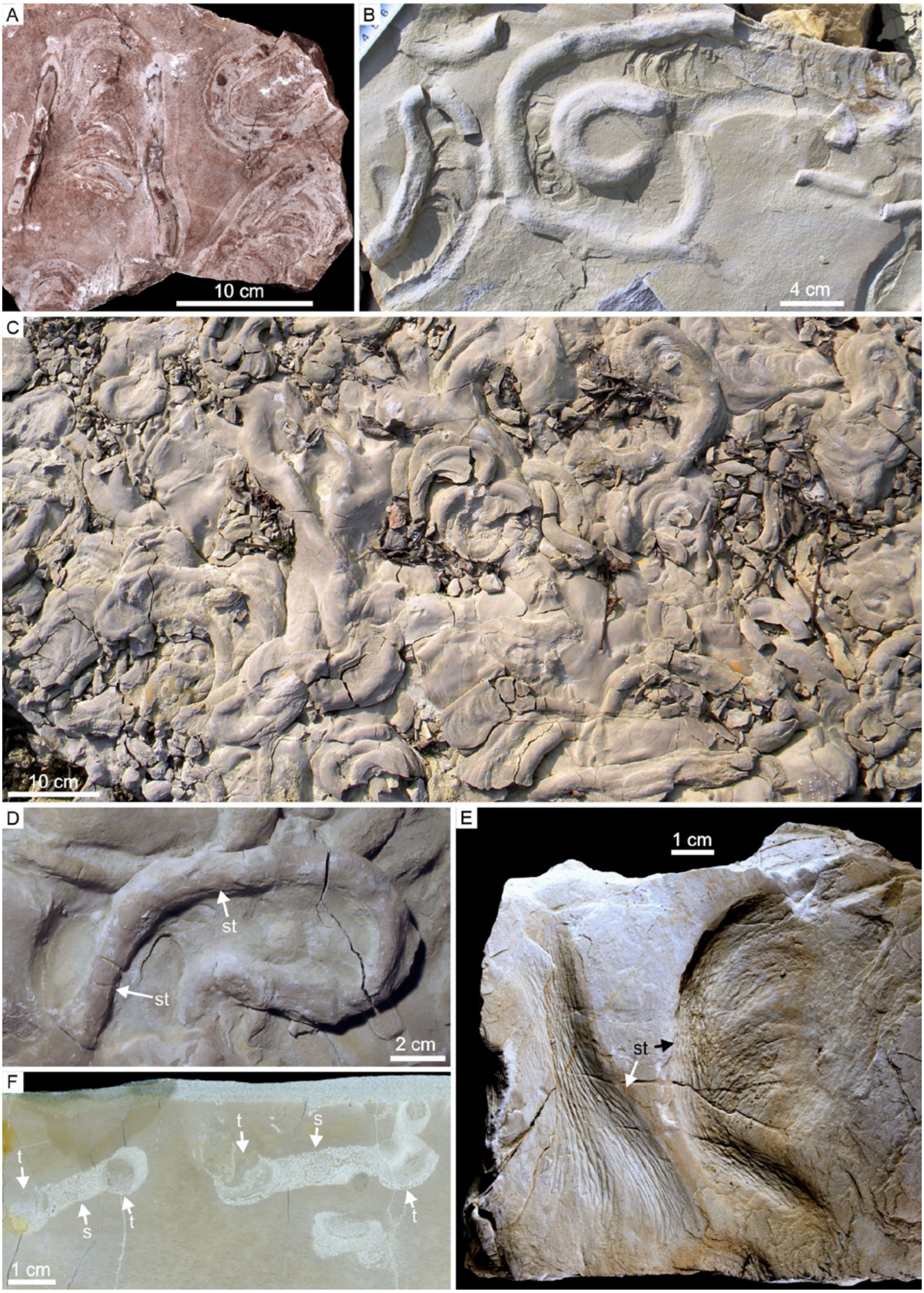

Fig. 3. Regular, horizontal to subhorizontal *Rhizocorallium commune* "*irregulare*" from the Gogolin Beds. **A.** Wide, smooth, tongue-like form with distinct spreite, Żyglin. **B.** Curved form, Żyglin. **C.** Crowded burrows, composed of curved tongues, Ząbkowice; photograph taken by Michał Matysik. **D.** Burrow with sparse scratches (st) parallel to the marginal tube, Wygiełzów. **E.** Net-like scratches (st) on marginal tunnels, Sadowa Góra. **F.** vertical section of horizontal burrows with visible marginal tubes (t) and spreiten area (s) filled with coprolites, Żyglin.

