3D MORPHOLOGY OF *POST MORTEM* ACROTHORACICAN BORINGS IN FAMENNIAN HETEROCORALS – A MORPHOLOGICAL DIVERSIFICATION OR A CONTINUUM ICHNOSPECIES?

Patrycja G. DWORCZAK [1, 2*], Emilia JAROCHOWSKA [2, 3],
Matthias LÓPEZ CORREA [2, 4] & Błażej BERKOWSKI [1]

[1] *Institute of Geology, Adam Mickiewicz University, ul. B. Krygowskiego 12 Poznań 61-680, Poland;*
e-mails: patrycja.dworczak@amu.edu.pl; bbrk@amu.edu.pl
[2] *Geozentrum Nordbayern, Universität Erlangen-Nürnberg, Erlangen, Germany;*
Loewenichstr. 28, 91054 Erlangen, Germany; e-mail: matthias.lopez@fau.de
[3] *Department of Earth Sciences, Utrecht University, Princetonlaan 8a, 3584 CS Utrecht,*
the Netherlands; e-mail: e.b.jarochowska@uu.nl
[4] *Consiglio Nazionale delle Ricerche, Istituto di Scienze Marine, Via Gobetti 101, 40129 Bologna, Italy*
* Corresponding author: patrycja.dworczak@amu.edu.pl

Abstract: Barnacle borings were found in six heterocoral skeletons. They are present as small (up to 2.9 mm long), slender, pouch-shaped borings with tapering, slit-like openings. The investigated borings were made by acrothoracican cirripedes, which mostly do not have a shell and bore into hard substrates to protect their "naked" bodies. The first occurrence of borings in skeletons of the heterocoral *Oligophylloides* Różkowska, 1969 from the Upper Devonian Tafilalt Platform was reported recently by Weyer in 2016. Here, the authors present the results of a detailed study of heterocoral remains with numerous acrothoracican borings from Jebel Bou Ifarherioun (Famennian, Anti-Atlas, Morocco). The borings were found on the basal part but also on broken branches and stems of the heterocoral corallum and occurred *post mortem*. There is no indication of a *syn vivo* coral-barnacle interaction with borings in tissue-covered areas. The authors used micro-CT scans to visualize the 3D morphology of the pits, their orientation, and distribution. Additionally, the 3D morphology of an assemblage of 75 pits was used to carry out ordination and cluster analyses, which showed that previously proposed ichnospecies may be a continuum of morphological variability. In the basis of measurements by the present authors, the studied borings do not fit any known ichnotaxa. The absence of bourrelets excludes the possibility that the borings studied belong to the ichnogenus *Rogerella* Saint-Seine, 1951. Hence, the results seem to contradict a synonymization that was proposed by Bromley and D'Alessandro (1987) and subsequent authors and leave room for further research and discussion on this topic. Although the inferred boring organism is a filter feeder and, thus, depends on currents, the authors did not find a preferential orientation of the borings. The samples considered here are the best-preserved Devonian barnacle borings to date.

Key words: Acrothoracican barnacles, Heterocoralia, bioerosion, Late Devonian, Morocco.

INTRODUCTION

Trace fossils produced by the erosional activity of organisms in hard substrates (such as drilling, grinding, scratching) are referred to as borings (Wilson, 2007). In the fossil record, they are found in the skeletons of various organisms, in rocks, and in wood (e.g., Wilson and Palmer, 1998; Huggett *et al.,* 2000; Vinn and Toom, 2016; Claussen *et al.,* 2019). Recently, bioerosion is found even in plastic fragments (e.g., Davidson *et al.,* 2018, and references therein). Its occurrence and diversity have been changing considerably during

the Phanerozoic (e.g., Seilacher, 1977; Buatois *et al.*, 2005; Wilson, 2007; Buatois *et al.*, 2016; Mángano and Buatois, 2016; Mángano *et al.*, 2016). The oldest record of bioerosion is described from the Precambrian and the process is common today (e.g., Bromley, 1975; Golubic *et al.*, 1975; Voigt, 1977; Radtke and Golubic, 2005; McLoughlin *et al.*, 2009; Donovan, 2011; Meyer *et al.*, 2022). After the Great Ordovician Biodiversification Event, bioerosional diversity and disparity were almost constant during the Devonian

Period (Bromley, 2004; Buatois and Mángano, 2016) and the most common ichnospecies was *Trypanites* Mägdefrau, 1932 (Goldring and Kaźmierczak, 1974; Pemberton *et al.*, 1980, 1988; Wood, 2000; Taylor and Wilson, 2002). Macro- and microborings are essential tools for reconstructing the interactions between organisms (parasitism, commensalism, symbiosis), as well as their spatial and temporal distribution. Furthermore, when the producer is unknown, borings very often are the only evidence of their existence in the fossil record.

Most acrothoracican barnacles do not have an external skeleton (e.g., Lambers and Boekschoten, 1986; Lin *et al.*, 2016; Nielsen *et al.*, 2016; Chan *et al.*, 2021), thus they bore in calcareous hard substrates and form dwelling traces (dom- ichnia; Wisshak *et al.*, 2019; Kočová Veselská *et al.*, 2021; Mikuláš *et al.*, 2022). When a larva settles on a hard sub- strate, it begins the chemical dissolution of it. Subsequently, the adult organism bores through the use of cirri and the body is located in a pit upside-down, so that the cirri sweep food to its mouth (Chan *et al.*, 2014). Only female speci- mens bore, males attach themselves to the female mantle sack or to the wall of boring (e.g., Seilacher, 1969; Lambers and Boekschoten, 1986; Lin *et al.*, 2016). Their pouch- shaped borings are common in fossil and modern, marine environments, especially in calcareous hard substrates, such as brachiopod shells (e.g., Rodriguez and Gutschick, 1970, 1977), bivalve shells (e.g., Tomlinson, 1963), gastropod shells (Schlaudt and Young, 1960; Tomlinson, 1963; Baird *et al.*, 1990; Bałuk and Radwański, 1991), coral skeletons (e.g., Rodriguez and Gutschick, 1970; Delamette, 1989; El-Hedeny and El-Sabbagh, 2018; Toom *et al.*, 2019), bry- ozoan colonies (e.g., Kobluk and Nemcsok, 1982; Delamette, 1989), echinoderms (e.g., Saint-Seine, 1951; Donovan and Jagt, 2013), belemnite rostrae (e.g., Seilacher, 1968; Delamette, 1989), algae (Bassi *et al.*, 2013; Botha *et al.*, 2020) and oncoids (Rodriguez and Gutschick, 2000). They appear as the tapered slits, a few millimetres long, but the internal shape of the boring is characteristic for the family of the organism producing it; this is known from observations of recent material (Seilacher, 1969; Kobluk and Nemcsok, 1982; Grygier and Newman, 1985). Some members of this group of barnacles have a calcareous, basal plate and struc- tures formed by secreted cementum, which may be also de- posited in the apertural regions, but these structures do not seem to preserve well in the fossil record (see Grygier and Newman, 1985; Plewes, 1996).

The bioerosional activity of barnacles has a rich and long fossil record. It is known from the Late Ordovician until today. The oldest evidence was described by Vogel and Brett (2009) from the USA. However, barnacle ero- sional activity was rather frequent in the Devonian period (Middle–Late Devonian), but unknown in the Frasnian (see Table 1). Studies of the diversity and distribution of acrothoracican barnacle borings are hindered by taxonom- ic difficulties. The same organism may produce multiple, different trace fossils and identical trace fossils may be produced by multiple biological taxa (James *et al.*, 1977; Bertling, 2007; Rindsberg, 2012; Lopes and Pereira, 2018). Furthermore, because borings are known to change shape between substrates (e.g., Tapanila *et al.*, 2004; Mikuláš *et* *al.*, 2022), with certain substrates (hosts) occurring only in the fossil record (e.g., belemnites). A final challenge is fossil preservation, for example, under conditions of ero- sion (see Schlaudt and Young, 1960; Abletz, 1993; Plewes, 1996; El-Hedeny and El-Sabbagh, 2018). Additionally, some diagnoses of biological taxa included the shape of the borings, which has led to the use of biological taxonomy for isolated borings, e.g., fossil borings (e.g., Chan *et al.*, 2014). Borings are trace fossils and thus their nomenclature should follow the rules of ichnotaxonomy, regulated by the International Commission on Zoological Nomenclature (see also Bertling *et al.,* 2006; Buatois *et al.,* 2017; Rindsberg, 2018). Basically, the organism and the shape of its trace fos- sils do not match, although in the case of extant acrotho- racican barnacles, there is good correspondence between them (e.g., Tomlinson, 1969; Chan *et al.*, 2014). The rela- tionship between recent and fossil acrothoracican barnacle borings was studied by Lambers and Boekschoten (1986). Their results showed that both ichnotaxa had the same ra- tios of boring dimensions.

Several ichnotaxa have been erected for different mor- phologies of fossil acrothoracican borings, but owing to their similarity and limited morphometric information, which would allow a consistent classification, many authors have followed the approach of Bromley and D'Alessandro (1987) of lumping these ichnotaxa into the genus *Rogerella* Saint-Seine, 1951 as the oldest one. This approach is not followed here for following reason: among known acrothoracican borings, *Rogerella* stands out because of the presence of a narrow, peduncular slit and calcareous bourrelets (Saint-Seine, 1951; Tomlinson, 1969; Lambers and Boekschoten, 1986; Buatois *et al.*, 2016), absent in all other ichnogenera that have been synonymized with it (Bromley and D'Alessandro, 1987). Furthermore, Codez and Saint-Seine (1958) offered pre- liminary, morphometric measurements, indicating that the ichnogenera they erected, *Simonizapfes* and *Brachyzapfes*, as well as *Zapfella* Saint-Seine (1954), possibly may be distinguished consistently on the basis of their shapes. If this observation is upheld, it would offer the possibility of assessing the diversity of fossil acrothoracican barna- cles, if only through their ichnological record.

In the present study, the authors report the first 3D quan- titative morphometric analysis of acrothoracican borings in the heterocoral skeleton of *Oligophylloides maroccanus* Weyer, 2016 from the Upper Devonian carbonate Tafilalt Platform (Jebel Bou Ifarherioun, Anti-Atlas, Morocco). These borings were created by acrothoracican barnacles, which settled on the branches, stems, and the basal part (extended holdfast) of the heterocoral corallum. Ordinarily, the pits are secondarily filled with sediment and iron-man- ganese oxides. Previously, trace fossils in the skeletons of *O. maroccanus* were illustrated by Weyer (2016, fig. 5) Upper Famennian, Jebel Bou Ifarherioun) and deter- mined as borings, the tracemaker of which was unknown. The authors traced the morphology of the acrothoracican borings and their relationship with the heterocoral hosts using micro-computed tomography. This approach al- lowed measurement of the dimensions of 75 borings and quantification of their disparity, which the authors then

Table 1

Comparison of all known erosional activity of Devonian acrotoracican barnacles.

Source	Ichnotaxa	Boring			Aperture		Host	Strati-graphy	Locality	Relation-ship	Environ-ment
		length	width	depth	length	width					
		[mm]									
Baird *et al.*, 1990	unnamed	–	–	0.8–−1.5	0.25–−4.0	0.1–−1.0	gastropods	Givetian	The Hamilton Group, western New York	*syn vivo*	relatively shallow water
Codez and Saint-Seine, 1958	unnamed	–	–	–	–	–	brachiopods	Eifel	Germany	–	–
Ehlers and Kline, 1934	unnamed, undescribed	–	–	–	–	–	brachiopods	Givetian	Michigan	–	–
Muir-Wood and Cooper, 1960	unnamed, undescribed	–	–	–	–	–	brachiopods	Givetian	–	–	–
Rodriguez and Gutschick, 1970	unnamed	–	–	–	–	–	rugose corals, brachiopods	Fammenian	The Rocky Mountain area	*post mortem*	shallow water
Rodriguez and Gutschick, 1977	unnamed	–	–	–	1.1–−1.2	0.5–−0.7	brachiopods	Fammenian	The Louisiana Limestone of Missuori	*syn vivo* and *post mortem*	relatively shallow water
Stainbrook, 1938	unnamed, undescribed	–	–	–	–	–	brachiopods	Givetian	The Cedat Volley, Iowa	–	–
Weyer, 2016	unnamed	–	–	–	–	–	heterocorals	Fammenian	Jebel Bou Ifarherioun, Morocco	*syn vivo*	deep water

compared with published data on the morphology of fossil acrothoracican borings, which Bromley and D'Alessandro (1987) treated as subjective synonyms of *Rogerella* Saint-Seine, 1951, namely *Bascomella* Morningstar, 1922, *Brachyzapfes* Codez, 1957 (in Codez and Saint-Seine, 1958), *Seminolithes* Hyde, 1953, *Simonizapfes* Codez, 1957 (in Codez and Saint-Seine, 1958) and *Zapfella* Saint-Seine, 1954. The aims of the present study were 1) to document the relationship between heterocoral skeletons and acrothoracican barnacles, 2) to measure and document their morphology and distribution, 3) to establish their relationships with previously known ichnogenera, and 4) to revise the taxonomic position of *Rogerella*.

