

# Skeletobiosis on favositid corals: a case study from the Middle Devonian of the Mader Basin, Morocco

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## ABSTRACT:

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Tabulate corals of the genus *Favosites* Lamarck, 1816 from the Middle Devonian of Madène el Mrakib (eastern Anti-Atlas, Morocco) were qualitatively and quantitatively studied with respect to their encrusting and boring organisms (skeletobionts). The assemblage, comprising 18 taxa, is numerically dominated by bryozoans, microconchid tubeworms, and auloporid tabulates. Although less diverse, the recognised *Favosites*-hosted skeletobiont fauna contains taxa described previously from co-occurring brachiopods. As evidenced by the lower mean abundance and density of the skeletobionts, in contrast to the brachiopod hosts, the favositid corals were, however, not preferred substrates for colonisation. Although the skeletobionts occur on both the upper and lower sides of the host colonies, the majority of colonisers thrived on the latter. Such a colonisation pattern may indicate that the favositids were colonised first on the surfaces devoid of the hosts' soft tissue. The upper sides, in turn, were largely covered by polyps, so these areas might have been either colonised *post mortem*, or the larvae settled on those parts of the living hosts that were devoid of soft tissue. The lack of any skeletobiont group present exclusively on the lower sides indicates that none of the abundant taxa were obligate cryptobionts. The favositids lack any traces after parasitic endobionts, such as, e.g., *Chaetosalpinx* Sokolov, 1948 and allied cecidotaxa, which may either point to the general absence of such endobionts in the habitat, limited survival of their larvae, or an efficient immune system of the hosts, preventing their settlement.

**Key words:** Epibionts; Endobionts; Sclerobionts; Tabulata; Palaeoecology; Devonian.



## INTRODUCTION

The Middle Devonian was a unique interval in Earth's history, during which many invertebrates with calcitic skeletons flourished in marine habitats, starting to play important ecological roles. Tabulate corals and stromatoporoids constructed massive reef structures (Talent 1988; Wood 1998; Copper 2002; Edinger *et al.* 2002; Copper and Scotese 2003; Zapalski *et al.* 2017; Król *et al.* 2018; Jakubowicz *et al.* 2019). Along with the tabulates and stromatoporoids, diverse brachiopod and rugose coral assemblages inhabited reefs, peri-reef environments, and vast areas of both shallow and deeper parts of carbonate platforms and ramps (e.g., Baird and Brett 1983; Webb and Schneider 2013; Zapalski *et al.* 2017; Jakubowicz *et al.* 2019; Zatoń and Wrzolek 2020; Chang *et al.* 2021; Woźniak *et al.* 2022; Zatoń *et al.* 2022a). These organisms also provided 'benthic islands' in soft-bottom environments, and thus increased the small-scale habitat heterogeneity by serving as hard substrates for cementing and boring organisms, collectively known as skelotobionts (*sensu* Taylor and Wilson 2002). Both encrusters (episkelotobionts) and endobionts (endoskelotobionts) are preserved *in situ* with respect to their host, providing valuable information on the colonisers' spatial distribution, dominance, ecological preference, and relationships to the host organisms, as well as to the associated skelotobionts (e.g., Zapalski 2005, 2009; Taylor 2016; Peters *et al.* 2024; Zatoń and Nawrot 2024a; see also Taylor and Wilson 2003 for a comprehensive review).

For the Middle Devonian, the problem of skelotobiosis (see also Romero *et al.* 2022 for the term sclerobiosis), or the use of skeletal remains of other organisms by colonising biotas, has been much more extensively studied on rhynchonelliformean brachiopods (e.g., Sparks *et al.* 1980; Bordeaux and Brett 1990; Bose *et al.* 2011; Mistiaen *et al.* 2012; Zatoń *et al.* 2022a; Brychey *et al.* 2023) than on rugose (e.g., Baird and Brett 1983; Zatoń and Wrzolek 2020; Zatoń *et al.* 2022b, 2023a) and tabulate corals (e.g., Copper 1996; Zapalski 2009; Zatoń *et al.* 2018, 2023a). This difference may be related not only to the generally greater abundance of brachiopod shells in the Middle Devonian deposits, but also to their more common occurrence in siliciclastic and marly facies from which they are easily collected in large quantities.

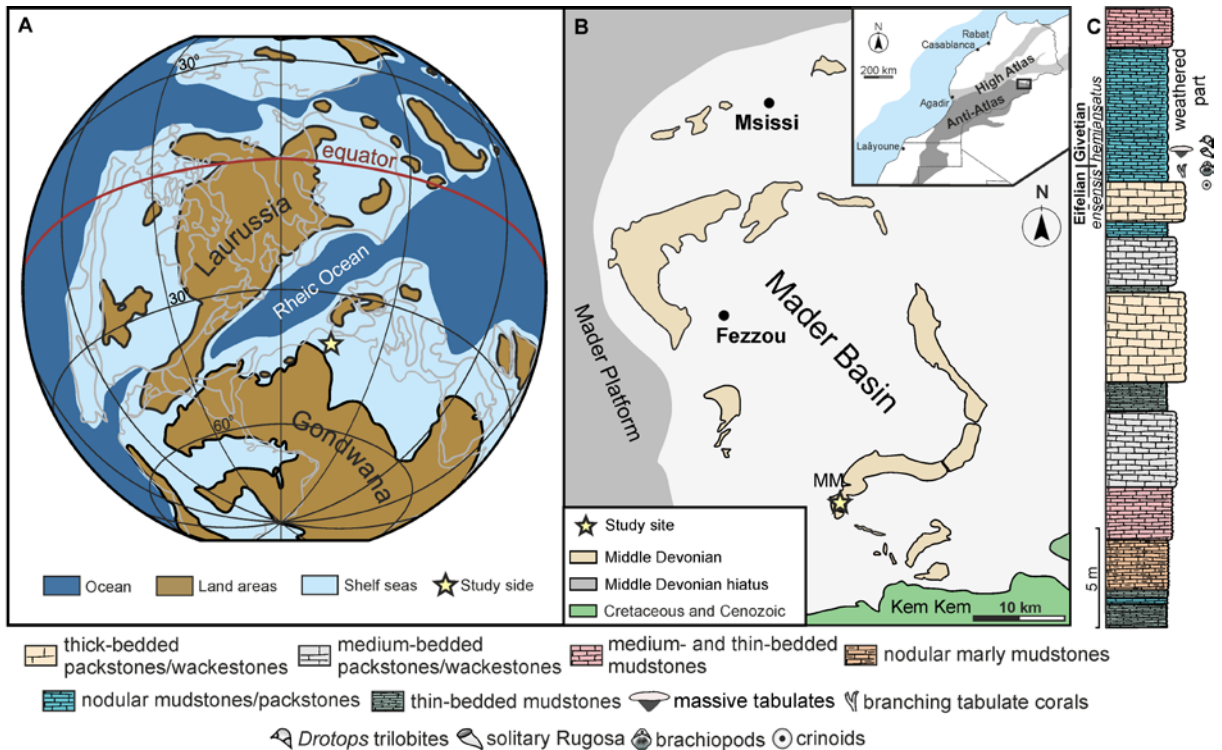
In the present paper, Middle Devonian favositid tabulate corals, which inhabited soft substrates preserved at the present day Madène el Mrakib locality