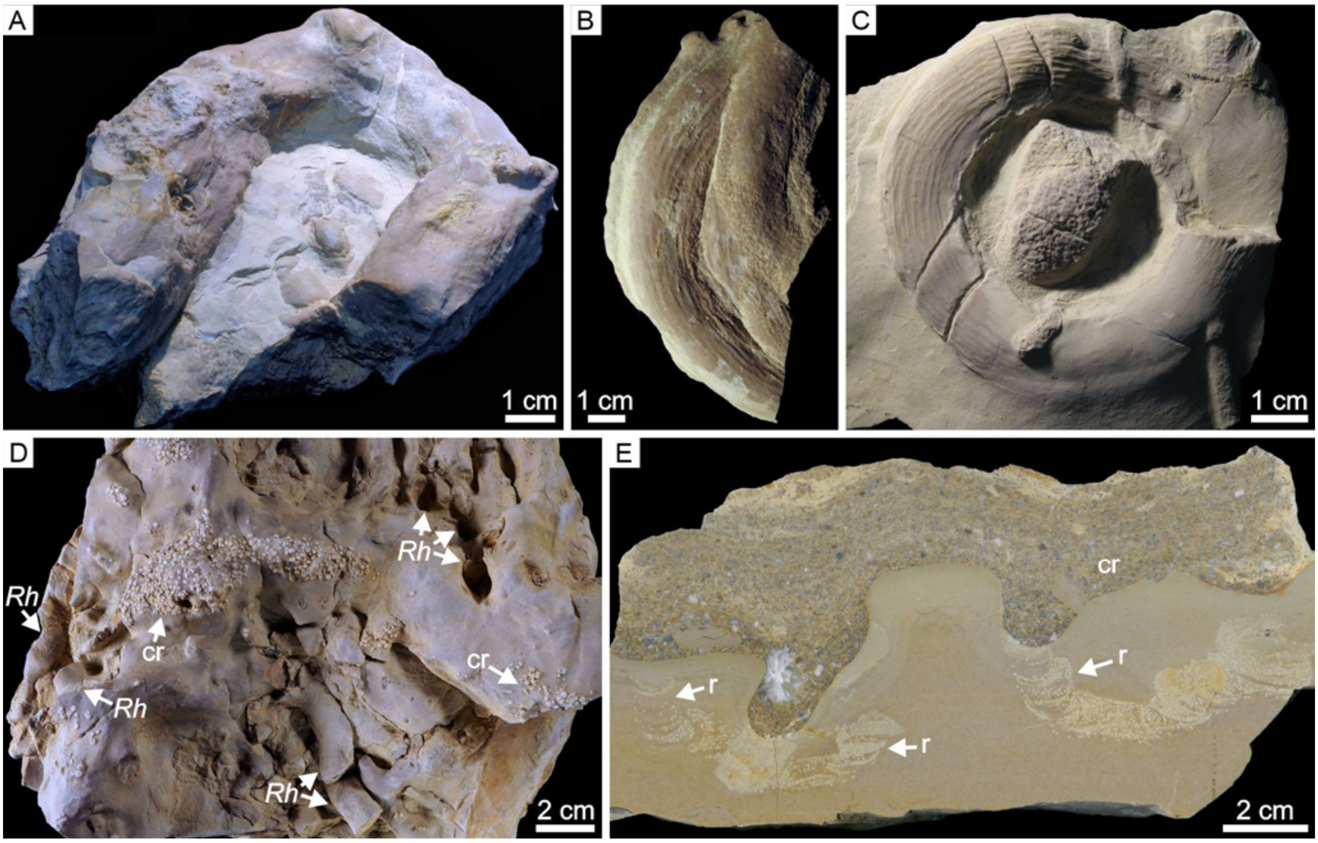

Fig. 4. Deep *Rhizocorallium* from the Gogolin Beds. **A, B.** Fragments of U-shaped burrows separated from the host rock, Wygiełzów; A – epichnial view; B – Hypichnial view, distinct scratches and coprolites are visible, hypichnial view. **C.** Spiral *R. commune ?uliarense* with crossing limbs, Żyglin, criss-crossing scratches and coprolites (c) are visible, hypichnial view. **D.** Amalgamated limestone bed with crinoid layer (cr) strongly bioturbated by *Rhizocorallium* (*Rh*), hypichnial view. **E.** Vertical cut of *Rhizocorallium* with retrusive limbs (r), eroded in the upper part and covered by crinoid layer (cr), Imielin.

(Figs 4E, 5, 6). Cross-sections of the burrows show that the faecal pellets occur in several different arrangements. The pellets within the horizontal or inclined limbs, as well as in the horizontal part between them, are generally densely packed in accordance with retrusive, or protrusive spreite patterns. Rarely, some limbs contain chaotically arranged pellets (e.g., Fig. 5D). The marginal tubes and some individual tunnels contain pellets in a different arrangement, i.e., as part of a distinct wall (e.g., Figs 5C, 6D). In another case, pellets are accumulated in a horizontal layer in the lower part of the burrow and some tunnels contain pellets, forming concentric layers that almost completely fill the tube (Fig. 6A–C). The faecal pellets are predominantly micritic, but rarely, some pellets contain partly corroded bioclasts, (crinoid ossicles, Fig. 6A–C). Also, some of the pellets, especially those filling the marginal tube, contain small calcite crystals (Fig. 6E). The pellets that form the wall usually are completely replaced by calcite crystals, up to 3 mm across (Figs 5, 6D; cf. Bodzioch and Kowal-Linka, 2001). The sediment, filling the marginal tubes, usually contains pyrite cubes as well (Fig. 5C). Moreover, one analysed burrow contains a single ?scolecodont and several placoid and ganoid fish scales.

The illustrated *Rhizocorallium commune problematica* come from the Lower Gogolin Beds at Żyglin, Wygiełzów, Imielin and Psary. Identical burrows were observed at Wojkowice, Sadowa Góra, Góra Świętej Anny and possibly at other localities in the same stratigraphic position (Fig. 1). Similar, deep forms of *Rhizocorallium* were observed in early diagenetic dolomite (Röt in the facies sense), directly below the Lower Gogolin Beds (Stachacz and Matysik, unpublished observations in 2017).

Horizontal to vertical *Rhizocorallium commune “auriforme”* (Hall, 1843)

U-shaped, horizontal, oblique to vertical, relatively short, tongue-like structure, which is composed of a marginal tunnel that forms limbs with a spreite between them (Fig. 8). The entire structure is 60–150 mm long and about 50–60 mm wide. The marginal tube, 5–10 mm in diameter, is filled mostly with quartz sand. The spreite area is generally filled with a finer deposit that has a higher carbonate content, similar to the host rock, although isolated ganoid fish scales and other skeletal remains occasionally occur. These trace fossils were observed only in the Miedary Beds at Miedary.