GEOLOGICAL SETTING

The investigated material was collected from the Upper Famennian (middle/upper *expansa* conodont Zone; see Ziegler and Sandberg, 1984) beds at Jebel Bou Ifarherioun (eastern Anti-Atlas, Morocco, 31°7′59.20″N; 4°17′9.84″W). The Jebel Bou Ifarherioun ridge constitutes a carbonate succession, formed during the Devonian in the south-western part of the Tafilalt Platform (Fig. 1). The succession shows the unique record of a well-preserved sea bottom, where the deposition of carbonates was controlled by syndepositional tectonics (e.g., Wendt, 1985). This tectonic activity resulted in several basins with different spatial and temporal sedimentation and diverse ecosystems. These basins included relatively shallow-water habitats, as well as impoverished faunas of deep, episodically anaerobic environments (e.g., Wendt and Belka, 1991; Belka *et al.,* 1997; Frey *et al.,* 2018; Jakubowicz *et al.,* 2019). The heterocoral skeletons come from the *Gonioclymenia* Limestone, upper Famennian grey and/or reddish, ammonoid-rich crinoid wackestones-packstones. The limestone contains pelagic organisms, especially abundant cephalopods, ostracods, conodonts (see, e.g., Korn and Bockwinkel, 2017), and reworked fragments of crinoids, bivalves, gastropods, and trilobites. Corals are represented by well-preserved small, undissepimented, solitary rugosans, tabulates (Weyer, 2002) and heterocorals with abundant epizoans (Dworczak *et al.,* 2020). The studied material is housed at the Institute of Geology, Adam Mickiewicz University, Poznań, Poland.
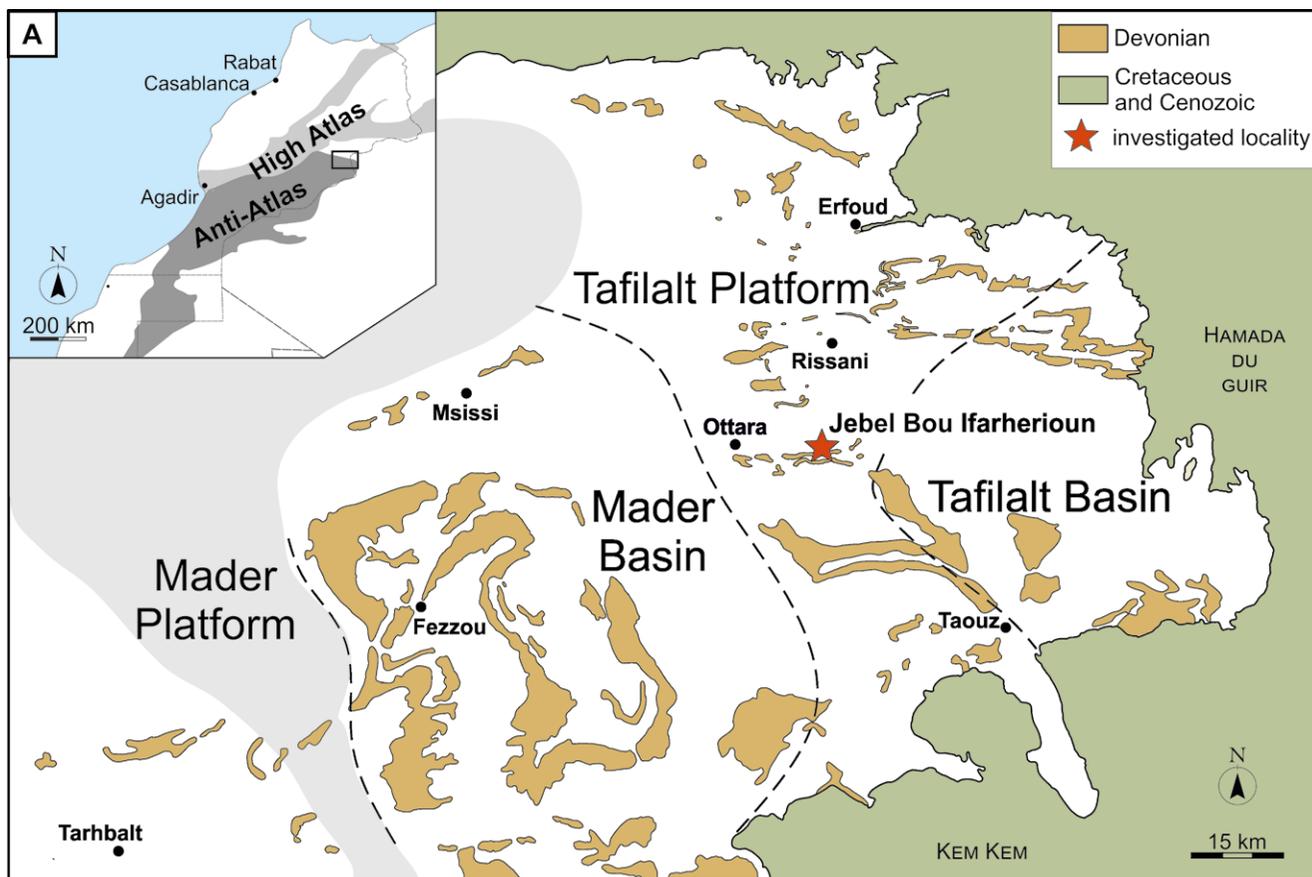
Fig. 1. Simplified geological map of the eastern Anti-Atlas with the outcrop distribution of the Devonian strata and the main Devonian sedimentary basins marked (slightly modified after Jakubowicz *et al.*, 2019; adapted from Dopieralska, 2009). The location of Jebel Bou Ifarherioun, where *Oligophylloides maroccanus* was collected, is indicated by a red star. Inset shows the general geological context of the study area.

MATERIAL AND METHODS

Materials

The material studied comprises six well-preserved fragments of skeleton of the heterocoral *Oligophylloides maroccanus* Weyer, 2016 with numerous borings on their surfaces. These corals belong to the problematic order of Palaeozoic corals, known as Heterocorallia Schindewolf, 1941. The origin and affinities of this group have for a long time been debatable [see discussions in Fedorowski (1991), Oliver (1966), Scrutton (1997)], but recent studies (Berkowski *et al.*, 2021) included heterocorals in the subclass Octocorallia. Heterocorals did not have calices nor an external theca (epitheca; Wrzołek, 1981; Fedorowski, 1991; Weyer, 1997, 2016; Chwieduk, 2001) and these characters distinguish them from Palaeozoic rugose and tabulate corals. The entire skeleton was presumably covered by soft tissue with numerous polyps (Berkowski *et al.*, 2021). Most heterocorals, and especially *Oligophylloides*, inhabited environments interpreted as oxygen-depleted and relatively deep-water (mesophotic and aphotic; e.g., Weyer, 2016; Dworczak *et al.*, 2020). The genus *Oligophylloides* Różkowska, 1969 is characterised by a thick wall of protoheterotheca type and a central core with septal apparatus that is composed of dichotomously dividing septa. The wall is built of lamellar, low-Mg calcite

crystals, which create a dense and compact microstructure (Chwieduk, 2001; Dworczak *et al.*, 2022). Colonies of *Oligophylloides* formed fan-shaped skeletons with relatively long and thin branches and were attached to the substrate by a massive holdfast (Weyer, 2016; Berkowski *et al.*, 2021). Hence, very often, only fragments (mostly branches) of colony are found in the fossil record. The material investigated contains six specimens: two fragments of branches UAM Ro/JBI/01 (1907), shown in Figure 2A–G, and UAM Ro/JBI/03 (1907), three fragments of the stem, UAM Ro/JBI/02 (1907), UAM Ro/JBI/04 (1907), and UAM Ro/JBI/05 (1907), and one proximal part (holdfast) of a colony, UAM He/JBI/03 (1907), in Figure 3A–D.

METHODS

Micro-computed tomography

The best-preserved part of a heterocoral branch, UAM Ro/IBI/01 (1907) and proximal part of corallum UAM He/JBI/03 (1907) were investigated in more detail. The specimens were photographed using an Axiocam digital camera attached to a ZEISS AXIO Zoom-V16 microscope with ZEISS ZEN-2-core soft ware at the Friedrich-Alexander-Universität (FAU) in Erlangen, Germany.
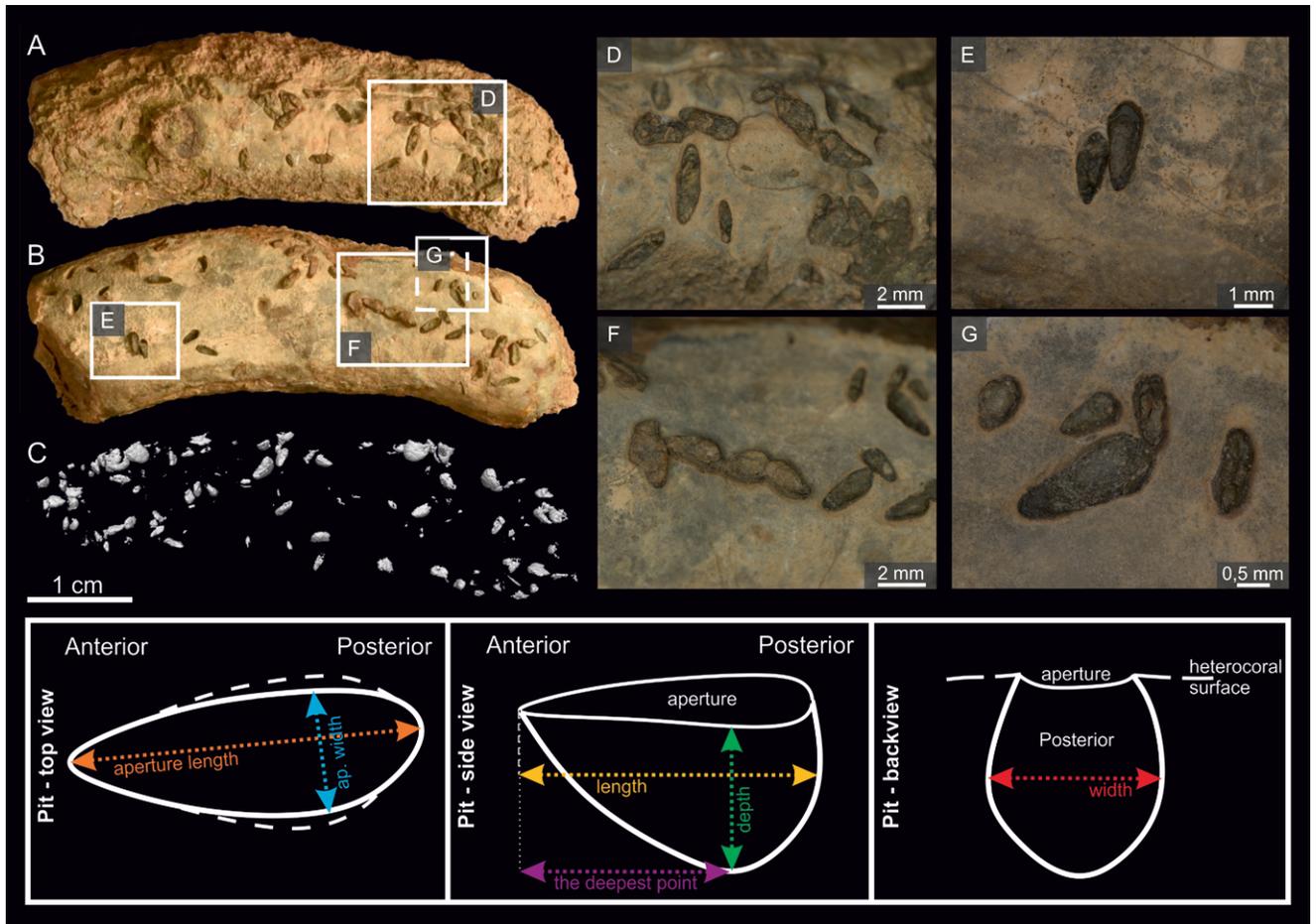
Fig. 2.   Fragment of an *Oligophylloides maroccanus* branch with acrothoracican borings UAM Ro/IBI/01 (1907). **A, B.** Overview of the specimen. The trace fossils are partially covered with sediment. Most borings are filled with iron-manganese oxides. The pits occur individually, create groups of borings, which contact and cross each other or form "pathways". **C.** Micro-CT images of all borings inside of heterocoral skeleton. **D–G.** Close-ups of the specimen demonstrating more details: **D.** The filled borings. Differences in size and shape of pits are visible. They touch and cross each other. **E.** A pair of two parallel borings filled with sediment. **F.** A "pathway" of pits. The filling of borings sticks out above heterocoral surfaces. **G.** Different shapes and sizes of borings. **H–J.** Drawings of borings with measurements marked. **H.** Top view of boring. **I.** side view of pit. **J.** Back view of boring.