in Morocco, have been analysed with respect to their preserved skelotobionts. Previously, a large collection of brachiopods from the same locality provided the first quantitative data on the diversity, abundance, and colonisation patterns of skelotobionts from the northern shelf of Gondwana (Zatoń *et al.* 2022a). A later inspection of the site furthermore revealed also that favositid tabulates were a conspicuous element of the local Devonian ecosystem. Thus, in order to trace the colonisation patterns, diversity, abundance, and distribution of the associated skelotobionts, their relation to the hosts, and their similarity to the assemblage present on the co-occurring brachiopods, the newly collected favositids have been studied. The resulting data are compared to the colonisation patterns documented for other hosts, and used for deciphering the possible steps of colonisation of the tabulate corals. The gathering and analysis of such data on sclerobionts preserved on different but co-occurring hosts provide a wider and more detail picture of hard substrate communities and their palaeoecology in a given palaeoenvironment.

This paper is addressed to the jubilee of Prof. Michał Szulczewski, who is especially known for his work concerning the Devonian system.

## GEOLOGICAL BACKGROUND

The Madène el Mrakib section is located in the eastern Anti-Atlas, Morocco, in the southern part of the Mader Basin, ~30 km SE of the village of Fezzou (Text-fig. 1B). The basin formed during the Devonian as a result of the extensional breakup of the broad shelf marking the passive margin of NW Gondwana (Text-fig. 1A; Wendt 1985, 2021). By the Middle through Late Devonian, a distinct platform-and-basin topography originated, with several basins typified by different sedimentary histories and accompanying rich, partially endemic faunas adapted to a variety of bathymetries, insolation, current regimes, and substrates (e.g., Wendt and Belka 1991; Berkowski 2008; Lubeseder *et al.* 2010; Frey *et al.* 2018; Berkowski *et al.* 2019; Dworzak *et al.* 2020). The Middle Devonian deposits of the Mader Basin are predominantly neritic, argillaceous wackestones to mudstones; the most fossiliferous, shallowest facies, rimming the partially emerged Mader Platform, occur along the southern, western, and northern margins of the basin (Kaufmann 1998). During the latest Eifelian–early Givetian, these areas contained rich coral-stromatoporoid communities, forming small bioherms and bios-



Text-fig. 1. Location of the study site. A – Palaeogeographic map for the Middle Devonian (adapted from Scotese 2001; slightly modified after Jakubowicz *et al.* 2019) with the position of the study site indicated. B – Schematic geological map of the Mader Basin showing the distribution of the Middle Devonian outcrops and the study site at Madène el Mrakib (MM) (adapted from Döring and Kazmierczak 2001 and Jakubowicz *et al.* 2019). C – Lithostratigraphic column of the Middle Devonian deposits at Madène el Mrakib with the studied fossiliferous interval indicated (slightly modified after Zatoń *et al.* 2022a).

tromes (Schröder and Kazmierczak 1999; Döring and Kazmierczak 2001; Fröhlich 2003; Berkowski *et al.* 2023; Majchrzyk *et al.* 2024), and a single, large reefal buildup (Aferdou el Mrakib; Kaufmann 1998; Król *et al.* 2018; Jakubowicz *et al.* 2019; Majchrzyk *et al.* 2022, 2023; Zatoń *et al.* 2023a).

The Madène el Mrakib section exposes Middle Devonian carbonates and Upper Devonian siliciclastics (Kaufmann 1998; Döring and Kazmierczak 2001; Becker *et al.* 2018). The lower part of the section, attributed to the lower Eifelian, comprises a fossil-poor succession of marls, shales, and hemipelagic carbonate mudstones with rare bioclast-rich intercalations (Text-fig. 1C). Throughout the upper Eifelian–lower Givetian, a general shallowing-upward trend is marked by the up-section increase in the thickness and number of increasingly fossiliferous, carbonate intervals, culminating with a diverse, shallow-water reef assemblage, dominated by branching tabulate corals (Majchrzyk *et al.* 2024). The upper, Frasnian–Famennian, siliciclastic part of the succession is widely known owing to its remarkably well-preserved

chondrichthyan fishes (e.g., Frey *et al.* 2019, 2020) and cephalopods (e.g., Klug *et al.* 2016).

The studied favositids have been collected from an interval of fossiliferous, thin-bedded, nodular carbonates (mudstones to packstones) which contains, in its upper part, abundant remains of the phacopid trilobite *Drotops megalomanicus* Struve, 1990 (Text-fig. 1C). The deposit represents the transition between the uppermost Eifelian (*ensensis* Zone) and lowermost Givetian (*hemiansatus* Zone; Zatoń *et al.* 2022a); coeval *Drotops*-rich strata are exposed in several parts of the southern Mader Basin, providing a locally important marker horizon (Kaufmann 1998; Jakubowicz *et al.* 2019). The horizon can be easily traced in both the field and satellite images owing to the extensive commercial exploitation of the *Drotops* fossils. The studied limestones contain abundant brachiopods, branching and, more rarely, massive tabulate corals, solitary rugose corals, tentaculitoids, as well as fragments of bryozoans, gastropods, crinoids and ostracods (Struve 1990; Halamski and Baliński 2013; Jakubowicz *et al.* 2015; Zatoń *et al.* 2022a, 2023b).

## MATERIAL AND METHODS

In total, 86 colonies of favositids were collected from the scree closely adjacent to the section at Madène el Mrakib. After cleaning, the specimens were inspected under a Nikon SMZ1000 binocular microscope, and all detected fossils of encrusters and traces left by boring organisms were identified to the lowest possible taxonomic level and counted. Such a procedure was applied separately to the upper (exposed) and lower/inwardly sloping sides (usually forming the hidden surfaces; from now on referred to as the lower sides) of the colonies. As in previous similar studies (e.g., Zatoń and Wrzolek 2020; Zatoń *et al.* 2022a, 2023b), each well-separated colony of colonial encrusters was counted as one specimen. In order to obtain accurate data on the size of the specimens, the volume of each of the 47 best-preserved colonies was measured by displacement of water using measuring cylinders. Later, the colonies were cut transversely to the growth direction, polished, and further inspected for additional skeletobionts (especially borings and bioclaustrations) which might have potentially been present in older parts of the favositids.