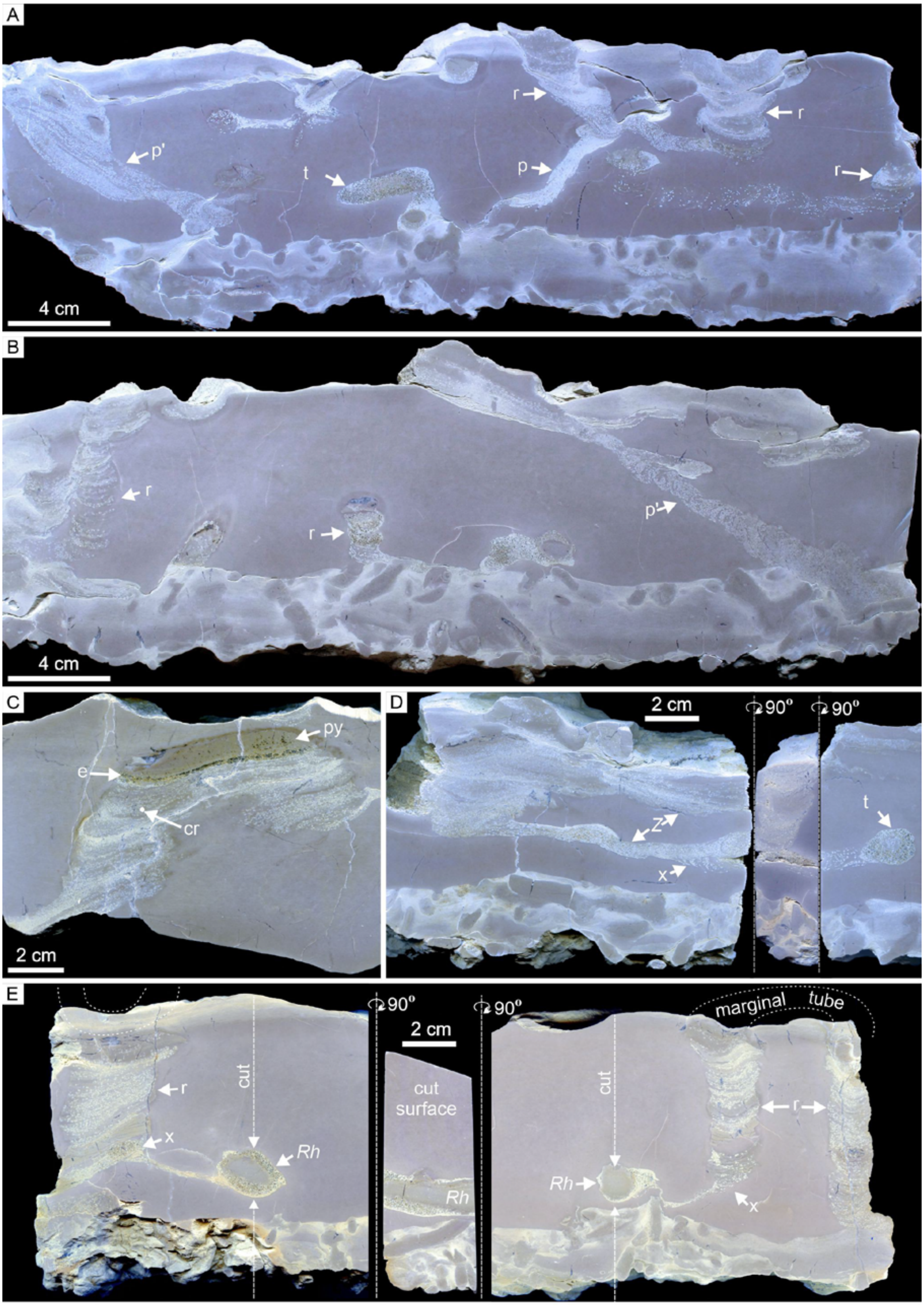

Fig. 5. *Rhizocorallium commune problematica* in vertical sections, Gogolin Beds, Żyglin. **A, B.** Slabs with the burrows of different depth, both, with retrusive (r – dominated) and protrusive (p, p', p' – the same burrows in different cuts, 50 mm apart) limbs filled with coprolites, and marginal tubes formed a tunnel (t). **C.** Retrusive limbs terminated by tunnel in the uppermost part, formed by marginal tube. The tunnel is partly filled by calcite pseudomorphoses after evaporites (e – green crystals) and pyrite crystals (py – dark spots), crinoid remain occur within a spreiten. **D.** Three different views of specimen with strongly developed subhorizontal, *Zoophycos*-like part of the limbs (*Z*), large retrusive spreite (r) and a secondary branch (x) with large tube (t). **E.** Three different views of inverted U-shaped burrow with deep retrusive limbs (r), cut (x) by shallow, horizontal burrow (*Rh*).