The specimen UAM Ro/IBI/01 (1907) was analysed with computed tomography (CT; micro-CT phoenix v/tome/x s research/edition and the software VGstudio Max 3.0) at the Friedrich-Alexander-Universität (FAU) in Erlangen, Germany. The branch was scanned at 1500 projections, each with a tube voltage of 120 kV, a tube current of 350 µA, a filter of 0.5 mm Sn. The authors visualized 3D images of pit morphology, orientation, and distribution without destroying the samples. The largest dimensions of borings were measured in the software VGstudio Max 3.0. Only borings with good contrast were measured. A summary of the measurements is presented in Table 2. Definitions of the measured variables are presented in Figure 2H–J: the anterior and posterior ends are defined as the narrower and wider ends of the aperture, respectively. Aperture length and width were measured as the major and minor axes, respectively, assuming that the aperture is treated as an imperfect ellipse. Boring length was measured as the major axis in a projection of the boring on a plane, i.e. corresponding to the distance between the anteriormost and posteriormost points. Similarly, width was measured at the widest point

Table 2

Summary of measurements of acrothoracican borings on the heterocoral branch [UAM Ro/IBI/01 (1907)] in this study (N = 93). Mean values were in all cases equal to median values. For explanations of variables, see Figure 2.

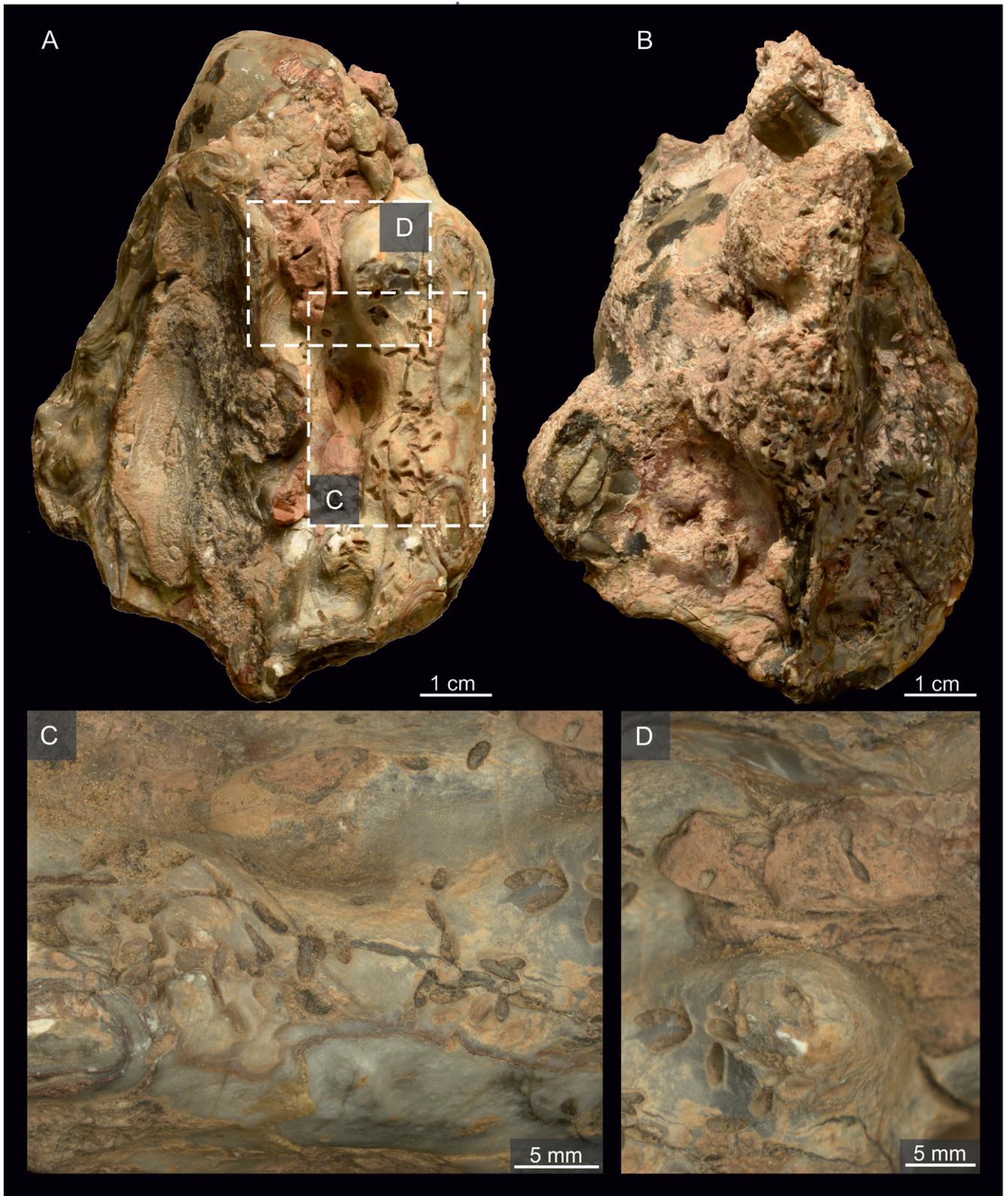| Variable		Minimum	Mean	Maximum	Standard deviation
Depth	[mm]	0.5	1.2	2.5	0.4
Length		0.6	1.7	2.9	0.5
Length of aperture		0.4	1.5	2.6	0.4
The deepest point		0.3	0.9	1.8	0.3
Width		0.3	0.7	1.1	0.2
Width of aperture		0.2	0.6	1.2	0.2

Fig. 3. Proximal part of heterocoral skeleton *Oligophylloides maroccanus* with acrothoracican borings UAM He/JBI/03 (1907). **A.** The trace fossils occur without any pattern of arrangement. They create a large group of borings which contact and cross each other. They are partially filled by sediment or iron-manganese oxides. **B.** The borings create a dense group of pits, which are chaotically distributed on the surface of the skeleton. They occur close to each other, some in contact or crossing each other. Most of them are not filled and differ in size and depth. **C, D.** Close-ups of the specimen demonstrating more detail: **C.** Surface of the heterocoral corallum with empty and sediment-filled borings. Some of them are crossed by cracks. **D.** Surface of sediment, which was bored by acrothoracican barnacles. The borings occur individually or together.

of the boring along the minor axis. The deepest point of the boring was calculated as the distance between the anterior-most end of the aperture and the projection of the deepest point of the boring on the aperture plane. The measurements are compared with those reported in the literature. Sources are listed in Table 3.

Appendix 1 presents new measurements carried out on the specimens reported here and Appendices 2 and 3 contain measurements extracted from Codez and Saint-Seine (1958), used to create Figures 4–6.

Table 3

Dimensions of ichnotaxa of acrothoracican borings as reported by previous authors.
Where different values had been reported, the maximum range is shown.

Ichnospecies	Boring			Aperture		Host	Stratigraphy	Locality	Source of measurements
	length	width	depth	length	widt				
	[mm]								
Bascomella fusiformis Elias and Condra, 1957	1.5	0.3–0.4	–	–	–	Invertebrates	Late Pennsylvanian	Douglas Group, Kansas	Elias, 1957
Bascomella gigantes Morningstar, 1922	1.6–2.0	0.8–0.9	–	–	–	Invertebrates	Early Permian	Pottsville, Alabama	Elias, 1957
Brachyzapfes elliptica Codez, 1957	1.1–2.0	0.4 – 0.9	0.6–1.2	0.9–1.8	0.3–05	Brachiopods, pelecypods, belemnites	Cretaceous	France	Codez and Saint-Seine, 1958 (length and depth), Grygier and Newman, 1985 (depth and aperture), Tomlinson, 1963 (all measurements)
Rogerella cragini Schlaudt and Young, 1960	≤ 1.9	≤ 0.7	0.9	0.8–1.9	0.3–0.7	Gastropods	Middle Albian	Colorado River, Texas	Schlaudt and Young, 1960
Rogerella lecointrei Saint-Seine, 1951	0.5–3.0	–	–	–	–	Echinoids	Cretaceous	France	Saint-Seine, 1951
Rogerella mathieui Saint-Seine, 1955	1.3–2.9	0.5–1.3	3.1	1.0–2.0	0.3–0.8	Echinoids, belemnites, corals, bivalves	Middle Jurassic, Upper Cretaceous, Miocene, Pliocene	France	Codez and Saint-Seine, 1958 (length and width), Grygier and Newman, 1985 (depth and aperture)
Rogerella polonica Bałuk and Radwański, 1991	5.0–13.0	4.0–10.0	–	2.8–5.5	0.5–0.8	Gastropods	Middle Miocene	Holy Cross Mountains, Poland	Bałuk and Radwański, 1991
Seminolithes clarkei Elias, 1957	1.2	0.6	–	–	–	Brachiopods	Late Mississippian	the Redo-ak Hollow formation, Oklahoma	Elias, 1957

| Ichnospecies	Boring			Aperture		Host	Stratigraphy	Locality	Source of measurements
	length	width	depth	length	widt				
	[mm]								
Seminolithes linii Hyde, 1953	2.0	0.3–0.5	–	–	–	Invertebrates	Early Carboniferous	The Logan Formation, Ohio	Elias, 1957
Simonizapfes elongata Codez, 1957	2.0–4.5	0.5–1.1	1.3–2.7	1.0–2.3	0.3–0.65	Belemnites, pelecypods, gastropods, crinoids, etc.	Triassic, Jurassic	Europe, India	Codez and Saint-Seine, 1958 – (length and width) Tomlinson, 1969 (aperture)
Simonizapfes davenporti Tomlinson, 1969	–	–	0.3–0.96	1.15–2.16	0.3–0.65	Pelecypods, belemnite	Late Creta-ceous	Poricy Brook, New Jersey	Tomlinson, 1969
Zapfella pattei Saint-Seine, 1954	2.2–3.6	1.0–1.8	1.6–3.3	1.5–2.5	0.3–0.6	Gastropods, pelecypods, calcareous marls, bi-valves	Miocene, Pliocene	Vienna Basin, France, Italy, Algieria	Codez and Saint-Seine, 1958 (length and depth), Grygier and Newman, 1985 (depth and aperture), Tomlinson, 1963 (all mea-surements)
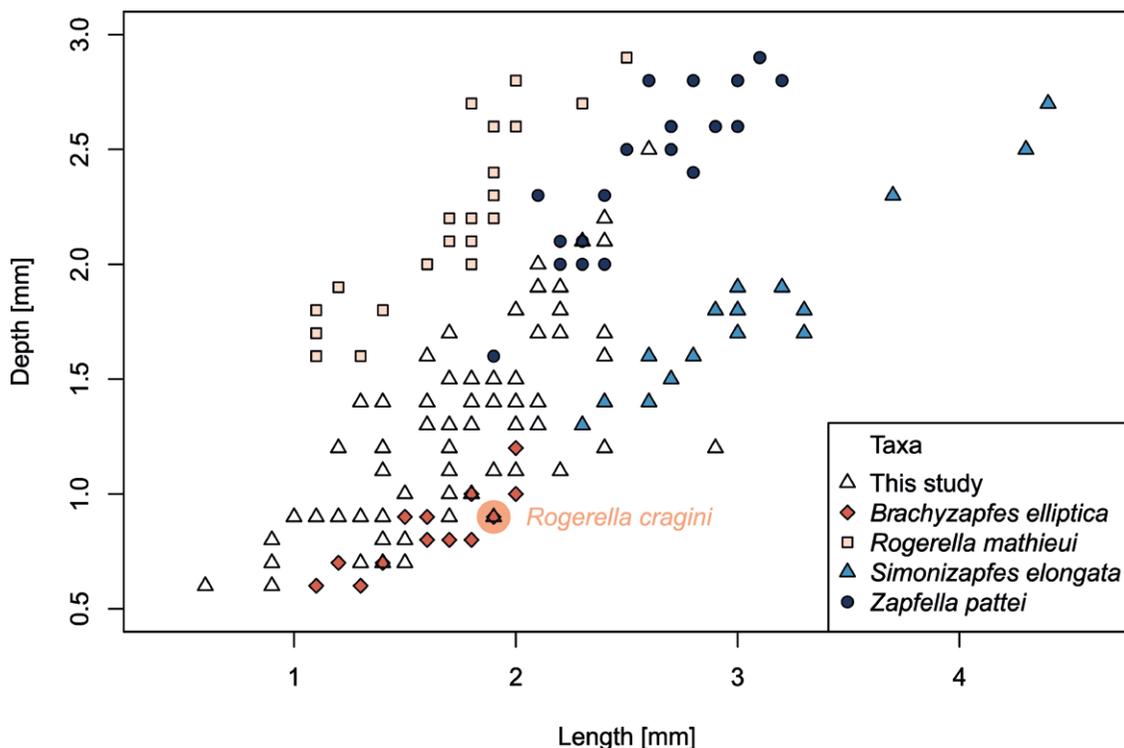
Fig. 4. Relationships between the lengths and depths of acrothoracican borings segmented from a micro-CT scan of specimen UAM Ro/IBI/01 (1907). The dimensions are compared with those reported for previously established taxa. Sources are listed in Table 2. Borings are assigned to four clusters, as defined in Figure 3. N = 75.
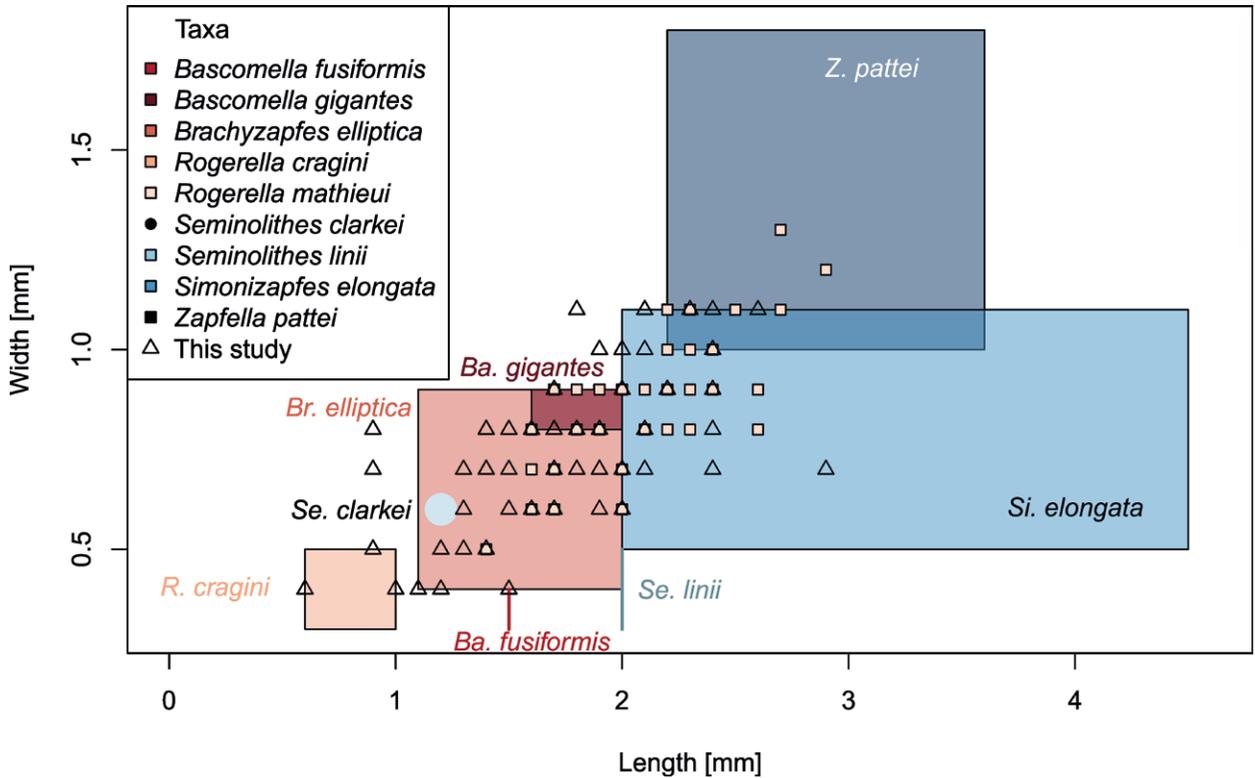
Fig. 5. Relationships between the lengths and widths of acrothoracican borings segmented from a micro-CT scan of specimen UAM Ro/IBI/01 (1907). The dimensions are compared with those reported for previously established species. Sources are listed in Table 2. Borings are assigned to four clusters, as defined in Figure 3. N = 75.