Selected skeletobionts were coated with ammonium chloride and photographed using a Canon EOS 350D digital camera. Some other specimens, however, were also photographed using a Nikon SMZ1000 equipped with an Imaging Source DFK NME 33UX265 camera and NIS-Elements D imaging software.

To evaluate the relationship between the colony size and skeletobiont colonisation patterns, we restricted the analyses to the well-preserved colonies whose volume had been measured. The same set of specimens was also used to compare the skeletobiont assemblages present on the lower and upper sides of the corals, and to assess the differences in colonisation metrics between the favositids and the co-occurring brachiopods. We quantified the colonisation frequency (proportion of corals hosting skeletobionts), abundance (the number of individuals) and richness (the number of genera/higher taxa) of the skeletobionts for both the entire coral colonies and for each side separately. To avoid overestimation of the skeletobiont richness, unidentifiable epibionts (Bryozoa indet., Brachiopoda indet. and other indeterminate taxa) were counted only when no other bryozoan, brachiopod, or skeletobiont taxon was present on a given host (as in Rodland *et al.* 2014; Zatoń *et al.* 2022a). However, undetermined specimens were still included in the analyses of the skeletobiont abundance, as they represent successful recruitment events. The surface

area of the corals potentially available for skeletobiont colonisation was approximated based on their volume by assuming a spherical shape of the colonies. The area of colonised and non-colonised specimens was compared using the non-parametric Wilcoxon test. Differences in the abundance and richness of skeletobionts present on the lower and upper side of the colonies were evaluated using the paired Wilcoxon test, while the diversity of the entire assemblages (abundance data from each side pooled together across the colonies) was compared with individual-based rarefaction and extrapolation curves (Colwell *et al.* 2012).

Rarefaction was also used to assess the differences in diversity of the skeletobiont assemblages present on favositids and brachiopods and was based on the pooled data from all specimens (see Zatoń *et al.* 2022a, and Zatoń and Nawrot 2024b for details of the brachiopod dataset). However, given the importance of substrate area in controlling colonisation patterns (Zatoń and Nawrot 2024a), we only used measured specimens when comparing colonisation metrics (average abundance and density of skeletobionts). Thus, the analysis was restricted to a sample of the best preserved and complete brachiopod shells representing the five most abundant brachiopod taxa (15 to 93 colonised shells per taxon depending on the available material, see Zatoń and Nawrot 2024a). In order to account for differences in host size, we calculated skeletobiont density for each colony and shell as the number of individuals per unit area ( $\text{ind}/\text{cm}^2$ ) and compared host area, skeletobiont abundance, and density between the favositids and brachiopods using the Wilcoxon test. Statistical analyses were performed in R 4.2.1 (R Core Team 2022) using ‘iN-EXT’ package (Hsieh *et al.* 2022).

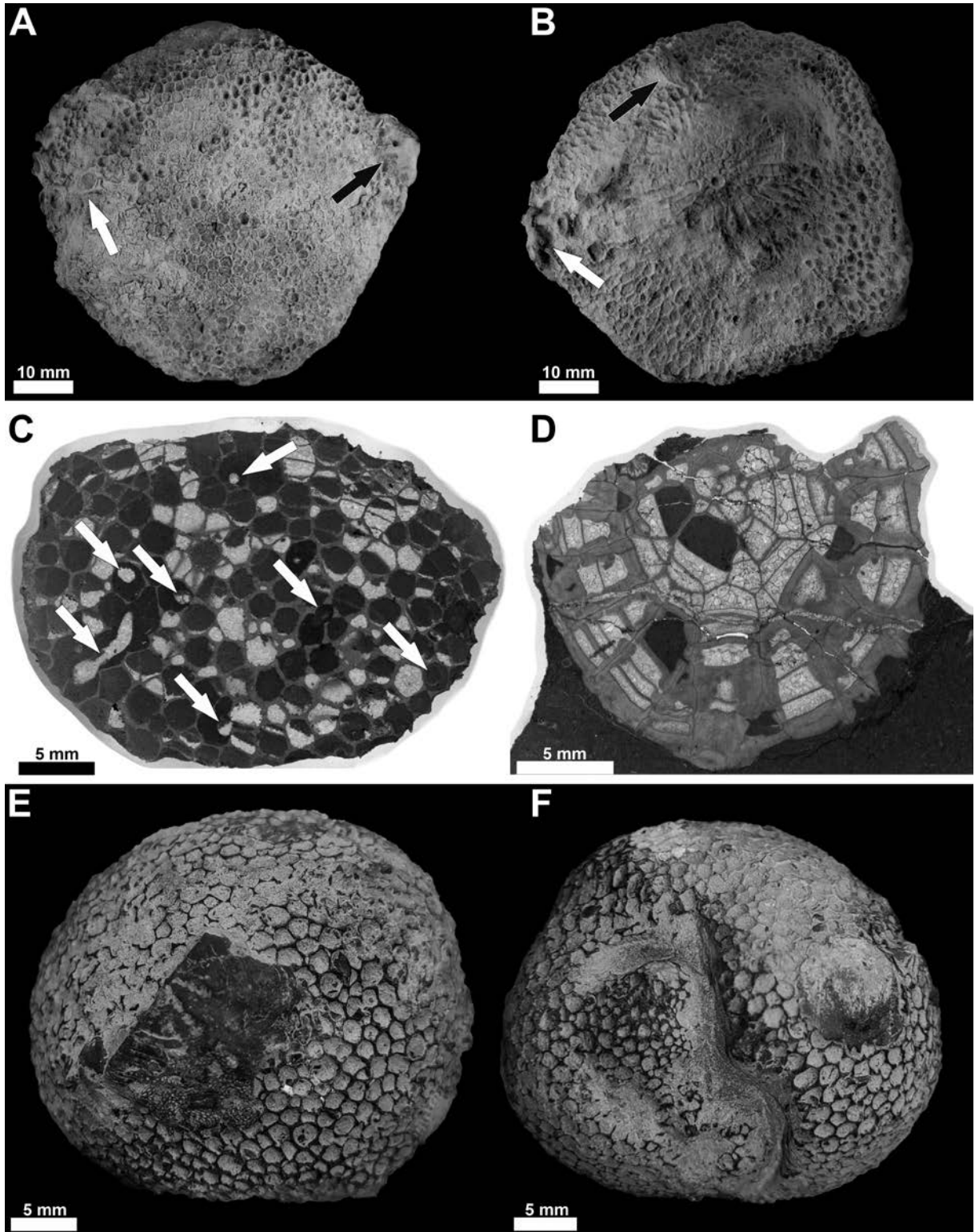
The material is housed at the Institute of Earth Sciences in Sosnowiec, abbreviated GIUS 4-3794.