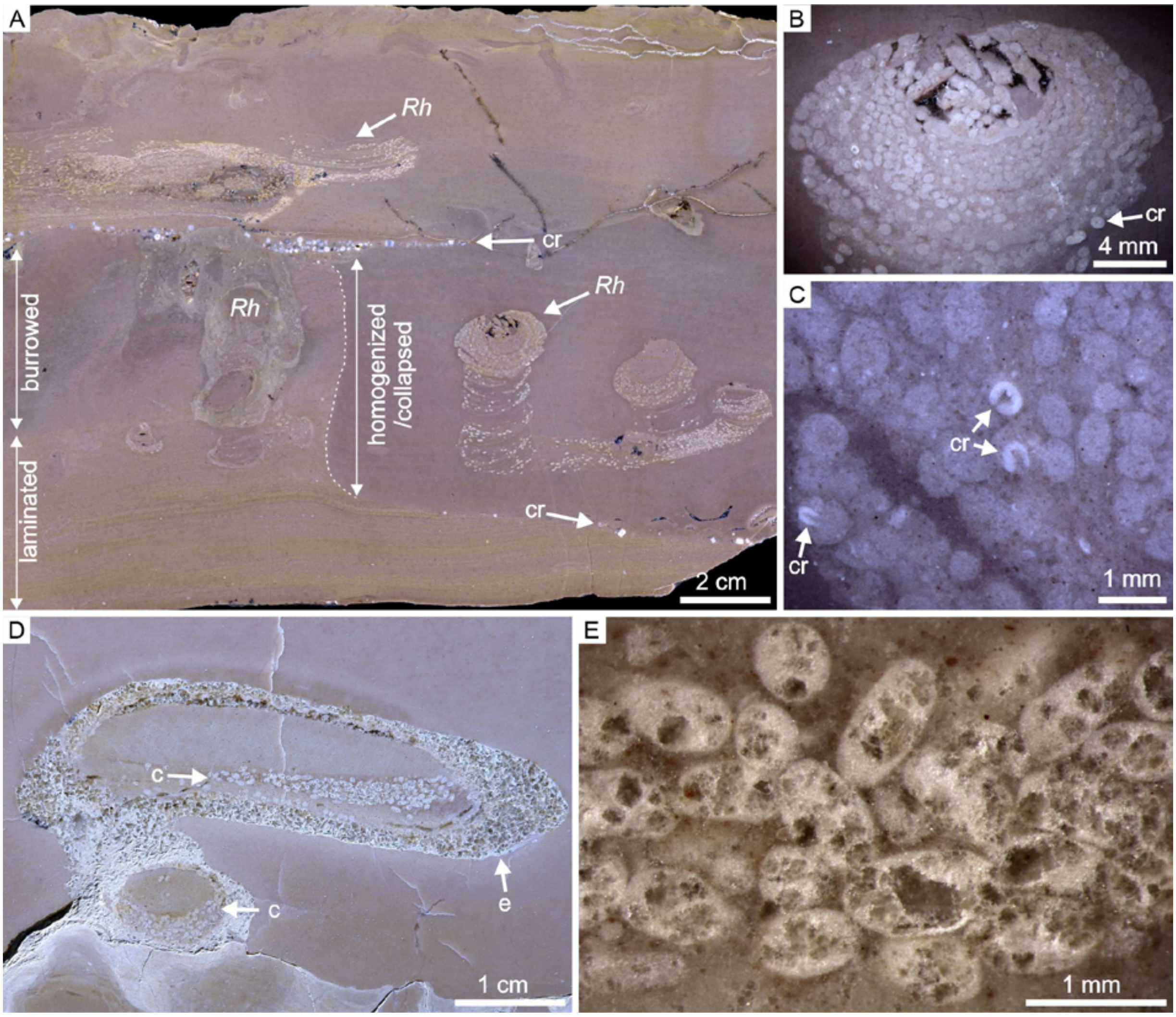

Fig. 6. Details of deep *Rhizocorallium commune problematica* associated with a crinoid layer, Gogolin Beds. **A.** Several burrows (*Rh*) in partly bioturbated tempestite with crinoid layer remains (cr), Psary. **B, C.** Details of the burrow from the A. The marginal tube is filled with coprolites and isolated, partly corroded crinoid remains (cr). **D.** Chamber formed by marginal tube filled with several generations of coprolites. The wall of the burrow is reinforced by coprolites replaced by calcite crystals (e). **E.** Coprolites (c) with small calcite crystals inside.

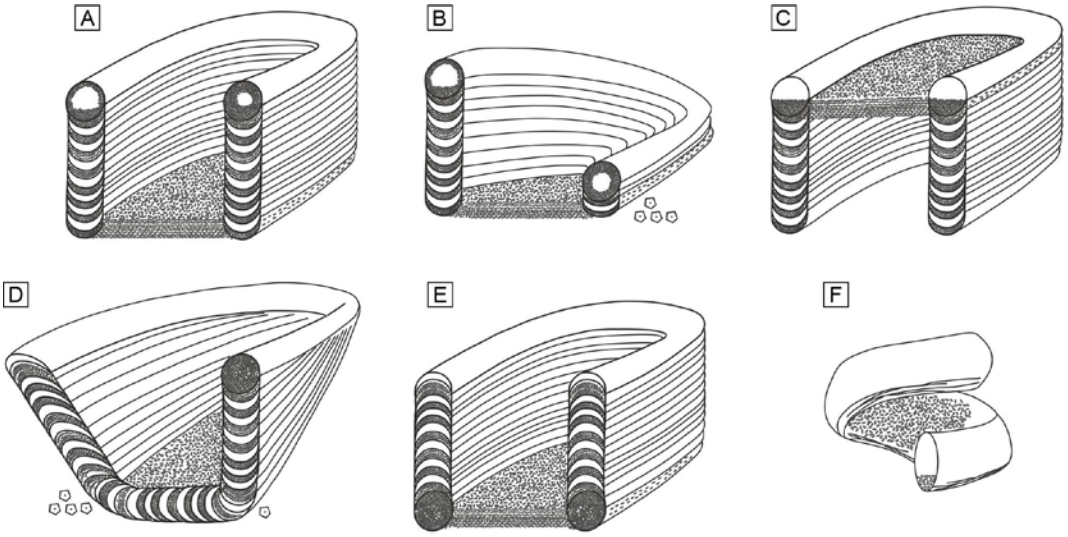

Fig. 7. Sketches of idealized, diverse forms of deep *Rhizocorallium commune.* **A.** Burrow with vertical, symmetrical, U-shaped retrusive limbs. **B.** Asymmetrical burrow with one underdeveloped limb. **C.** ∩-shaped burrow with retrusive limbs. **D.** Burrow consists of protrusive and retrusive limbs. **E.** Burrow with both protrusive limbs. **F.** Rare spiral form.

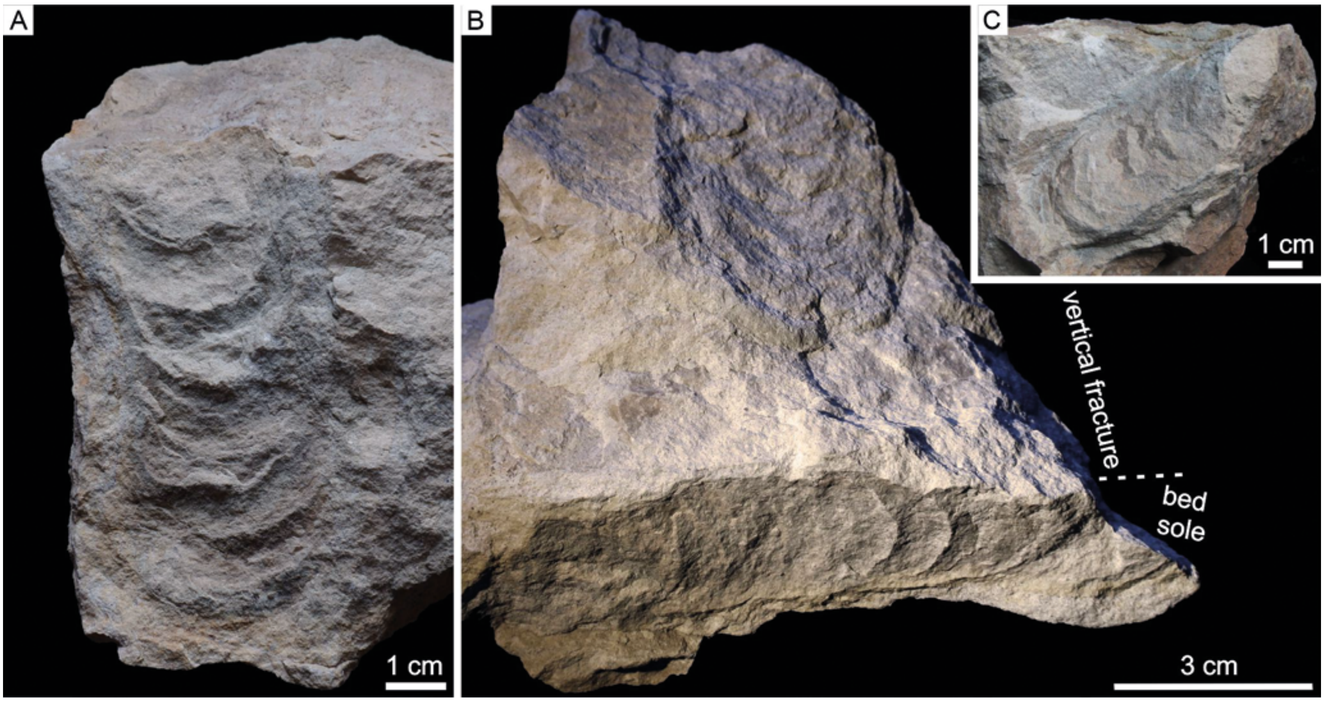

Fig. 8. *Rhizocorallium commune "auriforme"* from the Miedary Beds, Miedary. **A.** Vertical form similar to *Diplocraterion*. **B.** Both vertical, oblique (invisible) and horizontal burrows in one fragment of sandy dolomite. **C.** Oblique burrow.