Fig. 6 Relationships between the aperture lengths and widths of acrothoracican borings. The dimensions are compared with those reported for previously established species. Sources are listed in Table 2. Borings are assigned to four clusters, as defined in Figure 3. N = 75.
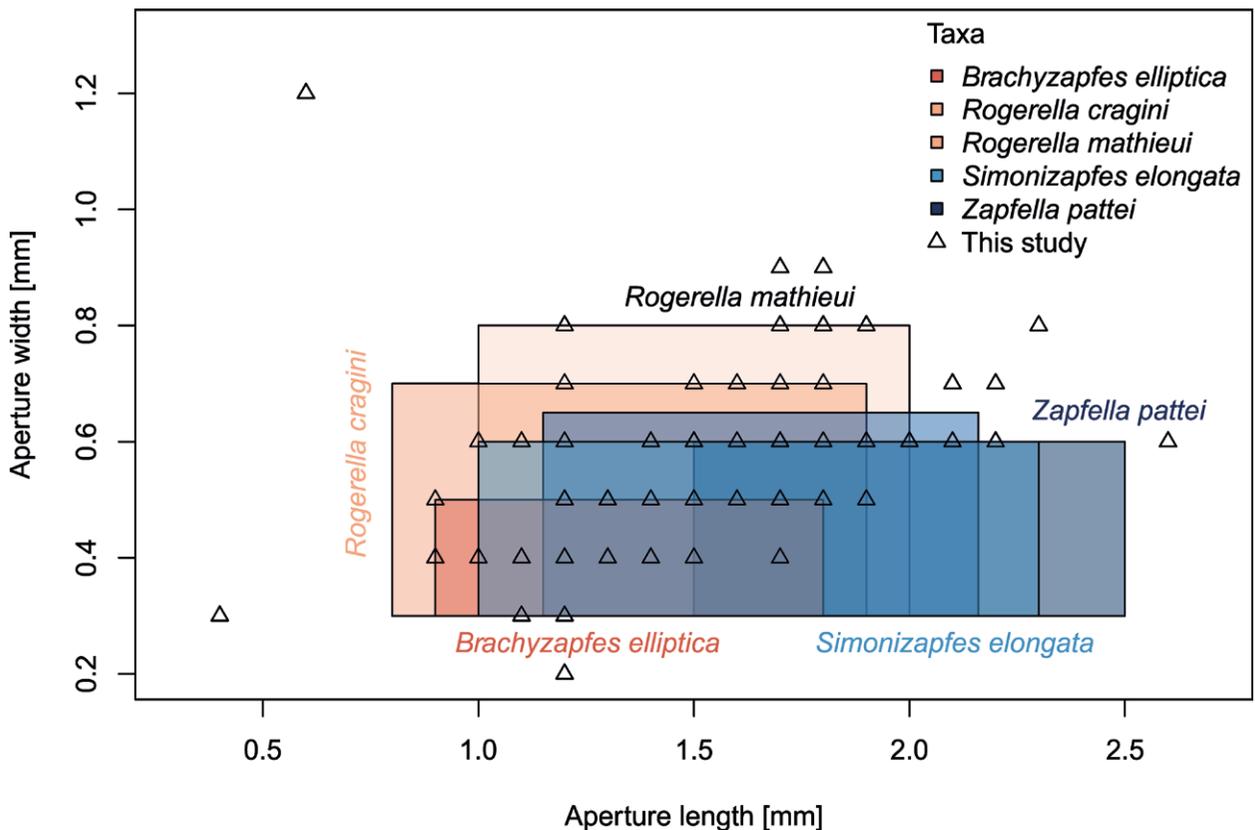
Statistical analyses

The aim of the analyses was to determine if the dimensions of the specimens match those of previously known ichnogenera and whether *Rogerella* Saint-Saine, 1951 is a synonym of other ichnogenera; 93 pits were measured, but only in 75 the contrast was sufficient to measure all dimensions reliably. This reduced dataset was used for analyses of the relationships between dimensions. The analyses have been carried out in R Software (R Development Core Team, 2020). Six variables measured in each pit were used to carry out Principal Component Analysis (PCA) using the covariance matrix as input, since all variables are measured on the same scale. All variables had approximately symmetrical distributions (Figs 4–6) and were strongly correlated with each other, therefore PCA was judged as a suitable type of analysis (for details of the decision process, see Bialik *et al.,* 2021). In order to identify morphotypes and potential distinct morphotaxa, the same restricted dataset was used to carry out K-means clustering, assuming four clusters.

RESULTS

General description of borings

The borings are narrow, pouch-shaped, and occur abundantly on the surfaces of *Oligophylloides maroccanus* Weyer, 2016. Most of them are empty, though some of them are filled with iron-manganese oxides (specimen UAM Ro/IBI/01 (1907), Fig. 2A–G) or with sediment, the surrounding reddish limestone (specimen UAM He/JBI/03 (1907), Fig. 3A–D). The lengths range from 0.6 to 2.9 mm, the widths from 0.3 to 1.1 mm and the depths from 0.5 to 2.5 mm (N = 93). The apertures are narrow, wedge-shaped, or elliptical and taper toward the opening. The boundaries of borings are rounded and smooth. The lengths of apertures range from 0.4 to 2.6 mm and widths from 0.2 to 1.2 mm. They do not have preserved bourrelets (secondary deposits around the aperture) or peduncular slits (in some cases, a curved,

extended slit, that gives the aperture a comma-like shape), which allows the exclusion of *Rogerella* Saint-Seine, 1951 and borings produced by the genus *Trypetesa* Norman, 1903. Usually, the pits are longer than deep. The deepest point of the boring is more or less inclined from the anterior to posterior ends. The deepest points of the pits are mostly in the interval between 45–70% of the length. This character correlates with the widest area of boring. The shape of the aperture reflects the shape of the boring and indicates where the deepest part of the pit occurs. The deeper the boring, the closer the point is to the anterior part.

Preservation

The studied samples of *Oligophylloides maroccanus* represent well-preserved fragments of colony. However, the surface of one branch, specimen UAM Ro/IBI/01 (1907), shown in Fig. 2A, B, D–G seems partially eroded, probably owing to dissolution. This is especially noticeable in this specimen because iron-manganese oxides filled the borings. The filling protrudes from the surfaces and precisely follows the shapes of apertures and borings. This feature allowed accurate measurement of the original boring depths. This type of preservation may obscure details of the apertural region, which are diagnostic for some taxa, such as *Rogerella* (Saint-Seine, 1951; Grygier and Newman, 1985). The borings in the proximal part of heterocoral skeleton (specimen UAM He/JBI/03 (1907)) are mostly empty or partially filled with lithified sediment. In either case, bourrelets could not be found and the apertures were oval or flax seed-shaped, without any evidence of peduncular slits.

Morphotypes

Four morphotypes are recognized among the borings studied (Fig. 7).

Morphotype I: Borings have a lenticular or flaxseed shape of apertures (Fig. 7A), with a length range from 0.6 to 2.1 mm and a width range from 0.2 to 1.2 mm. The anterior and
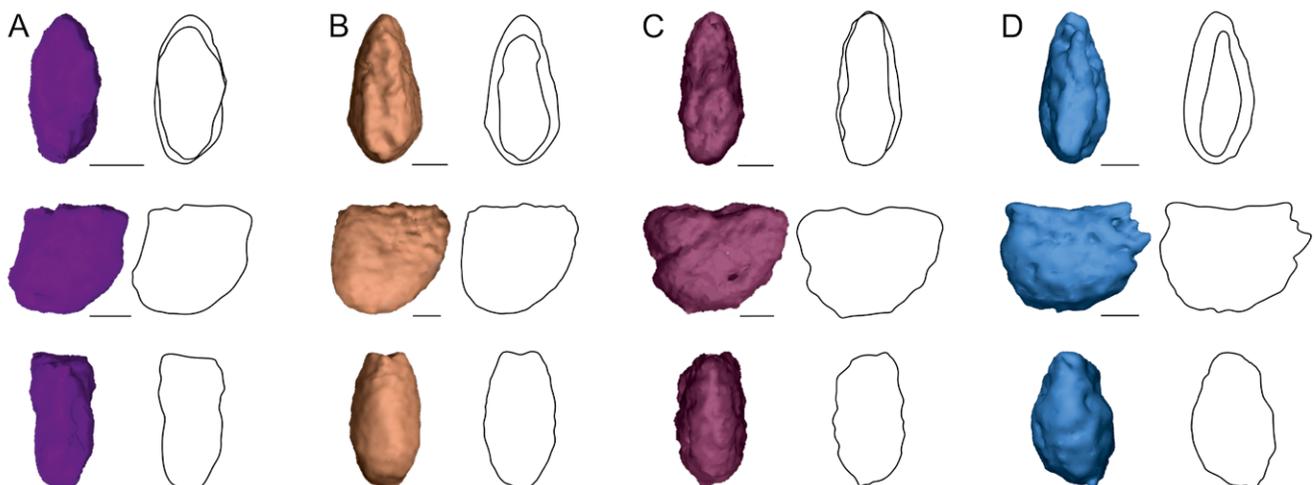

Fig. 7. The variety of shapes and sizes of acrothoracican borings in the *Oligophylloides maroccanus* skeleton. Scale bars = 1 mm.

posterior walls of pits are almost parallel to each other and oblique to the surface. In transverse view, the deepest point is in the middle or posterior part of boring. Borings vary substantially in terms of their dimensions. They are from 0.9 to 2.2 mm long, from 0.3 to 0.9 mm wide and from 0.5 to 1.9 mm deep.