## RESULTS

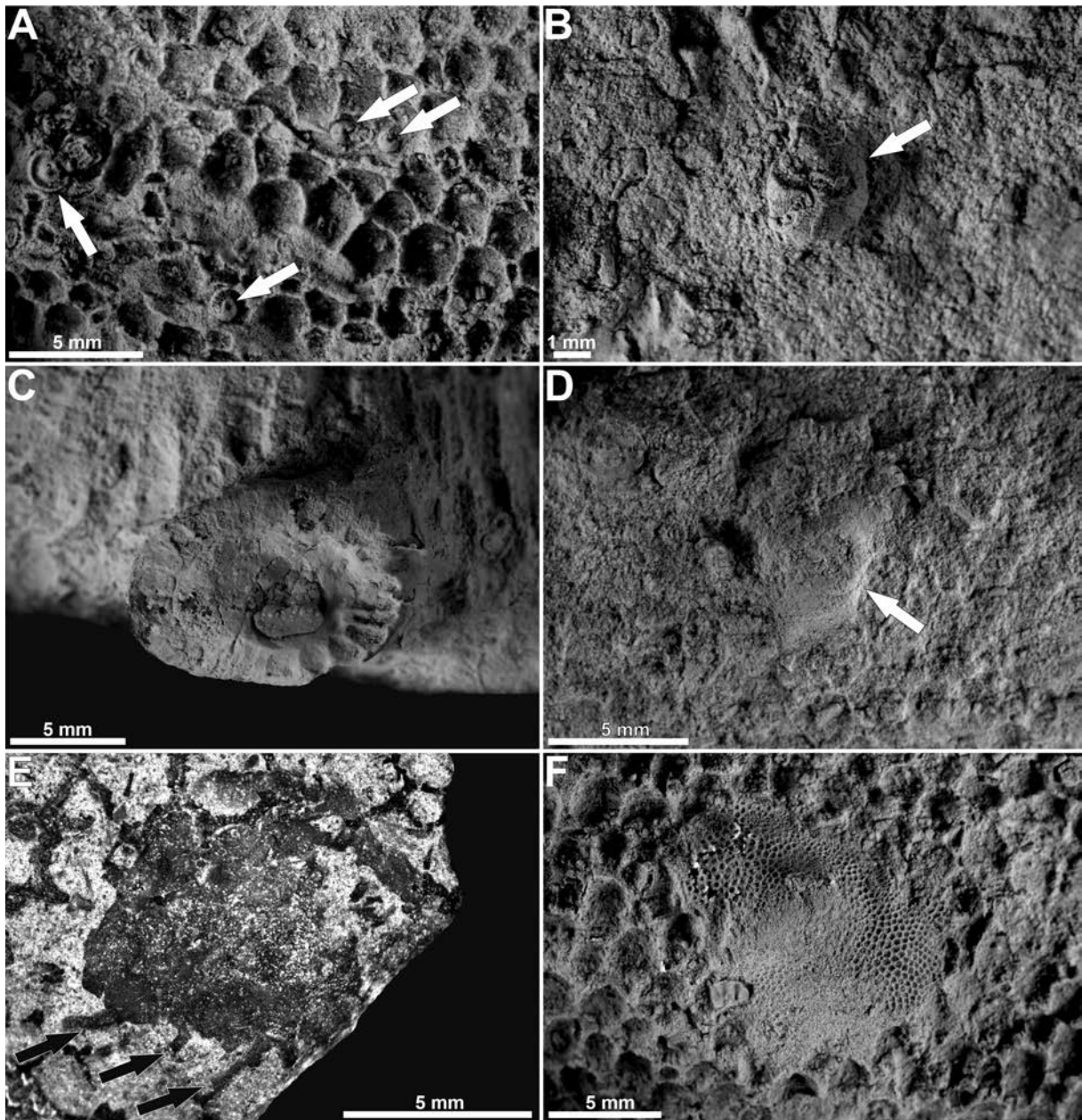
### Favositid hosts

Favositid tabulate corals are relatively abundant in the studied deposits and represented predominantly by *Favosites goldfussi* d’Orbigny, 1850 (Text-fig. 2A–C). Other species are rare, including only a single small, juvenile specimen of *F. ?bohemicus* Maurer, 1896 (Text-fig. 2D), and two specimens of *Favosites* sp. (Text fig. 2E, F) *sensu* Król *et al.* (2018), previously described from the Aferdou el Mrakib reef in the Mader Basin.





Text-fig. 2. Favositids from the Middle Devonian of Madène el Mrakib, Mader Basin, Morocco. A – Upper (exposed) side of *Favosites goldfussi* d’Orbigny, 1850. B – Lower (cryptic) side of *Favosites goldfussi* d’Orbigny, 1850; encrusting auloporids and rugose corals are indicated with white and black arrows, respectively. C – *Favosites goldfussi* d’Orbigny, 1850, transverse thin section. Arrows indicate *Trypanites*-like borings. D – Juvenile *Favosites bohemicus* Maurer, 1896, transverse thin section. E, F – Two views of a circumrotatory corallum of *Favosites* sp.