DISCUSSION

Remarks on ichnotaxonomy

According to Knaust's (2013) classification of *Rhizocorallium*, only two ichnospecies were recognized, *R. jenense* Zenker, 1836 and *R. commune* Schmidt, 1876, the latter of which is commonly represented by two "morphological variants", as well as two rare ichnosubspecies, both commented upon below. Other ichnospecies, proposed by Fürsich (1974), are assigned as synonyms of them. Formally, the International Commission on Zoological Nomenclature (1999) does not provide "variants" as available names and following Knaust (2013) proposition, these are used herein as informal ichnotaxa and written in quotation marks.

Shallow, horizontal to subhorizontal *Rhizocorallium* are very common in the Polish Muschelkalk and there is no doubt about its classification as *Rhizocorallium commune.* According to Knaust (2013), long, winding burrows represent *R. commune* "*irregulare"* (Mayer, 1954), whereas short, inclined forms are *R. commune* "*auriforme"* (Hall, 1843). Bayet-Gall et al. (2018) disagreed classification by Knaust (2013) and placed long and winding burrows in separate ichnospecies *R. irregulare*. The classification used in this paper generally follows the Knaust (2013) concept, although the structures that display features of both variants, i.e., short but horizontal burrows, are also observed (Fig. 3A, D). According to Knaust (2013), differences in burrow size show gradual transitions and therefore they cannot be a diagnostic feature at the ichnospecies level but should be separated as morphological variants that indicate different facies conditions. Nevertheless, small, horizontal burrows (Fig. 3D) are classified therein as a possibly underdeveloped form of *R. commune* "*irregulare"* and so the distinction between large and small forms is irrelevant because they occupy the same facies. Moreover, some essentially horizontal burrows have marginal tubes, covered by densely arranged, criss-crossing scratches (Fig. 3E; cf. Stachacz and Matysik, 2020), representing a transition between *Rhizocorallium commune* and *R. jenense*. The presence or absence of the scratches as well as their density and pattern varies even within individual burrows and the marginal tube sculpture depends on the substrate (soft to hard, see ecological part) and thus is not a strict taxonomic feature.

The spiral, short but deep forms (Fig. 4C) are placed herein in *R. commune*, but it is difficult to determine which of Knaust's (2013) variants they represent. These burrows could be placed in *R. commune uliarense* (Firtion, 1958), but do not form such deep, complex structures with parallel limbs and their limbs criss-cross at different levels. The spiral shape of the discussed burrow clearly results from avoiding neighbouring burrows. Other spiral or winding forms (Fig. 3B, C) are similar to *Rhizocorallium* from a deep-water environment (cf. Książkiewicz, 1977; Uchman, 1991; Kotlarczyk and Uchman, 2012) or *Zoophycos*. Even so, *Rhizocorallium* has a marginal tube of larger diameter in relation to the burrow width than *Zoophycos* and does not form semicircular lobes (Knaust, 2013 and references therein). These features indicate that the two ichnotaxa should be separated at the ichnogenus level (Bromley and Hanken, 2003). Gradual transitions between *Rhizocorallium* and *Zoophycos* do exist, e.g., long, tongue-like forms (Figs 3A–C, 5D) and could be considered as initial forms of a larger structure (cf. Knaust, 2013). Moreover, Knaust (2004) posited a single, possible producer for both ichnospecies in the Muschelkalk.

The deep *Rhizocorallium* burrows with vertically retrusive spreite, according to the classification proposed by Knaust (2013), are placed in *R. commune problematica* (Gümbel, 1861). This trace fossil originally was described by Gümbel as *Lithochela problematica,* a bent, horseshoe-shaped, burrow, similar to *Rhizocorallium* from the Upper Triassic of the Bavarian Alps; unfortunately, no type material survives (Knaust, 2013). The same Upper Triassic structure was recognized as *Rhizocorallium* by Fuchs (1895). In his *Rhizocorallium* review, Fürsich (1974) described deep, in nearly all cases protrusive burrows, with short, retrusive limbs, analogous to *R. commune problematica.* Moreover, he mentioned branched forms and simple tubes, connected to a complex, U-shaped burrow, similar to forms illustrated herein (Fig. 5E). Although in 1974, he postulated Gümbel's "*Lithochela problematica"* as a synonym of *R. jenense*, but Fürsich (1981) placed deep, vertically retrusive burrows of the Jurassic of Portugal in *R. irregulare* Mayer, 1954 (*R. commune* in Knaust's [2013] classification). Chisholm (1970) and Chamberlain (1977) placed U-shaped, vertically retrusive spreiten burrows respectively from the Carboniferous of Scotland and the Devonian of Nevada in *Teichichnus*. Chamberlain (1977) even erected a new ichnospecies *Teichichnus repandus,* for the discussed structure. According to Buckman (1994), these forms represent end-members of continuous morphotypes; small specimens should be placed in *R. jenense*, and large ones in *R. irregulare* (= *R. commune*). Another example of late Palaeozoic retrusive *Rhizocorallium* has been recognized in India and was assigned to *R. commune* by Bhattacharya and Bhattacharya (2007). Mesozoic burrows recently placed in *R. commune problematica* are represented mostly by Triassic trace fossils of the Germanic Muschelkalk, but several post-Triassic finds are also known (Knaust, 2013 and references therein).