Morphotype II: The posterior wall of the boring is almost perpendicular to the surface and extends only under the posterior end of the pit (Fig. 7B). The anterior wall extends obliquely to the surface. In transverse sections, the borings show that the deepest point is in the posterior part of the boring. The minimum length is 0.6 mm and the maximum 2.6 mm, but most of the lengths fall between 1.0 and 2.6 mm. The width ranges from 0.4 to 1.1 mm and the depth ranges from 0.6 to 2.5 mm. The aperture is wedge-shaped (Fig. 7B) and tapers toward the anterior end.

Morphotype III: The borings are narrow, and their outline is similar to a bowl shape, where the walls extend laterally and obliquely to the surface (Fig. 7C, D). This morphotype is the largest and the most common. The length ranges from 0.9 to 2.9 mm, the width from 0.4 to 1.1 mm, and the depth from 0.6 to 2.3 mm. The aperture can be wedge-shaped or oval, which reflects the position of the deepest part of the boring on the posterior or interior side. The length ranges from 0.9 to 2.6 mm and the width from 0.4 to 0.9 mm.

Morphotype IV: Only four borings display this shape. The pits are narrow and extend laterally (Fig. 7E). They are from 1.7 to 2.1 mm long, 0.8–1.1 mm wide, and 1.2–1.9 mm deep. The lengths of apertures range from 1.2 to 1.9 mm and the width from 0.5 to 0.9 mm. The borings have a characteristic prolongation of the aperture.

Morphotypes identified on the basis of their disparity were then compared with dimensions reported for fossil acrothoracican pouch-shaped borings, which are summarized in Table 3. The dimensions of borings produced by *Trypetesa* sp. were not included because these borings are morphologically distinct (see Tomlinson, 1969; Bałuk and Radwański, 1991; Nielsen *et al.,* 2016). Species of *Trypetesa* produce borings with narrow slits lined with cementum, which led Grygier and Newman (1985) to suggest that they are extant analogues of the ichnogenus *Rogerella*, also specifically excluded here because of the lack of the characteristics listed above. Wisshak *et al.*, (2019) additionally included in their synonymization as *Rogerella* the following species: *Cliona oostoma* Seguenza, 1879 and *Clionoida arbiglandensis* Smith, 1910. These species are excluded from the present comparison, because for the former no morphometric data could be found and the latter was an order of magnitude larger than all other taxa considered here. The relationships of clusters identified in this study to these taxa are presented in Figures 4–6.

Figures 4 and 5 support the opinion of Codez and Saint-Seine (1958) that ichnotaxa covered in this analysis have different ratios of boring dimensions. Their proportions allow discrimination, in particular there are no overlaps between the positions occupied by these taxa in the morphospace described by the length and depth (Fig. 4) and only minimal overlap between the fields occupied by *Zapfella pattei* Saint-Seine, 1954 and *Simonizapfes elongata* Codez, 1957 (in Codez and Saint-Seine, 1958) in the morphospace

described by length and width (Fig. 5). The proportions of length *versus* width and length *versus* depth of the borings studied here do not match those of any of these taxa. The proportions of the length and depth include in their lower range those of the short and shallow *Brachyzapfes elliptica*, but the range of depths is much deeper, excluding, however, the range occupied by the much deeper *Rogerella cragini* Schlaudt and Young (1960). The relationship between the length and depth in the pits studied here was similar to that of *Zapfella pattei*, but both dimensions were smaller. Lengths and widths of the pits span the range occupied by *R. cragini*, *B. elliptica* and *S. elongata*. They overlap with the range reported for *Rogerella mathieui* Saint-Seine, 1955, but extend to include smaller pits below the values reported for this species.

The dimensions of apertures are not distinctive for those taxa, for which they had been reported (Fig. 6; Tab. 3).

Distribution of borings in heterocoral skeletons

The borings are visible only on the external surfaces of the heterocorals studied. They usually occur as clustered and commonly adjacent, small, pouch-shaped pits. Their arrangement is chaotic, without any preferred orientation on the entire surface. They occur separately (Figs 2A–D, F, G, 3A–D), in pairs (Fig. 2B, E) or create numerous contiguous and overlapping pits (Figs 2A–D, F, G, 3A–D). In pairs, the two borings are almost parallel to each other and, very often, they are similar in size (Fig. 2B, E). Additionally, borings in such pairs are close and touch each other (Fig. 2B, E). Groups consist of numerous, different sizes (Figs 2A–G, 3A–D). Moreover, they can form "pathways", which consist of a few borings occurring in one line (single file; Fig. 2B, F). They comprise 5–7 borings, which sometimes touch each other (Fig. 3F). The distribution of borings differs between specimens. On the specimen UAM Ro/IBI/01 (1907), bioerosion covers most of the stem, illustrated in detail by micro-CT images (Fig. 2C). The borings occupy mainly three sides of the stem. Specimen UAM He/JBI/03 (1907) shows numerous barnacle trace fossils, mainly on two sides of the extended holdfast, and they are restricted to outer surface of the holdfast (Fig. 3A, B). Moreover, on the specimen UAM He/JBI/03 (1907), the borings are visible in the sediment (Fig. 3A, D), where they are not as numerous as in the skeletons. They occur individually or in small groups, where they contact each other.

Principal component analysis and K-means clustering

Principal Component 1 (PC1) explained 78% of the total variability, with its high values driven by high loadings of length, aperture length and depth (Fig. 8). PC2 explained 11% of the total variability and was mostly driven by a negative loading of the depth. In total, PC1 and PC2 explained 89% of the total dataset, supporting the strong correlation of the dimensions. It also revealed that depth was relatively independent of the size of the pit and its aperture.

Quantification of dimensions in 3D offers the possibility of objectifying the description and classification of morphotaxa. K-means clustering, assuming four groups, revealed
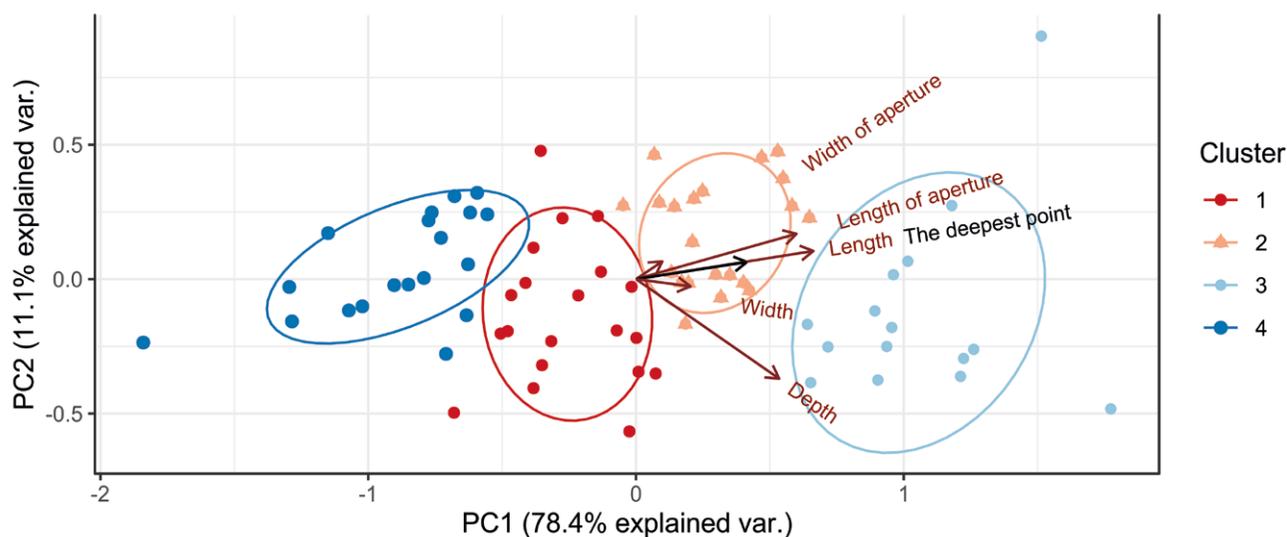
Fig. 8. Principal Component Analysis of acrothoracican borings. The graph shows the borings divided into four clusters, using the K-means algorithm. Ellipses mark 95% confidence intervals for each cluster. N = 75.

that they represent sections of the size continuum, summarized by PC1 (Fig. 8). The ratio between the cluster-sum of squares to the total sum of squares was 71.6%.

DISCUSSION

The skeletons of *Oligophylloides maroccanus* Weyer, 2016 presented demonstrate acrothoracican borings from the Upper Devonian of Morocco. The investigated material, combined with 3D micro-CT scanning and segmentation, allowed tracing of the morphology of pits quantitatively, as well as the description of their orientation and distribution.

Taxonomic affinity of the borings

On the basis of the absence of peduncular slits and bourrelets, which, however, are rarely preserved, the authors exclude the possibility that the borings described here belong to the ichnogenus *Rogerella*. This argument holds also for the other genera that are included in *Rogerella* by Bromley and D'Alessandro (1987) and many subsequent authors. The morphometric comparison of fossil barnacle borings in the present study shows that the dimensions of borings described here differ from measurements from the literature in their proportions of boring depth to length. The relationship between the lengths and the widths of the pits showed fewer differences between these forms. Grygier and Newman (1985) documented that the relationship between lengths and widths of the pits and additional features, such as trails and cementum, support the differences between borings produced by taxa with different morphologies. Such differences in apertural regions also support distinguishing different ichnotaxa (Codez and Saint-Seine, 1958). Unfortunately features of the apertures were not preserved sufficiently in the pits documented here, but even morphological comparison of the dimensions was

sufficient to show that they were distinct from previously described taxa. Importantly, the comparison of just the width and length of the borings would indicate that they belong to *Rogerella mathieui* (Fig. 5), but with neither slits nor bourrelets preserved, which could be attributed to the corrosion of specimen surfaces. But inclusion of the third dimension, the depth, shows a much wider disparity than reported for this ichnospecies (Fig. 4).

Biological underpinning of ichnodisparity

The present analysis is limited by the number of measurements available for the taxa that are discussed and it will hopefully stimulate further quantitative analyses to ground-truth the interpretations by the present authors. But even if ichnotaxa have consistent proportions, this does not automatically mean that they were made by different biological species. Depending on the substrates, the shapes of borings differ (Grygier and Newman, 1985; Plewes, 1996). Breton *et al.* (2020) noticed that borings are oblique to the surface in thin shells and Nielsen *et al.* (2016) described the size differences of borings with regard to the thickness of substrates (gastropod shell). This implies that some ichnotaxa might be produced by the same biological taxon, boring in different substrates. This is a common situation in ichnology and allows recording and documenting existing disparity, when no biological information is available to the palaeontologist. It is unlikely that all ichnotaxa discussed here (Tab. 3 and Figs 5–6) are produced by one acrothoracican genus, because no living taxon of this group inhabits such a wide range of hosts (G. Kolbasov, personal communication, 2021).

As shown by Grygier and Newman (1985), characterizing pits produced by extant acrothoracicans offers a tool for evaluation of the extent to which ichnodisparity translates to biological disparity. Thus, more 3D quantitative descriptions of populations of pits, bored by known taxa of barnacles, would benefit palaeontologists enormously, but currently

this data is limited (see e.g., Nielsen *et al.,* 2016). On the basis of the similarity between Recent acrothoracicans, belonging to the order Lithoglyptida, family Lithoglyptidae (G. Kolbasov, personal communication, 2021), the authors hypothesise the same family as a potential producer of the borings presented in this study. With more data on extant borings, it may become possible to constrain this assignment further.

Morphological variability within the ichnofossil assemblage

Prior to this study, ichnotaxonomy of acrothoracican borings was based on 2D characters, mostly observed on the surfaces of the substrates (e.g., Saint-Seine, 1951; Rodriguez and Gutschick, 1977; Baird *et al.*, 1990). Here, the authors revise it on the basis of the 3D morphology of the borings acquired through micro-CT. To identify potential disparate ichnospecies, the authors carried out cluster analysis, assuming four morphotypes (Fig. 7). In an ordination space derived from all six dimensions, it becomes clear that these clusters lie on a morphological continuum (Fig. 8). Probably, the morphotypes result from modification of the shapes of the borings during the development of barnacles (see Plewes, 1996). Apart from differences in the method of measurement, the number of pits analysed here allows a more nearly complete representation of variability than in previous studies (e.g., Codez and Saint-Seine, 1958; Rodriguez and Gutschick, 1977), which were mostly based on smaller datasets.