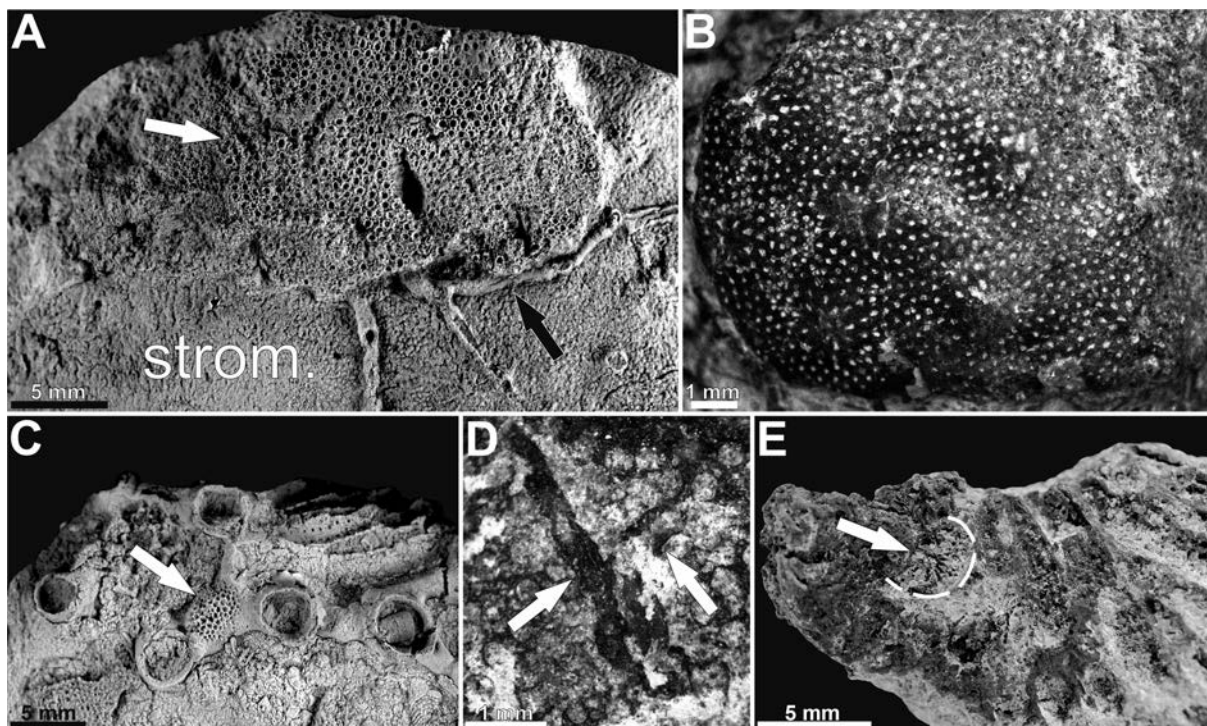


Text-fig. 3. Selected skeletobionts colonising favositids from the Middle Devonian of Madène el Mrakib, Mader Basin, Morocco. A – Tentaculitoid microconchids (arrowed). B – Tentaculitoid *Anticalyptrea* Quenstedt, 1867 (arrowed). C – Rugose coral. D – Crinoid holdfast (arrowed). E – Productid brachiopod with preserved lateral spines (arrowed). F – Trepostome bryozoan *Eostenopora* aff. *clivosa* (Schlüter, 1889).

*Favosites goldfussi* is characterised by cerioid coralla comprised of polygonal, 3- to 9-sided corallites with diameters of 1.9–3.0 mm (mean = 2.45 mm). The corallite walls are typically 0.15–0.25 mm thick. The mural pores are circular and reach 0.38 mm in diameter. The septal spines are very abundant, sharp, and relatively short. The tabulae are thin, complete, and irregularly spaced. *Favosites ?bohemicus*

differs from *F. goldfussi* in having larger corallites (up to 5.3 mm in diameter), rare septal spines, and more variable wall thickness (0.1–1.1 mm). The latter characteristic could, however, be related to the juvenile age of the specimen (cf. Berkowski *et al.* 2023). *Favosites* sp., on the other hand, is typified by smaller corallites, 1.2–2.4 mm in diameter, and fewer septal spines compared to *F. goldfussi*.





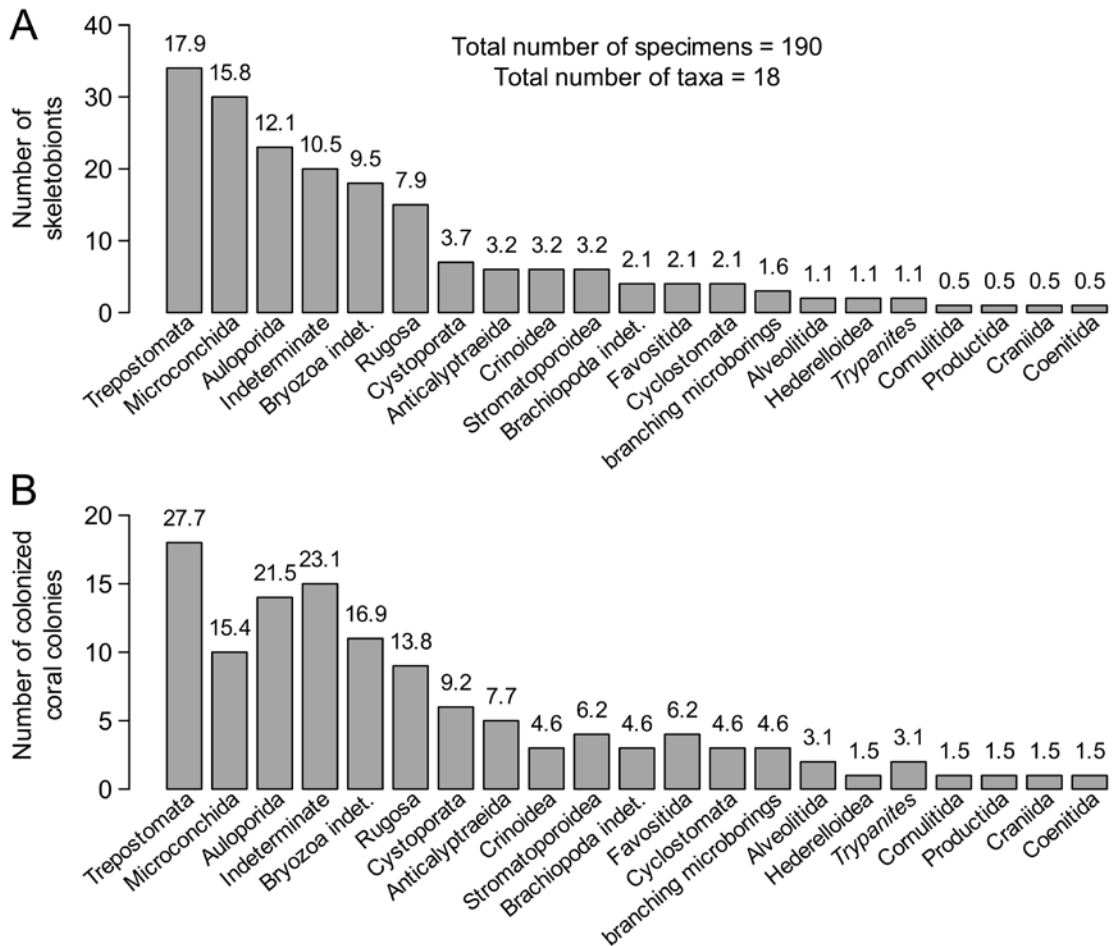
Text-fig. 4. Selected skeletobionts colonising favositids from the Middle Devonian of Madène el Mrakib, Mader Basin, Morocco. A – Sheet stromatoporoid (strom.) encrusted by the cyclostome bryozoan *Corynotrypa* sp. (black arrow) and the cystoporate bryozoan *Cyclotrypa cyclostoma* (Schlüter, 1889) (white arrow). B – Cystoporate bryozoan *Fistulipora* sp. C – *Aulopora* sp. tabulate encrusted by a trepostome bryozoan *Eostenopora* aff. *clivosa* (Schlüter, 1889) (arrowed). D – Abraded hederelloid colony (arrowed). E – Rugose coral (arrowed) embedded within a favositid skeleton.