The illustrated specimens of *Rhizocorallium commune "auriforme"* from the Ladinian of the Miedary Beds (Fig. 8), including both horizontal and vertical forms, show similar proportions of the burrow size and the marginal tube as well as similar spreite patterns. These burrows therefore show a smooth transition from *Rhizocorallium* Zenker, 1836 to *Diplocraterion* Torell, 1870, which belong to the same ichnofamily Rhizocoralliidae Richter, 1926. The dilemma of these two ichnogenera is known and already was discussed; by consensus, *Rhizocorallium* is represented by horizontal and inclined burrows, whereas *Diplocraterion* exhibits vertical burrows (Knaust, 2013). However, burrows composed of both horizontal (lower) and vertical (upper) portions were mentioned by Rodríguez-Tovar *et al.* (2012) and illustrated by Knaust (2013). Schlirf (2011) introduced the terms "single-spreite lamina", for burrows with only spreite between the limbs of the U shape (U-spreite lamina), and "double-spreite lamina" for burrows with a combination of U-spreite lamina and an additional, mostly retrusive shift of the U limb (limb spreite lamina). In Schlirf's concept, U-shaped, the single-lamina, vertical to oblique burrows should be placed in *Diplocraterion*, wedge-shaped structures with double-spreite laminae in *Rhizocorallium*, and horizontal structures in *Ilmenichnus* Hecker, 1980. The latter ichnogenus does not differ from *Rhizocorallium* and is assigned as its younger synonym (Knaust, 2013). Moreover, Schlirf (2011) created *Ilmenichnus atherus* (synonymized with *R. commune* by Knaust, 2013), which clearly represents the same architecture as *R. commune problematica*. Nevertheless, *Rhizocorallium* occasionally reveals both subhorizontal and subvertical components and some of its ichnospecies could be considered as synonyms of *Diplocraterion*, if orientation within the sediment were to be disregarded as a diagnostic feature (see Knaust, 2013 for discussion).

Ethology and ecology

Commonly, horizontal to subhorizontal, shallowly penetrating *Rhizocorallium commune* "*irregulare"* is widely interpreted as being the result of deposit-feeding (e.g., Fürsich, 1974, 1981; Schlirf, 2011; Knaust, 2013 and references therein). Such burrows in the Triassic Germanic Basin were produced both in soft carbonate deposits (archetypal *Cruziana* ichnofacies) and in firmgrounds (*Glossifungites* ichnofacies *sensu* Seilacher, 1967), as evidenced by scratches (Figs 3D, E, 4B, C). The oblique and subvertical forms with a spreite (partly placed in *R. commune "auriforme"* herein) are assigned as the burrows of suspension-feeders, independently of ichnotaxonomy (e.g., Schlirf, 2011; Knaust, 2013). Differences in orientation of similar burrows within the same bed (Fig. 8) could be caused by a variable rate of deposition of siliciclastic-carbonate material, as well as in the supply of fresh water with nutrients and waste removal (Worsley and Mørk, 2001). It is noteworthy that the discussed assemblage of horizontal to subvertical burrows in the Miedary Beds appeared, when salinity most likely increased from oligohaline to polyhaline conditions (cf. Pawlak *et al.*, 2022). Nevertheless, rapid and significant changes in salinity during the deposition of even single dolomitic beds, caused by event deposition of eroded terrestrial material, are likely. Fish scales occurring within these burrows could indicate that the tracemaker (most likely polychaetes, Knaust, 2013) was a predator, feeding on fish. Indeed, fish remains and other non-carbonate bioclasts also occur outside of *Rhizocorallium*, but it seems they are less abundant in the host deposit. Although deposit and suspension feeders are generally accepted as *Rhizocorallium* (and *Diplocraterion*) tracemakers, predators similar to the contemporary "bobbit worm" (*Eunice aphroditois*) are also considered herein. L-shaped, subhorizontal to subvertical burrows *Pennichnus* Pan *et al.*, 2021, although produced by predatory worms, already were reported from the Miocene of Taiwan (Pan *et al.*, 2021). It seems likely that at least some of the vertical and oblique rhizocoralliids that contain no carbonate faecal pellets were produced by similar predators.