Timing of barnacle infestation

The detailed investigations of apparently well-preserved specimens of the heterocoral *O. maroccanus* demonstrating acrothoracican borings provide new evidence of *post mortem* encrustation by acrothoracican barnacles. It is commonly accepted that the skeleton of the heterocoral corallum was entirely enveloped by a thick layer of soft tissue, presumably with armoured polyps, which performed the function of armour against the larvae of boring and epibiontic organisms (Weyer, 2016; Dworczak *et al.*, 2020; Berkowski *et al.*, 2021). However, heterocorals could roll up their soft tissue, which resulted in exposure of the proximal part of the skeleton (Weyer, 2016; Dworczak *et al.*, 2020; Berkowski *et al.*, 2021). The exposed skeleton could be easily colonised by intruders. Furthermore, Heterocorallia could unroll the soft tissue towards distal part and progressively overgrew their infesting organisms (see Dworczak *et al.*, 2020). The borings are visible only on the outer surface of coral skeletons and there are not overgrown by the soft tissue of the colony. Moreover, in the polished transverse slabs of studied samples, the authors observed the absence of malformations. These two features indicate that the colonies had been dead at the time when the borings formed (cf. Kobluk and Nemcsok, 1982). Abletz (1993) and Miller (1970) described *syn vivo* interaction between corals and barnacles, which was indicated by the orientation and distribution pattern of borings and "an elevated ridge of coral tissue around the aperture of some borings". Therefore, it seems to be

unlikely that the larvae of barnacles could settle on live heterocoral skeletons. Among acrothoracican barnacles, there is an exception, the modern genus *Berndtia* bores in living corals (Chan *et al.*, 2014). Other *syn vivo* interaction was noted by Seilacher (1968), who observed the characteristic distribution pattern of acrothoracican borings on belemnite rostra (see discussion in Donovan and Jagt, 2013; De Baets *et al.*, 2020). Trace fossils that followed the host's swimming direction demonstrate that barnacles could benefit from this position and had better access to currents. However, the samples studied show a chaotic distribution and an absence of pit orientation. It seems that there was no dominant current direction on the sea bottom, which could control larval establishment (Kobluk and Nemcsok, 1982). According to Lambers and Boekschoten (1986) and Kočová Veselská *et al.* (2021), a lack of orientation and a chaotic distribution of borings can also indicate *post mortem* interaction. The massive heterocoral skeletons offered a stable and firm substratum for the attachment of barnacle larvae on a muddy sea bottom, although bioierosion by acrothoracican barnacles was most frequent in brachiopod shells during the Devonian period (see Table 1). This placement ensured better access to currents supplying nutrients, especially for barnacles, which are sessile filter-feeders. Many authors have discussed whether acrothoracican barnacles prefer live or dead hosts (see discussions in Kočová Veselská *et al.*, 2021, and Plewes, 1996). It seems that the most crucial factors for barnacle settlement are the character of the substrate, with carbonates being preferred, and the type of host, with epibenthonic, sessile hosts favoured (Seilacher, 1969).

Patterns of bioerosion in the skeletons of *O. maroccanus* show that the bottom currents could transport sediment, covering broken heterocoral colony on the seafloor, or even moving them. These cases limited the settlement of the coral by acrothoracican larvae. However, the abundant occurrences of borings on the skeleton, crossing each other or filled with the surrounding sediment, show that several generations of barnacles could settle on the heterocorals before the coral skeletons were turned over and/or finally buried.

CONCLUSIONS

The studied specimens of *Oligophylloides maroccanus* Weyer, 2016 from Jebel Bou Ifarherioun (Anti-Atlas, Morocco) display trace fossils that most likely were produced by acrothoracican barnacles. They are new evidence of barnacle activity in the Late Devonian. A detailed 3D investigation using micro-CT allowed retracing their distribution and orientation on heterocoral skeletons, as well as comparing their 3D morphology with known fossil acrothoracican borings.

A reevaluation of the morphological parameters of known ichnogenera, previously synonymized with *Rogerella*, revealed that they can be distinguished on the basis of the relationships between pit length *versus* depth. The borings described here do not fit any of the previously documented ichnotaxa but correspond to shapes produced by the extant acrothoracican family Lithoglyptidae. However, this topic deserves further research.

On the basis of the present analyses, it appears that aperture dimensions are not distinctive for fossil acrothoracican borings. Nonetheless, the authors see the need for further investigation..

Four morphotypes of borings have been observed on the heterocoral branch studied. Ordination analysis, carried out on a dataset of six dimensions measured in 75 pits, showed that these clusters do not represent four different ichnospecies but lie on a morphological continuum.

The interaction between the acrothoracican barnacles and heterocorals was *post mortem*. This is indicated by the chaotic orientation and distribution of the borings, their occurrence only on the external surface of skeletons, and the lack of malformations on coral heterotheca.

The massive heterocoral skeleton, devoid of soft tissue, was an easily available hard substrate for acrothoracican barnacles. The chaotic distribution and orientation of the pits show that there were no dominant bottom currents on the sea floor. Crosscutting borings reflect different colonization episodes.

Acknowledgments

REFERENCES

Abletz, V. V., 1993. Trace fossils of Acrothoracica (Cirripedia) from the Eocene of the Krivoy Rog Basin. *Paleontologicheski Zhurnal*, 27: 73–80.

Baird, G. C., Brett, C. E. & Tomlinson, J. T., 1990. Host-specific acrothoracid barnacles on Middle Devonian platyceratid gastropods. *Historical Biology*, 4: 221–244.

Bałuk, W. & Radwański, A., 1991. A new occurrence of fossil acrothoracican cirripedes: *Trypetesa polonica* sp. n. in hermitted gastropod shells from the Korytnica Basin (Middle Miocene: Holy Cross Mountains, Central Poland), and its bearing on behavioral evolution of the genus *Trypetesa*. *Acta Geologica Polonica*, 4: 1–36.

Bassi, D., Iryu, Y., Braga, J. C., Takayanagi, H. & Tsuji, Y., 2013. Bathymetric distribution of ichnocoenoses from recent subtropical algal nodules off Fraser Island, eastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 369: 58–66.

Belka, Z., Kaufmann, B. & Bultynck, P., 1997. Conodont-based quantitative biostratigraphy for the Eifelian of the eastern Anti-Atlas, Morocco. *Geological Society of America Bulletin*, 109: 643–651.

Berkowski, B., Zapalski, M. K., Jarochowska, E. & Alderslade, P., 2021. Early development and coloniality in *Oligophylloides* from the Devonian of Morocco – are Heterocorallia Palaeozoic octocorals?. *PLoS One*, 16 (9), doi:10.1371/journal.pone.0257523

Bertling, M., 2007. What's in a name? Nomenclature, systematics, ichnotaxonomy. In: Miller, W., III (ed.), *Trace Fossils. Concepts, Problems, Prospects*. Elsevier, Amsterdam & Oxford, pp. 81–91.

Bertling, M., Braddy, S. J., Bromley, R. G., Demathieu, G. R., Genise, J., Mikuláš, R., Nielsen, J. K., Nielsen, K. S. S., Rindsberg, A. K., Schlirf, M. & Uchman, A., 2006. Names for trace fossils: a uniform approach. *Lethaia*, 39: 265–286.

Bialik, O. M., Jarochowska, E. & Grossowicz, M., 2021 Ordination analysis in sedimentology, geochemistry and palaeoenvironment–background, current trends and recommendations. *The Depositional Record*, 7: 541–563.

Botha, T., Griffiths, C. L. & Maneveldt, G. W., 2020. Coralline red algae – a new host taxon for burrowing barnacles (Cirripedia, Acrothoracica). *Marine Biodiversity*, 50: 1–5.

Breton, G., Jäger, M. & Kocí, T., 2020. The sclerobionts of the Bajocian Oolithe ferrugineuse de Bayeux Formation from Calvados (Paris Basin, Normandy, France). *Annales de Paléontologie*, 106: 102361.

Bromley, R. G., 1975. Comparative analysis of fossil and recente-chinoid bioerosion. *Palaeontology*, 18: 725–739.

Bromley, R. G., 2004. A stratigraphy of marine bioerosion. In: McIlroy, D. (ed.), *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Geological Society of London, Geological Society, London, Special Publications*, 228: 455–479.

Bromley, R. G. & D'Alessandro, A., 1987. Bioerosion of the Plio-Pleistocene transgression of southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 93: 379–442.

Buatois, L. A., Carmona, N. B., Curran, H. A., Netto, R. G., Mángano, M. G. & Wetzel, A. 2016. The Mesozoic Marine Revolution. In: Mángano, M. & Buatois, L. (eds), *The Trace-Fossil Record of Major Evolutionary Events. Volume 2: Mesozoic and Cenozoic. Topics in Geobiology,* 40. Springer, Dortrecht, pp. 19–134.

Buatois, L. A., Gingras, M. K., MacEachern, J., Mángano, M. G., Zonneveld, J. P., Pemberton, S. G., Netto, R. G. & Martin, A., 2005. Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaios*, 20: 321–347.

Buatois, L. A. & Mángano, M. G., 2016. Recurrent patterns and processes: The significance of ichnology in evolutionary paleoecology. In: Mángano, M. G. & Buatois, L. A. (eds), *The Trace-Fossil Record of Major Evolutionary Events. Volume 2: Mesozoic and Cenozoic. Topics in Geobiology,* 40. Springer, Dordrecht, pp. 449–473.

Buatois, L. A., Wisshak, M., Wilson, M. A. & Mángano, M. G., 2017. Categories of architectural designs in trace fossils: A measure of ichnodisparity. *Earth-Science Reviews*, 164: 102–181.

Chan, B. K. K., Dreyer, N., Gale, A. S.,Glenner, H., Ewers-Saucedo, Ch., Perez-Losada, M., Kolbasov, G. A., Crandall,

K. A. & Høeg, J. S., 2021. The evolutionary diversity of barnacles, with an updated classification of fossil and living forms. *Zoological Journal of the Linnean Society*, 20: 1–58.

Chan, B. K. K., Kolbasov, G. A., Hirose, M., Mezaki. T. & Suwa, R., 2014. Biodiversity and biogeography of the coral boring barnacles of the genus *Berndtia* (Cirripedia: Acrothoracica) in the West Pacific, with description of three new species. *Journal of Natural History*, 48: 1503–1541.

Chwieduk, E., 2001. Biology of the Famennian heterocoral *Oligophylloides pachythecus*. *Palaeontology*, 44: 1189–1226.

Claussen, A. L., Munnecke, A., Wilson, M. A. & Oswald, I., 2019. The oldest deep-boring bivalves? Evidence from the Silurian of Gotland (Sweden). *Facies*, 65: 1–15.

Codez, J. & Saint-Seine, R. de, 1958. Révision des Cirripèdes acrothoraciques fossiles. *Bulletin de la Société Géologique de France,* 7: 699–719.

Davidson, T. M., Altieri, A. H., Ruiz, G. M. & Torchin, M. E., 2018. Bioerosion in a changing world: a conceptual framework. *Ecology Letters*, 21: 422–438.

De Baets, K. D., Hoffmann, R. & Mironenko, A., 2021. *Evolutionary history of cephalopod pathologies linked with parasitism*. In: Baets, K. D., de & Huntley, J. W. (eds), *The Evolution and Fossil Record of Parasitism. Coevolution and Paleoparasitological Techniques. Topics in Geobiology*, 50. Springer, Dordrecht, pp. 203–249.

Delamette, M., 1989. Trace fossil assemblages from the Albian phosphate-rich sandstones of the Helvetic Shelf (Western Alps). *Cretaceous Research*, 10: 207–219.

Donovan, S. K., 2011. The Recent boring *Gastrochaenolites ornatus* Kelly & Bromley, 1984, in a Chalk cobble from Cromer, England. *Bulletin of the Mizunami Fossil Museum*, 37: 185–188.

Donovan, S. K. & Jagt, J. W. M., 2013. *Rogerella* isp. infesting the pore pairs of *Hemipneustes striatoradiatus* (Leske) (Echinoidea: Upper Cretaceous, Belgium). *Ichnos*, 20: 153–156.

Dopieralska, J., 2009. Reconstructing seawater circulation on the Moroccan shelf of Gondwana during the Late Devonian: evidence from Nd isotope composition of conodonts. *Geochemistry, Geophysics, Geosystems*, 10: 1–13.

Dworczak, P. G, Berkowski, B. & Jakubowicz, M., 2020. Epizoans immured in the heterocoral *Oligophylloides maroccanus* Weyer, 2017: a unique record from the Famennian (Upper Devonian) of Morocco. *Lethaia*, 53: 452–461.

Dworczak, P. G., Jakubowicz, M., López Correa, M., Munnecke, A., Joachimski, M., Mazzoli, C. & Berkowski, B., 2022. Carbon and oxygen isotope fractionation in the Late Devonian heterocoral *Oligophylloides:* Implications for the skeletogenesis and evolution of the Heterocorallia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 598: 111017, https://doi.org/10.1016/j.palaeo.2022.111017

Ehlers, G. M. & Kline V., 1934. Revision of Aleksander Winchell's types of brachiopods from the Middle Devonian Traverse Group of rocks of Michigan. *Contributions from the Museum of Paleontology, University of Michigan*, 4: 143–176.

El-Hedeny, M. & El-Sabbagh, A., 2018. *Entobia* ichnofacies from the Middle Miocene carbonate succession of the northern Western Desert of Egypt. *Annales Societatis Geologorum Poloniae*, 88: 1–19.

Elias, M. K., 1957. Late Mississippian fauna from the Redoak Hollow Formation of southern Oklahoma, part I. *Journal of Paleontology*, 31: 370–427.