The favositids exhibit predominantly bulbous growth forms with convex bases and commonly flattened tops. Tabular and irregular morphologies are also relatively common. The size of the colonies varies widely. The smallest ones have only 4 cm<sup>3</sup>, whereas the largest measured colony has 355 cm<sup>3</sup> (mean = 71.11 cm<sup>3</sup>). Their horizontal outlines range from circular to oval. Growth interruption surfaces and rejuvenations were not observed, despite the common occurrence of sediment infills in the corallites. The growth axes of the coralla are commonly tilted in one direction or curved. Two small, spherical specimens exhibit a circumrotatory mode of growth.

### Skeletobionts

Skeletobionts were found on 65 favositid colonies. The remainder of the colonies is either worn or does not possess visible encrusters (episkeletobionts *sensu* Taylor and Wilson 2002) and borer (endoskeletobionts *sensu* Taylor and Wilson 2002) traces. The detected skeletobionts comprise 18 taxa. Due to their preservation state, however, some bryozoans and brachio-

pods are difficult to identify to lower taxonomic levels and thus have been left as Bryozoa/Brachiopoda indet. Some other encrusters are also preserved as remnants of their attachment bases and thus have been grouped together as indeterminate fossils. Identified solitary encrusters are numerically dominated by spirally-coiled microconchids (Text-fig. 3A). Although usually preserved as attachment bases, the complete specimens are very similar to the species *Palaeoconchus sanctacrucensis* Zatoń and Krawczyński, 2011, recently noted on brachiopods from the same locality (Zatoń *et al.* 2023b). With respect to abundance, the next solitary skeletobionts are represented by rugose corals (Text-figs 2A, B, 3C, 4E), tentaculitoid anticalyptraeids (likely *Anticalyptraea madenensis* Zatoń, Słowiński, Vinn and Jakubowicz, 2023b; Text-fig. 3B), crinoids (holdfasts, Text-fig. 3D) and brachiopods. The latter are represented by remnants of attachment valves of indeterminate forms, as well as by productids (Text-fig. 3E) and craniids (*Deliella* sp.). Conical tentaculitoids, assigned to cornulitids, are rare. When we take the number of the favositids colonised by these encrusters into account,



Text-fig. 5. Abundance of skeletobionts on the favositid corals. A – Abundance of the skeletobiont taxa (all are shown). B – Number of coral colonies colonised by each skeletobiont taxon. In A the number above the bars represents the percentage abundance of each taxon, and in B they refer to the percentage of colonies in the entire coral sample ( $n = 65$ ) which are colonised by a given skeletobiont taxon.

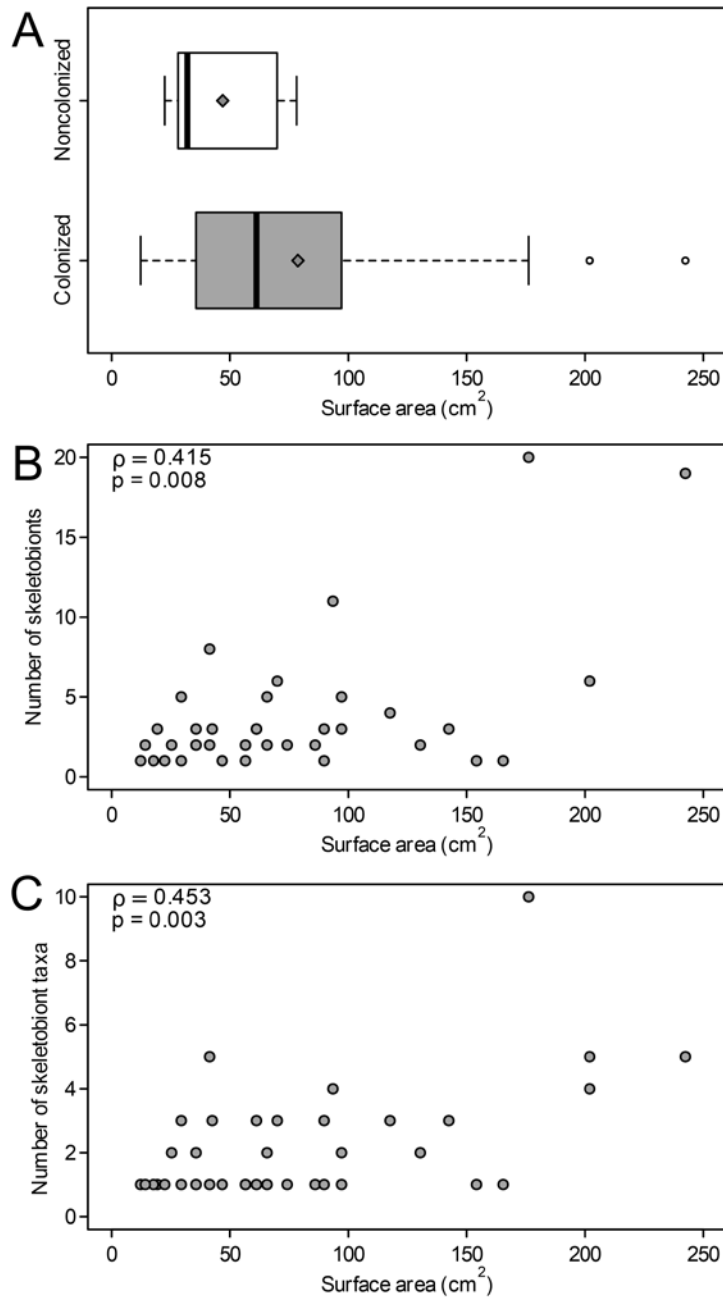
the pattern is quite similar (Text-fig. 5). Compared to the other abundant taxa, microconchids occur on a lower number of coral colonies, suggesting their tendency to aggregate on selected hosts.