The deep burrows placed in *Rhizocorallium commune problematica* are the most problematic in interpretation. According to Kowal-Linka and Bodzioch (2011), deep *Rhizocorallium* isp. (therein) from the Gogolin Beds at Żyglin is made in two stages: the protrusive part of the burrow in quiet conditions, and the retrusive limbs during rapid deposition. They considered *Rhizocorallium* with vertically retrusive limbs as escape structures. They also stated that the lowest 2–3 cm of the micritic layer of amalgamated beds, as well as the partly eroded firmground below, contain no *Rhizocorallium*. However, this micritic layer does contain numerous *Rhizocorallium* and the firmground below contains sparse *Rhizocorallium* but a mass occurrence of *Oravaichnium* (cf. Stachacz *et al.*, 2022) with some *Thalassinoides* (Fig. 5A, B, D, E; see also Kowal-Linka and Bodzioch, 2011, fig. 3B). This micritic layer, as well as the cross-laminated layer (Fig. 6A) in many exposures of the Lower Gogolin Beds (Fig. 1), represents partly bioturbated tempestite beds with relics of cross-stratification, in some cases similar to hummocky or swaly stratification (Fig. 6A), which is most clearly visible on weathered surfaces in the field. Deposition of such tempestites was very brief, i.e., several hours to several days (Dott, 1983), and the development of *Rhizocorallium* during deposition is dubious. Slower sedimentation of horizontal lamination or low-angle cross-lamination (cf. Kowal-Linka and Bodzioch, 2011, fig. 3A) as well as the slow formation of the burrows with a vertically retrusive spreite, as proposed by earlier authors (Fürsich, 1974; Schlirf, 2000), is more likely. Moreover, the distinct walls, presumably reinforced by mucus, in the vertical part of the burrow, observed by Kowal-Linka and Bodzioch (2011), confirm the gradual formation of this structure, whereas rapidly formed escape structures display no walls. The presence of deep, oblique, protrusive limbs, full of faecal pellets in the same layers (Fig. 5A, B) is also significant. This is evidence that some animals needed to go deeper by several centimetres into the sediment, not to escape from this depth. Therefore, all *Rhizocorallium* with their horizontal and oblique portions, as well as vertical, protrusive and retrusive limbs, here are interpreted as post-depositional feeding- or dwelling-feeding structures. The buried animal had to escape upwards as quickly as possible, rather than feed with simultaneous pellet formation. Obviously, defaecation may be caused by stress, but the production of such an amount of faecal pellets throughout the U-shaped horizontal burrow is unlikely. It is also noteworthy that the horizontal, protrusive spreite with faecal pellets (Kowal-Linka and Bodzioch, 2011, fig. 3C, D) are not the limbs of a U-shaped structure, but reworked deposits between the limbs (U-spreite lamina *sensu* Schlirf, 2011; see Figs 5A, D, 6A). Smaller, ‘normal’ *Rhizocorallium commune* that cut (or branch out) the burrow with a deep, vertically retrusive spreite (Fig. 5D, E) are evidence that the worm could exist and burrow close to the bottom of the tempestite without forming a vertically retrusive section. Moreover, the burrows penetrate the tempestite and reach the firmground below, which is documented by scratches at the base (Fig. 4B, C). Although intersection of the burrows, produced by two different animals, is rare because of phobotaxis, branching to avoid an older spreite is more likely (Knaust, 2013). The presence of both, U- and ∩-shaped burrows (in vertical plane, cf. Figs 5A, C, D, E, 6A) with horizontal spreite in the lower and upper parts of the construction respectively indicate that the animal was searching for a food-rich layer and reworking the selected layer. Fürsich (1974) noticed that food buried within the deposit is usually concentrated within the selected layer, necessitating that the animal burrows sideways. Identification of such a layer by the animal and subsequent feeding caused development of a horizontal, *Zoophycos*-like spreite (Fig. 5A, D). According to Fürsich (1981, fig. 5), who illustrated deep, ∩-shaped (in the vertical plane) *Rhizocorallium*, these structures show that the animal was digging downwards, as indicated by a protrusive lobe, but subsequently started digging at a slightly different level. Changing the depth of excavation may be stimulated by erosion of the deposit near the surface and formation of *Diplocraterion*, or may reflect obstacles within the sediment, such as neighbouring burrows, causing retrusive movement of the animal (cf. Fig. 5A, B). Nevertheless, searching for food within the tempestite had priority, as evidenced by burrows completely filled with coprolites. As noted by Kowal-Linka and Bodzioch (2011), the studied, rapidly deposited bed was rich in organic matter. Specifically, the bottom of the tempestite and the layer below contained an abundance of buried organic matter, including small live or deceased animals. The presence of a crinoid layer in some tempestite beds (Figs 4D, E, 6A), as well as partly corroded crinoid ossicles within the faecal pellets (Figs 5C, 6B, C), indicates that these animals were an important part of the *Rhizocorallium*-makers diet. Obviously, the crinoid remains had to be found and eaten in the short time before soft tissue decomposition occurred. A scolecodont find indicates the potential burrow maker, while placoid and ganoid fish scales inside the burrow could represent additional food remains. Scolecodonts and fish scales also occur outside the burrows, but their frequency in the host sediment seems to be lower (the author’s own observations; cf. Antczak *et al.*, 2020).

Some of the studied burrows show tunnels filled with faecal pellets, forming several generations (Fig. 6), which indicates that they were dwelling-feeding structures revisited by the animal many times. The coprolites contain calcite crystals, interpreted as pseudomorphs after evaporites; in some cases, coprolites are entirely replaced by crystals (Figs 5, 6D, E; cf. Bodzioch, 2005; Bodzioch and Kowal-Linka, 2001). Such pseudomorphs within the coprolites occur both in the burrows and in the surrounding deposit, but additional pyritization (Fig. 5C) and dolomitization occur only in the burrows and their halos (Bodzioch and Kowal-Linka, 2001; Bodzioch, 2005). According to the cited authors, the presence of pyrite, especially framboids, was caused by redox conditions, but sulphate crystallization took place earlier. Crystallization of pyrite is related to the decomposition of soft tissues, associated with the aragonite and magnesium-calcite remains of buried organisms, rapidly accumulated during storms (Bodzioch and Kowal-Linka, 2001; Bodzioch, 2005). These chemical features are typical of crinoids and the rapidly buried animals are proposed herein as the main food source of the *Rhizocorallium* tracemaker in a “fresh”tempestite. The presence of crinoid fragments and other stored food remains, as well as the burrow maker mucus, favour anoxic conditions within the burrow. Biochemical processes within the coprolites, burrows and their halos have been illustrated and discussed in detail by Bodzioch and Kowal-Linka (2001) and Bodzioch (2005).

Mass occurrences of *Rhizocorallium* in some intervals of the Muschelkalk, especially its lower part, together with the near absence of other burrows, indicate unfavourable conditions for most infaunal organisms, and occurrence of specialized worms in great numbers. Such worm behaviour seems to be an opportunistic, r-selected strategy, if the burrow density exceeds 50/m^2 (Rodríguez-Tovar and Pérez-Valera, 2008), which is quite common in the case of the Gogolin Beds of the lower Muschelkalk (Fig. 3C). Indeed, unstressful parameters are recorded in the studied facies, but the *Rhizocorallium* makers functioned much better in these conditions than other burrowing fauna. It is noteworthy that the deep form of *Rhizocorallium* also occurs below the Lower Gogolin Beds within the dolomite of the Röt facies, which points to hypersaline conditions (Stachacz and Matysik, unpublished observations in 2017). Almost monoichnospecific accumulations of these burrows could also be interpreted as a taphonomic product of intense deep-tier bioturbation, although, shallow, horizontal *Rhizocorallium* is likewise abundant in the studied interval. Similar *Rhizocorallium* accumulations in the lower Middle Triassic of southern China were illustrated by Feng *et al.* (2018) and the presence of *Rhizocorallium* in a hypersaline environment of the Middle Triassic is likewise known from the Polish Tatra Mountains (Jaglarz and Uchman, 2010).