Elias, M. K. & Condra, G. E., 1957. *Fenestella* from the Permian of west Texas. *Geological Society of America. Memoirs*, 70: 1–158.

Fedorowski, J., 1991. Dividocorallia, a new subclass of Palaeozoic Anthozoa. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique,* 61: 21–105.

Frey, L., Rücklin, M., Korn, D. & Klug, C., 2018. Late Devonian and Early Carboniferous alpha diversity, ecospace occupation, vertebrate assemblages and bio-events of southeastern Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 496: 1– 17.

Goldring, R. & Kaźmierczak, J., 1974. Ecological succession in intraformational hardground formation. *Palaeontology*, 17: 949–962.

Golubic, S., Perkins, R. D. & Lukas, K. J., 1975. Boring microorganisms and microborings in carbonate substrates. In: Frey, R. W. (ed.), *The Study of Trace Fossils*. Springer, Berlin, Heidelberg, pp. 229–259.

Grygier, M. J. & Newman, W. A., 1985. Motility and calcareous parts in extant and fossil Acrothoracica (Crustacea: Cirripedia), based primarily upon new species burrowing in the deep-sea scleractinian coral *Enallopsammia. Transactions of the San Diego Society of Natural History*, 21: 1–22.

Huggett, J. M., Gale, A. S. & Evans, S., 2000. Carbonate concretions from the London Clay (Ypresian, Eocene) of southern England and the exceptional preservation of wood- boring communities. *Journal of the Geological Society*, 157: 187–200.

Hyde, J. E., 1953. Mississippian formations of central and southern Ohio. *Ohio Geological Survey Bulletin*, 51: 214–221.

Jakubowicz, M., Król, J., Zapalski, M. K., Wrzołek, T., Wolniewicz, P. & Berkowski, B., 2019. At the southern limits of the Devonian reef zone: Palaeoecology of the Aferdou el Mrakib reef (Givetian, eastern Anti-Atlas, Morocco). *Geological Journal*, 54: 10–38.

Kobluk, D. R. & Nemcsok, S., 1982. The macroboring ichnofossil *Trypanites* in colonies of the Middle Ordovician bryozoan *Prasopora*: population behaviour and reaction to environmental influences. *Canadian Journal of Earth Sciences*, 19: 679–688.

Kočová Veselská, M., Kočí, T., Jäger, M., Mikuláš, R., Heřmanová, Z., Morel, N. & Šamánek, J., 2021. Sclerobionts on tubes of the serpulid *Pyrgopolon* (*Pyrgopolon*) *deforme* (Lamarck, 1818) from the upper Cenomanian of Le Mans region, France. *Cretaceous Research*, 125: 104873.

Korn, D. & Bockwinkel, J., 2017. The genus *Gonioclymenia* (Ammonoidea; Late Devonian) in the Anti-Atlas of Morocco. *Neues Jahrbuch für Geologie und Paläontologie*, 285: 97–115.

Lambers, P., Boekschoten, G. J., 1986. On fossil and recent borings produced by acrothoracic cirripeds. *Geologie en Mijnbouw*, 65: 257–268.

Lin, H. C., Kolbasov, G. A. & Chan, B. K. K., 2016. Phylogenetic relationships of Darwin's "Mr. Arthrobalanus": The burrowing barnacles (Cirripedia: Acrothoracica). *Molecular Phylogenetics and Evolution*, 100: 292–302.

Lopes, R. P. & Pereira, J. C., 2018. Molluscan grazing traces (ichnogenus *Radulichnus* Voigt, 1977) on a Pleistocene bivalve

from southern Brazil, with the proposal of a new ichnospecies. *Ichnos*, 26: 141–157.

Mägdefrau, K., 1932. Über einige Bohrgänge aus dem Unteren Muschelkalk von Jena. *Palaontologische Zeitschrift*, 14: 150–160.

Mángano, M. G. & Buatois, L. A., 2016. The Cambrian explosion. In: Mángano, M. G. & Buatois, L. A. (eds), *The Trace-Fossil Record of Major Evolutionary Events. Topics in Geobiology,* 39. Springer, Dordrecht, pp. 73–126.

Mángano, M. G., Buatois, L. A., Wilson, M. & Droser, M., 2016. The Great Ordovician Biodiversification Event. In: Mángano, M. G. & Buatois, L. A. (eds), *The Trace-Fossil Record of Major Evolutionary Events. Topics in Geobiology,* 39. Springer, Dordrecht, pp. 127–156.

McLoughlin, N., Furnes, H., Banerjee, N. R., Muehlenbachs, K. & Staudigel, H., 2009. Ichnotaxonomy of microbial trace fossils in volcanic glass. *Journal of the Geological Society*, 166: 159–169.

Meyer, N., Wisshak, M., Edinger, E. N., Azetsu-Scott, K. & Freiwald, A., 2022. Ichnodiversity in the eastern Canadian Arctic in the context of polar microbioerosion patterns. *Polar Research*, 41: 8083, https://doi.org/10.33265/polar.v41.8083

Mikuláš, R., Kočová Veselská, M., Kočí, T., Šamánek, J., Jäger, M., Heřmanová, Z. & Bruthansová, J., 2022. Domichnial borings in serpulid tube walls: Prosperous benthic assemblages in the Cretaceous of France and the Czech Republic. *Frontiers in Ecology and Evolution*, 10, https://doi.org/10.3389/fevo.2022.882450

Miller, W. H., 1970. Additions to the fauna of the Niobrara Formation of Kansas. *Transactions of the Kansas Academy of Science*, 72: 533–546.

Morningstar, H., 1922. Pottsville fauna of Ohio. *Ohio Division of Geological Survey Bulletin*, 25: 1–312.

Muir-Wood, H. & Cooper, G. A., 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *Geological Society of America, Memoirs,* 81: 1–447.

Nielsen, S. K. D., Høeg, J. T. & Yusa, Y., 2016. Host relation, size and reproduction in the burrowing barnacle *Trypetesa lampas* (Hancock) (Crustacea Cirripedia Acrothoracica). *Zoological Studies*, 55: 1–10.

Norman, A. M., 1903. New generic names for some Entomostraca and Cirripedia. *Annals of Natural History*, 11: 367–369.

Oliver, W. A., 1966. Origins and relationships of Paleozoic coral groups and the origin of the Scleractinia. *Paleontological Society Papers*, 1: 107–134.

Pemberton, S. G., Jones, B. & Edgecombe, G., 1988. The influence of *Trypanites* in the diagenesis of Devonian stromatoporoids. *Journal of Paleontology*, 62: 22–31.

Pemberton, S. G., Kobluk, D. R., Ross, K. Y. & Risk, M. J., 1980. The boring *Trypanites* at the Silurian–Devonian disconformity in southern Ontario. *Journal of Paleontology*, 54: 1258–1266.

Plewes, C. R., 1996. *Ichnotaxonomic Studies of Jurassic Endoliths*. Unpublished PhD Thesis. Aberystwyth University, Aberystwyth, Great Britain, pp. 1–354.

R Development Core Team, 2020. R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. http://www.r- project.org/index.html.

Radtke, G. & Golubic, S., 2005. Microborings in mollusk shells, Bay of Safaga, Egypt: Morphometry and ichnology. *Facies*, 5: 118–134.

Rindsberg, A. K., 2012. Ichnotaxonomy: Finding patterns in a welter of information. In: Knaust, D. & Bromley, R. G. (eds), *Trace Fossils as Indicators of Sedimentary Environments. Developments in Sedimentology*, 64: 45–78.

Rindsberg, A. K., 2018. Ichnotaxonomy as a science. *Annales Societatis Geologorum Poloniae*, 88: 91–110.

Rodriguez, J. & Gutschick, R. C., 1970. Late Devonian-Early Mississippian ichnofossils from western Montana and northern Utah. In: Crimes, T. P. & Harper, J. C. (eds), *Trace Fossils. Geological Journal, Special Issue*, 3: 407–438.

Rodriguez, J. & Gutschick, R. C., 1977. Barnacle borings in live and dead hosts from the Louisiana Limestone (Famennian) of Missouri. *Journal of Paleontology*, 51: 718–724.

Rodriguez, J. & Gutschick, R. C., 2000. Late Famennian *Wetheredella* in oncoids from Montana and Utah, USA. *Brigham Young University Geology Studies*, 45: 69–86.

Różkowska, M., 1969. Famennian tetracoralloid and heterocoralloid fauna from the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica*, 14: 5–187.

Saint-Seine, R. de, 1951. Un cirripède acrothoracique du Crétacé; *Rogerella lecointrei*, nov. gen., nov. sp. *CompteRendu del'Academie des Sciences,* 223: 1051–1053.

Saint-Seine, R. de, 1954. Existence de Cirripedes acrothoraciques des le Lias: *Zapfella pattei*, nov. gen., nov. sp. *Bulletin de la Société Géologique de France*, 4: 447–451.

Saint-Seine, R. de, 1955. Les Cirripedes acrothoraciques Echinocoles. *Bulletin de la Société Géologique de France*, 5: 299–303.

Schindewolf, O. H., 1941. Zur Kenntnis der Heterophylliden, einereigentümlichen paläozoischen Korallengruppe. *Paläontologische Zeitschrift*, 22: 213–306.

Schlaudt, C. M. & Young, K., 1960. Acrothoracic barnacles from the Texas Permian and Cretaceous. *Journal of Paleontology*, 34: 903–907.

Scrutton, C. T., 1997. The Palaeozoic corals, I: origins and relationships. *Proceedings of the Yorkshire Geological Society*, 51: 177–208.

Seguenza, G., 1879. *Le formazioni Terziarie nella Provincia di Reggio (Calabria)*. Coi tipi del Salviucci, Rome, 416 pp.

Seilacher, A., 1968. Swimming habits of belemnites – recorded by boring barnacles. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 4: 279–285.

Seilacher, A., 1969. Paleoecology of boring barnacles. *American Zoologist*, 9: 705–719.

Seilacher, A., 1977. Evolution of trace fossil communities. In: Hallam A. (ed.), *Patterns of Evolution as Illustrated by the Fossil Record. Developments in Palaeontology and Stratigraphy*, 5: 359–376.

Smith, J., 1910. Carboniferous rocks of the Solway, Scotland. *The Geological Society of Glasgow*, 14: 30–59.

Steinbrook, M. A., 1938. *Atrypa* and *Stropheodonta* from the Cedar Valley Beds of Iowa. *Journal of Paleontology*, 12: 229–256.

Tapanila, L., Roberts, E. M., Bouare, M. L., Sissoko, F. & O'leary, M. A., 2004. Bivalve borings in phosphatic coprolites and bone, Cretaceous–Paleogene, northeastern Mali. *Palaios*, 19: 565–573.

Taylor, P. D. & Wilson, M. A., 2002. A new terminology for marine organisms inhabiting hard substrates. *Palaios*, 17: 522–525.

Tomlinson, J. T., 1963. Acrothoracican barnacles in Paleozoic myalinids. *Journal of Paleontology,* 37: 164–166.

Tomlinson, J. T., 1969. The burrowing barnacles (Cirripedia: Order Acrothoracica). *Bulletin of the United States National Museum*, 296: 1–162.

Toom, U., Vinn, O. & Hints, O., 2019. Ordovician and Silurian ichnofossils from carbonate facies in Estonia: a collection-based review. *Palaeoworld*, 28: 123–144.

Vinn, O. & Toom, U., 2016. Borings in phosphatized siltstone pebbles from the Cambrian of Estonia (Baltica). *Geological Magazine*, 153: 635–642.

Vogel, K. & Brett, C. E., 2009. Record of microendoliths in different facies of the Upper Ordovician in the Cincinnati Arch region USA: The early history of light-related microendolithic zonation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 281: 1–24.

Voigt, E., 1977. On grazing traces produced by the radula of fossil and recent gastropods and chitons. In: Crimes, T. P. & Harper, J. C. (eds), *Trace Fossils 2. Geological Journal, Special Issue*, 9: 335–346.

Wendt, J., 1985. Disintegration of the continental margin of north-western Gondwana: Late Devonian of the eastern Anti-Atlas (Morocco). *Geology*, 13: 815–818.

Wendt, J. & Belka, Z., 1991. Age and depositional environment of Upper Devonian (early Frasnian to early Famennian) black shales and limestones (Kellwasser facies) in the eastern Anti–Atlas, Morocco. *Facies*, 25: 51–89.

Weyer, D., 1997. News about Famennian Heterocorallia in Germany and Morocco. *Boletín de la Real Sociedad Española de Historia Natural*, 91: 145–151.

Weyer, D., 2002. Famennium-Anthozoa aus Marokko. 1. *Czarnockia* Różkowska, 1969 (Rugosa). *Mitteilungen aus dem Museum für Naturkunde in Berlin. Geowissenschaftliche Reihe*, 5: 75–92.

Weyer, D., 2016. Solitary and/or colonial growth in the Palaeozoic superorder Heterocorallia Schindewolf, 1941 (Eifelian–Serpukhovian). *Freiberger Forschungshefte*, 23: 59–101.

Wilson, M. A., 2007. Macroborings and the evolution of marine bioerosion. In: Miller, W., III (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 356–367.