The colonial encrusters are dominated by bryozoans, of which trepostomes (Text-figs 3F, 4A, C) are the most numerous. Apart from some indeterminate colonies, the trepostomes are represented by such species as *Leioclema decipiens* (Hall, 1883) and *Eostenopora* aff. *clivosa* (Schlüter, 1889) (Text-fig. 3F). Cystoporates are represented by *Cyclotrypa cyclostoma* (Schlüter, 1889) (Text-fig. 4A), as well as *Fistulipora* sp. (Text-fig. 4B), and Cyclostomata are represented by the uniserial genus *Corynotrypa* sp. (Text-fig. 4A). Except *Cyclotrypa cyclostoma*, the above genera were also detected on the co-occurring brachiopods (Zatoń *et al.* 2022a). Less numerous are auloprid tabulates (small and slender, and larger ro-

bust species, Text-figs 2A, B, 4C), stromatoporoids (Text-fig. 4A) and favositids, whereas alveolitids, coenitids (*?Roseoporella* sp.) and hederelloids (Text-fig. 4D) are relatively rare. With respect to the number of coral colonies colonised, the pattern is also similar (Text-fig. 5).

The traces after endoskeletobionts consist of branching microborings and circular, deep pits likely representing the ichnogenus *Trypanites* isp. (Text-fig. 2C). Both traces occur rather rarely compared to the majority of skeletobionts present (Text-fig. 5). A single favositid specimen also records a *syn vivo* interaction with a rugose coral in the form of distinct embedment of the epibiont within the tabulate skeleton (Text-fig. 4E). Symbiotic relationship between these coral groups is already known from the Silurian, but generally such relationship is rarely noticed (see Vinn *et al.* 2017). The observed interac-





Text-fig. 6. Relationship between the skeletobiont assemblages and favositid colony size. A – Comparison of the size of non-colonised and colonised corals. Thick horizontal lines and diamond points denote median and mean values, respectively. B – Relationship between the skeletobiont abundance and host colony surface area. C – Relationship between the richness of skeletobionts and host colony surface area. In B and C only the colonised colonies are shown.  $\rho$  – Spearman rank-order correlation coefficient,  $p$  –  $p$ -value for Spearman correlation.

tions between particular episkeletobionts consist of non-reciprocal overgrowths and thus they rather do not indicate any competition for space.

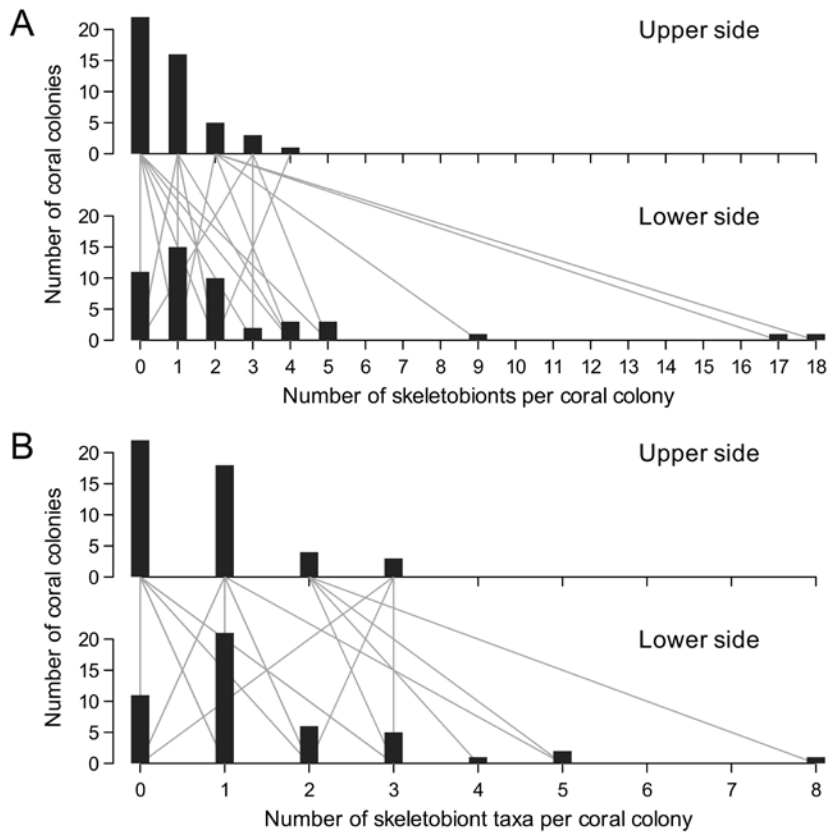
For the 55 favositid colonies (47 with skeletobionts) having both the upper and lower sides preserved, the mean skeletobiont abundance per host

colony is low (3.11), and the mean skeletobiont richness per host colony is even lower (1.80). Restricting the analyses to the 47 measured specimens gives similar results (Table 1).

A comparison of the size of the non-colonised and colonised corals, as well as the relationship

Parameter	Whole colony	Lower side	Upper side
Colonization frequency	0.85	0.77	0.53
Number of skeletobionts	151	112	39
Number of skeletobiont taxa	18	16	14
Mean skeletobiont abundance per colony	3.21	2.38	0.83
Mean skeletobiont richness per colony	1.83	1.49	0.74
Mean skeletobiont abundance per colonized colony	3.78	2.80	0.98
Mean skeletobiont richness per colonized colony	2.15	1.75	0.88
Mean colony volume (cm <sup>3</sup> )	71.11	NA	NA
Mean colony area (cm <sup>2</sup> )	73.99	NA	NA
Mean skeletobiont density (ind/cm <sup>2</sup> )	0.05	NA	NA
Mean volume of colonized specimens (cm <sup>3</sup> )	77.80	NA	NA
Mean area of colonized specimens (cm <sup>2</sup> )	78.72	NA	NA
Mean skeletobiont density on colonized specimens (ind/cm <sup>2</sup> )	0.06	NA	NA

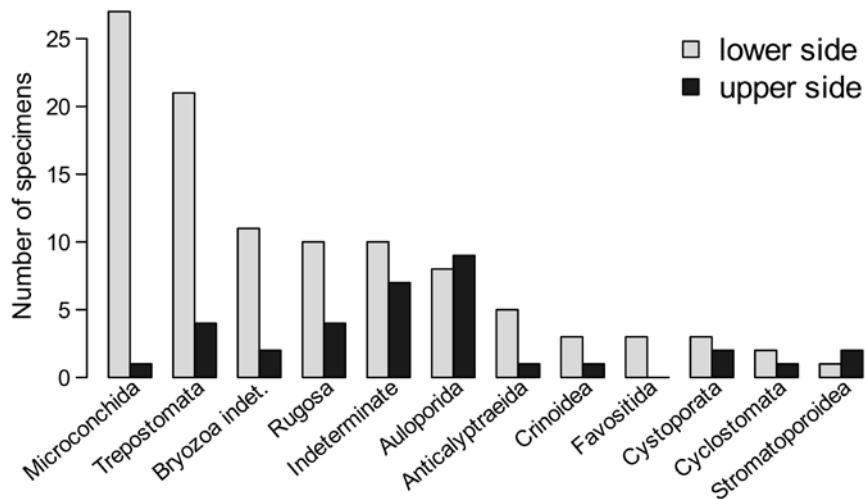
Table 1. Colonisation metrics for *Favosites* Lamarck, 1816 colonies from the Devonian of Morocco with measured volume. The approximate area of the colonies is calculated from the volume by assuming a spherical shape.