Rhizocorallium and Triassic infaunalisation

The described *Rhizocorallium* occurs *en masse* in the lower Gogolin Beds (Aegean, Sequence Anl; see Szulc, 2000) of the lower Muschelkalk, where they form a typical *Rhizocorallium* ichnofabric. The upper parts of the Muschelkalk, i.e., the Upper Gogolin Beds and higher units (Bithynian to Illyrian), contain an abundance of *Rhizocorallium,* but other ichnogenera are also frequent, and the *Oravaichnium* and *Thalassinoides* ichnofabrics become predominant (Stachacz and Matysik, 2020). Generally, the ichnological record of the Polish Muschelkalk reveals a predominantly high degree of bioturbation with relatively low ichnodiversity. Although 26 ichnogenera have been recognized in the Muschelkalk of the Germanic Basin, including Poland and Germany (Szulc, 2000; Knaust, 2007; Kowal-Linka and Bodzioch, 2011; Stachacz and Matysik, 2020), ichnocoenoses are dominated by one or two ichnotaxa, including *Rhizocorallium*, *Oravaichnium* or *Thalassinoides*. Other ichnotaxa usually are uncommon or rare (Stachacz and Matysik, 2020). This record is one of the earliest records of activity of burrowing marine animals in Earth history, in the aftermath of the Permian/Triassic mass extinction, and shows a gradual, long-term recovery of benthic communities, following the great biotic crisis (cf. Wang *et al.*, 2006). The full recovery of the Triassic burrowing fauna was generally longer in terms of ichnodiversity and sizes than that of nekton or even skeletal benthos (Twitchett and Wignall, 1996; Twitchett, 1999; Pruss and Bottjer, 2004; Fraiser and Bottjer, 2009; Knaust, 2010; Chen *et al.*, 2011; Chen and Benton, 2012; Zhao *et al.*, 2015; Luo *et al.*, 2016; Feng *et al.*, 2017a). This situation also pertains to organisms boring the rocky substrate (Uchman *et al.*, 2017; Matysik *et al.*, 2022). Such a long, gradual, ecologic recovery trend is well known for the entire marine ecosystem after the Permian/Triassic mass extinctions (Chen and Benton, 2012). The Polish Muschelkalk shows a clear example of this biotic recovery because conditions were constant during the deposition of the studied facies, which is evidenced by analysed facies and stable C and O isotope data (Stachacz and Matysik, 2020). Obviously, the entire Muschelkalk reveals varied facies, caused by sea-level changes, which easily can be recognized in this part of the Germanic Basin (Szulc, 2000).

The study of the analogous *Rhizocorallium* assemblages from China reveals that both size and penetration depth increased during the Spathian–Anisian (Luo *et al.*, 2017; Feng *et al.*, 2018), whereas the Anisian Polish Muschelkalk contains *Rhizocorallium* of more or less constant size, but varying in penetration depth (Stachacz and Matysik, 2020). Evolution of *Rhizocorallium* assemblages in Poland and China is distinctly diachronous and the maximum observed burrow depth reached up to 80 mm in the Aegean and the Pelsonian, respectively (Feng *et al.*, 2018). The abundance of large *Rhizocorallium* in the lower part of the transgressive sequence of the Polish Muschelkalk points to optimal conditions for their tracemakers during the Aegean (or even Olenekian, in case of the Röt facies), including development of crinoid meadows as a potential main food source. The Lower Gogolin Beds show that *Rhizocorallium* numbers even increased in the maximum flooding zone (sequence An1, upper part of the Żyglin section, Fig. 2A, see Stachacz and Matysik, 2020, fig. 2), whereas deep penetration of *R. commune problematica* was caused by deeper burial of organic remains in tempestites.

According to Feng *et al.* (2018), the abundance of large *Rhizocorallium* in the Anisian recorded the final stage (stage 4 of Twitchett, 2006) of burrowing faunal recovery, after the Permian/Triassic mass extinction. Nevertheless, Stachacz and Matysik (2020) recognised the occurrence of large *Rhizocorallium* (together with medium-sized *Thalassinoides*) in the Anisian (Aegean) as the penultimate stage of recovery, and only the common appearance of large *Thalassinoides,* associated with less abundant *Rhizocorallium* (middle-late Pelsonian), as the final recovery of the burrowers. The full recovery of the burrowing fauna is diachronous worldwide, but in the Polish part of the Germanic Basin, it took place in the middle to late Pelsonian. Owing to diachronism, the final stage of the burrowing benthos recovery proposed by Twitchett (2006) is subdivided for the Polish part of Germanic Basin into two stages: (1) common large *Rhizocorallium* and medium-sized *Thalassinoides* in stage 4, and (2) large *Rhizocorallium* and large *Thalassinoides* in stage 5 (Stachacz and Matysik, 2020). Nevertheless, the return of pre-extinction dimensions of *Rhizocorallium* and *Thalassinoides* is indicative of full recovery, rather than the diversification of ichnocoenoses. Exceptionally, in remote areas, such recovery took place later, i.e., in the Ladinian (Zonneveld *et al.*, 2001; Mørk and Bromley, 2008; Knaust and Costamagna, 2012), whereas in the English part of the Germanic Basin, recovery was earlier, i.e., Scythian/Anisian (Early/Middle Triassic boundary; Pollard, 1981).

The high abundance of *Rhizocorallium* in transgressive, hypersaline facies of the Röt (Olenekian, uppermost Lower Triassic; see Nawrocki and Szulc, 2000) and regressive facies of the uppermost Middle Triassic, in deposits that distinctly differ from the typical lower Muschelkalk, indicates that both before and after the final Triassic benthos recovery, *Rhizocorallium* was a pioneer burrow in unfavourable conditions. Also, the presence of unusual forms of *Rhizocorallium,* i.e., displaying smooth transitions to *Diplocraterion*, in the uppermost Middle Triassic, confirms its variability of form and adaptability to dynamic conditions of various salinities.

CONCLUSIONS

1. Details of deep *Rhizocorallium* with both retrusive and protrusive vertical spreite of diverse forms are presented. These trace fossils are common in several horizons of the Polish Muschelkalk, but are relatively rare elsewhere. The former interpretation of these structures as rapidly made fugichnia is challenged and instead, it is proposed that they were complex fodinichnia.
2. Scavengers, often feeding on crinoid remains, as well as predators, are indicated as potential tracemakers in at least part of the Middle Triassic *Rhizocorallium* at in special circumstances.
3. The abundance of *Rhizocorallium,* including its unusual forms, is typical of the transgressive system of the lowermost Muschelkalk, as well as the regressive, marginal-marine facies with varying salinity of the lower Keuper. Such a distribution of *Rhizocorallium* indicates that burrowing polychaetes acted as opportunistic pioneers in generally unfavourable conditions, including the long-term benthic recovery after the P-T crisis.
4. Mixed clastic-carbonate deposits of dynamic conditions and varied salinity conditions favoured the development of the trace fossils that appear with smooth transitions between *Rhizocorallium* and *Diplocraterion*.
5. The illustrated record of evolution of the Middle Triassic *Rhizocorallium* assemblage in Poland documents the last stages of benthic recovery after the P-T boundary, which is comparable to many sections of similar age around the world. In many cases, great abundance of *Rhizocorallium* seems to be an indication of pioneer burrowing in dynamic, unfavourable environments.

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