Wilson, M. A. & Palmer, T. J., 1998. The earliest *Gastrochaenolites* (Early Pennsylvanian, Arkansas, USA): an upper Paleozoic bivalve boring? *Journal of Paleontology*, 72: 769–772.

Wisshak, M., Knaust, D. & Bertling, M., 2019. Bioerosion ichnotaxa: review and annotated list. *Facies*, 65: 1–39.

Wood, R., 2000. Palaeoecology of a Late Devonian back reef: Canning Basin, Western Australia. *Palaeontology*, 43: 671–703.

Wrzołek, T., 1981. Coral growth in *Oligophylloides pachythecus* Różkowska, 1969. *Acta Palaeontologica Polonica*, 25: 513–517.

Ziegler, W. & Sandberg, C., 1984. *Palmatolepis*-based revision of upper part of standard Late Devonian conodont zonation. *Geological Society of America, Special Paper*, 196: 179–194.

Appendix 1

Measurements (in mm) of the acrothoracican borings on the heterocoral branch [UAM Ro/IBI/01 (1907)].

Number of boring	Length	Depth	Width	The deepest point	Length of aperture	Width of aperture	Morphotype	Shape of apperture
1	2.1	1.9	1.1	1.4	1.9	0.6	4	pouch
2	2.0	1.8	1.0	1.3	1.8	0.5	2	pouch
3	2.0	1.4	0.9	1.0	1.7	0.5	4	pouch
4	1.4	1.2	0.7	0.7	1.2	0.4	2	elliptical
5	1.8	1.5	0.8	1.1	1.7	0.7	3	pouch
6	1.3	1.0	0.6	NA	1.1	0.3	NA	elliptical
7	2.2	1.8	0.9	1.2	2.0	0.6	3	pouch
8	2.1	2.0	1.1	1.3	1.8	0.7	2	elliptical
9	1.8	1.5	1.1	1.2	1.7	0.9	3	pouch
10	1.8	1.4	0.8	1.2	1.7	0.6	2	elliptical
11	1.4	1.4	0.7	0.7	1.3	0.5	1	pouch
12	2.2	1.7	0.9	1.5	2.1	0.7	3	elliptical
13	1.4	1.4	0.8	0.9	1.1	0.3	2	pouch
14	2.4	2.1	1.1	1.1	2.2	0.7	3	elliptical
15	2.1	1.4	0.7	1.3	2.0	0.6	3	elliptical
16	1.7	1.3	0.8	1.2	1.6	0.5	2	elliptical
17	1.0	0.9	0.4	0.6	1.0	0.4	2	pouch

Number of boring	Length	Depth	Width	The deepest point	Length of aperture	Width of aperture	Morphotype	Shape of apperture
18	2.4	1.6	1.0	1.4	2.3	0.8	2	elliptical
19	1.8	1.4	0.8	0.8	1.7	0.8	3	pouch
20	1.7	1.5	0.6	0.8	1.5	0.6	3	elliptical
21	1.7	1.7	0.8	0.9	1.2	0.2	1	pouch
22	1.3	1.4	0.7	0.8	0.6	1.2	1	elliptical
23	1.3	1.9	0.5	NA	1.7	0.6	1	pouch
24	1.4	1.1	0.8	0.6	1.4	0.4	1	pouch
25	2.0	1.3	0.6	0.6	1.9	0.5	3	elliptical
26	1.5	0.7	0.8	0.9	1.6	0.7	3	pouch
27	1.2	0.9	0.4	0.7	1.0	0.6	1	elliptical
28	2.0	1.5	0.7	0.8	1.5	0.5	3	pouch
29	1.6	1.2	0.7	0.8	1.5	NA	3	elliptical
30	0.9	0.6	0.8	0.4	1.2	0.6	3	pouch
31	1.9	1.9	0.8	0.0	1.5	0.8	2	pouch
32	1.8	1.3	0.7	0.8	1.5	0.6	3	elliptical
33	1.4	1.1	0.8	0.7	1.4	0.6	2	pouch
34	1.7	1.2	0.8	0.7	1.5	0.7	1	elliptical
35	1.6	1.6	0.8	1.1	1.4	0.5	3	pouch
36	1.1	0.9	0.4	0.7	0.9	0.5	3	elliptical
37	1.1	0.6	0.3	NA	0.8	0.3	1	elliptical
38	1.3	0.9	0.6	0.9	1.1	0.5	NA	pouch
39	0.8	0.6	0.5	0.0	0.8	0.4	NA	pouch
40	0.9	0.7	0.5	0.5	0.9	0.4	2	pouch
41	0.6	0.6	0.4	0.4	0.4	0.3	2	pouch
42	0.9	0.8	0.7	0.3	0.9	0.4	3	elliptical
43	2.2	1.1	0.9	1.2	1.9	0.8	2	pouch
44	1.6	1.2	0.6	1.0	1.3	0.6	3	NA
45	1.1	0.8	0.6	NA	1.0	0.4	3	NA
46	2.6	2.5	1.1	1.7	2.2	0.6	2	pouch
47	1.2	0.9	0.5	0.7	1.1	0.4	2	pouch
48	1.5	0.8	0.6	0.8	1.3	0.5	3	elliptical
49	2.3	1.3	0.8	1.2	2.2	0.5	?	elliptical
50	2.4	1.2	0.8	1.0	1.8	0.8	3	elliptical
51	2.5	1.8	0.7	NA	2.1	0.6	3	elliptical
52	1.5	0.7	0.8	0.8	1.2	0.8	3	pouch
53	1.9	1.4	0.6	1.0	1.6	0.6	2	pouch
54	2.1	1.7	0.8	1.3	1.7	0.5	3	elliptical
55	1.7	1.1	0.9	0.9	1.8	0.9	2	pouch
56	1.9	1.1	0.8	1.0	1.7	0.6	3	pouch
57	1.3	0.7	0.6	0.7	1.3	0.4	3	pouch
58	1.7	1.0	0.7	1.0	1.5	0.6	3	pouch
59	2.1	1.9	0.8	1.1	1.7	0.4	2	elliptical
60	1.6	1.6	0.6	0.9	1.5	0.4	2	pouch
61	2.4	2.2	0.7	1.2	2.1	0.6	3	elliptical
62	2.3	2.1	1.1	1.3	2.1	0.7	2	pouch

Number of boring	Length	Depth	Width	The deepest point	Length of aperture	Width of aperture	Morphotype	Shape of apperture
63	1.6	1.3	0.8	0.7	1.2	0.5	1	pouch
64	2.2	1.9	0.9	1.1	2.1	0.6	1	pouch
65	1.6	1.4	0.6	1.2	1.3	0.5	3	elliptical
66	1.9	1.5	0.7	1.1	1.8	0.6	2	pouch
67	2.0	1.1	0.7	1.5	1.9	0.6	3	pouch
68	1.9	1.1	1.0	1.0	1.8	0.8	2	pouch
69	1.9	1.1	0.8	1.2	1.7	0.6	3	elliptical
70	1.4	1.1	0.5	0.6	1.2	0.3	2	pouch
71	1.8	1.0	0.7	1.1	1.5	0.6	2	pouch
72	1.9	0.9	0.7	1.1	1.7	0.6	3	elliptical
73	1.4	0.7	0.7	0.7	1.1	0.6	3	pouch
74	2.9	1.2	0.7	1.8	2.6	0.6	3	pouch
75	1.2	1.2	0.5	0.7	1.1	0.4	2	pouch
76	1.4	0.7	0.5	0.8	1.3	0.5	2	pouch
77	1.4	1.2	0.8	0.7	1.2	0.5	1	pouch
78	2.0	1.0	0.8	1.1	1.5	0.7	NA	NA
79	1.7	1.2	0.8	0.9	1.2	0.7	4	pouch
80	1.3	0.9	0.5	0.7	1.1	0.4	3	elliptical
81	2.1	1.3	1.0	1.2	1.9	0.8	4	pouch
82	1.5	1.0	0.7	0.8	1.4	0.6	2	pouch
83	1.7	0.9	0.7	1.1	1.3	0.4	1	pouch
84	1.4	0.9	0.8	0.8	1.1	0.6	2	pouch
85	0.8	0.5	0.4	0.4	0.7	0.3	NA	NA
86	1.4	0.8	0.5	0.7	1.0	0.4	NA	NA
87	0.9	0.5	0.5	0.7	0.7	0.3	1	NA
88	1.0	0.6	0.4	0.7	0.9	0.3	NA	NA
89	1.1	0.7	0.4	0.6	0.8	0.4	NA	NA
90	1.3	0.5	0.4	0.6	1.1	0.4	NA	pouch
91	1.4	0.8	0.5	0.7	1.2	0.4	3	elliptical
92	1.5	0.8	0.4	0.6	1.4	0.4	3	pouch
93	2.4	1.7	0.9	1.2	2.0	0.6	3	elliptical

Appendix 2

Lengths and widths of apertures (in mm) from the literature.

Length	Width
2.0	0.6
2.2	0.8
2.6	0.9
2.5	1.1
2.2	0.9
1.6	0.6
1.7	0.6
2.0	0.7

Length	Width
1.6	0.8
1.8	0.8
1.7	0.9
1.9	0.9
2.1	0.8
2.3	0.8
2.6	0.8
2.2	1.1

Length	Width
2.7	1.1
2.9	1.2
2.7	1.3
2.3	1.1
2.2	1.0
2.3	1.0
2.4	1.0
2.4	0.9

Length	Width
2.3	0.9
2.1	0.9
2.0	0.9
1.8	0.9
1.9	0.8
1.7	0.7
1.6	0.7
1.4	0.5

Measurements (in mm) of acrothoracican borings from the literature.

Species	Length	Depth
Brachyzapfes elliptica	1.1	0.6
Brachyzapfes elliptica	1.2	0.7
Brachyzapfes elliptica	1.3	0.6
Brachyzapfes elliptica	1.4	0.7
Brachyzapfes elliptica	1.5	0.9
Brachyzapfes elliptica	1.6	0.9
Brachyzapfes elliptica	1.6	0.9
Brachyzapfes elliptica	1.6	0.8
Brachyzapfes elliptica	1.7	0.8
Brachyzapfes elliptica	1.7	0.8
Brachyzapfes elliptica	1.8	0.8
Brachyzapfes elliptica	1.8	1.0
Brachyzapfes elliptica	1.9	0.9
Brachyzapfes elliptica	2.0	1.0
Brachyzapfes elliptica	2.0	1.2
Simonizapfes elongata	2.3	1.3
Simonizapfes elongata	2.4	1.4
Simonizapfes elongata	2.6	1.4
Simonizapfes elongata	2.7	1.5
Simonizapfes elongata	2.6	1.6
Simonizapfes elongata	2.8	1.6
Simonizapfes elongata	2.9	1.8
Simonizapfes elongata	3.0	1.7
Simonizapfes elongata	3.0	1.8
Simonizapfes elongata	3.0	1.8
Simonizapfes elongata	3.0	1.9
Simonizapfes elongata	3.2	1.9
Simonizapfes elongata	3.3	1.8
Simonizapfes elongata	3.3	1.7
Simonizapfes elongata	3.7	2.3
Simonizapfes elongata	4.3	2.5
Simonizapfes elongata	4.4	2.7
Zapfella pattei	1.9	1.6
Zapfella pattei	2.2	2.0
Zapfella pattei	2.3	2.0
Zapfella pattei	2.4	2.0

Species	Length	Depth
Zapfella pattei	2.3	2.1
Zapfella pattei	2.2	2.1
Zapfella pattei	2.2	2.1
Zapfella pattei	2.1	2.3
Zapfella pattei	2.4	2.3
Zapfella pattei	2.5	2.5
Zapfella pattei	2.8	2.4
Zapfella pattei	2.7	2.5
Zapfella pattei	2.7	2.6
Zapfella pattei	2.9	2.6
Zapfella pattei	3.0	2.6
Zapfella pattei	3.2	2.8
Zapfella pattei	3.1	2.9
Zapfella pattei	3.0	2.8
Zapfella pattei	2.8	2.8
Zapfella pattei	2.6	2.8
Rogerella mathieui	2.5	2.9
Rogerella mathieui	2.3	2.7
Rogerella mathieui	2.0	2.8
Rogerella mathieui	2.0	2.6
Rogerella mathieui	1.9	2.6
Rogerella mathieui	1.8	2.7
Rogerella mathieui	1.9	2.4
Rogerella mathieui	1.9	2.3
Rogerella mathieui	1.9	2.2
Rogerella mathieui	1.8	2.2
Rogerella mathieui	1.8	2.1
Rogerella mathieui	1.8	2.0
Rogerella mathieui	1.7	2.2
Rogerella mathieui	1.7	2.1
Rogerella mathieui	1.6	2.0
Rogerella mathieui	1.4	1.8
Rogerella mathieui	1.3	1.6
Rogerella mathieui	1.2	1.9
Rogerella mathieui	1.1	1.8
Rogerella mathieui	1.1	1.7
Rogerella mathieui	1.1	1.6