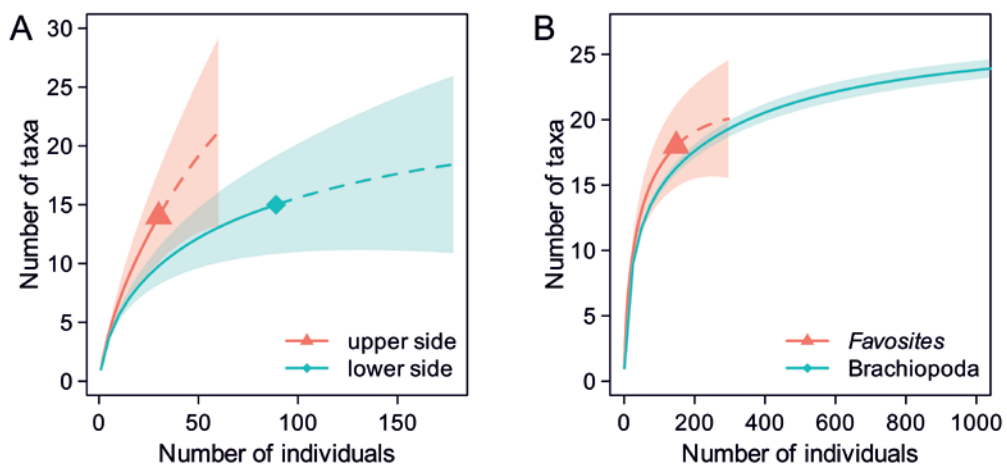
Text-fig. 7. Skeletobiont abundance (A) and richness (B) on each side of coral colonies, plotted as frequency distributions, i.e., as the number of corals hosting a given number of skeletobionts or skeletobiont taxa on their lower and upper side. Grey lines connect abundance/richness values observed on each side of individual coral specimens.

between the skeletobiont abundance/richness and host colony surface area, is shown in Text-fig. 6. Although the average area of the colonised corals (78.7 cm<sup>2</sup>) is larger than that of the non-colonised colonies (46.9 cm<sup>2</sup>), the difference is not statistically

significant (Wilcoxon test:  $W = 183, p = 0.204$ ) likely due to the small sample size of the latter (7 specimens). The same result was obtained when using volume instead of the surface area. However, there is a significant positive correlation between the colony



Text-fig. 8. Total abundance of the skelotobiont taxa represented by at least 3 specimens (~2% of the total assemblage from measured corals) on the lower and upper sides of the colonies.



Text-fig. 9. Individual-based rarefaction-extrapolation curves for skelotobiont assemblages inhabiting the upper and lower sides of coral colonies (A), and coral colonies vs. brachiopod shells (B). Shading indicates 95% confidence intervals. Bryozoa indet., Brachiopoda indet., and other undetermined skelotobionts were excluded from the analysis. The curve for the brachiopod-hosted assemblage is truncated at 1000 individuals.

size and skelotobiont abundance and richness (Text-fig. 6B, C).

The analysis of the skelotobiont distribution on the upper and lower sides of the coral colonies showed that the lower sides tend to be more frequently colonised (Table 1; Pearson's chi-squared test:  $\chi^2 = 4.6696$ ,  $df = 1$ ,  $p = 0.031$ ) and host more skelotobionts (paired Wilcoxon test:  $p < 0.001$  for both abundance and richness). Although the skelotobiont richness is only slightly higher on the lower sides of the colonised colonies (Table 1), the skelotobiont abundance tends to be evidently higher there (Table 1; Text-figs 7, 8). This observation is especially valid for

the microconchids, bryozoans, rugose corals, anticalyptraeids, and even crinoids; in contrast, the auloporids and stromatoporoids are more common on the upper sides (Text-fig. 8). Pooling data across the colonies suggests, however, that the total richness of the skelotobiont assemblage is similar on both sides (16 vs. 14 taxa, Table 1) and not significantly different when standardized to the same number of individuals (Text-fig. 9A).

In comparison to the skelotobiont assemblage colonising the brachiopods from the same strata (Zatoń *et al.* 2022a), the relative abundances of the skelotobionts present on the favositids are distinctly different

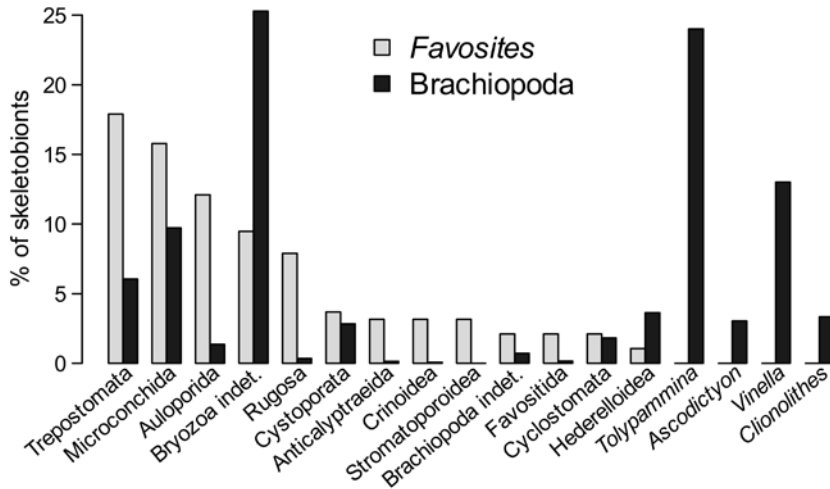


(Text-fig. 10). However, the higher total richness observed in the brachiopod-hosted assemblages (26 vs. 18 taxa on brachiopods and corals, respectively) can be largely explained by the sample-size effect (Text-fig. 9B). Although the favositid colonies have a greater surface area than the brachiopod shells (Text-fig. 11A), the skeletobiont abundance and density per host colony are significantly lower (Text-fig. 11B, C, Wilcoxon test;  $p < 0.001$  for all three comparisons).

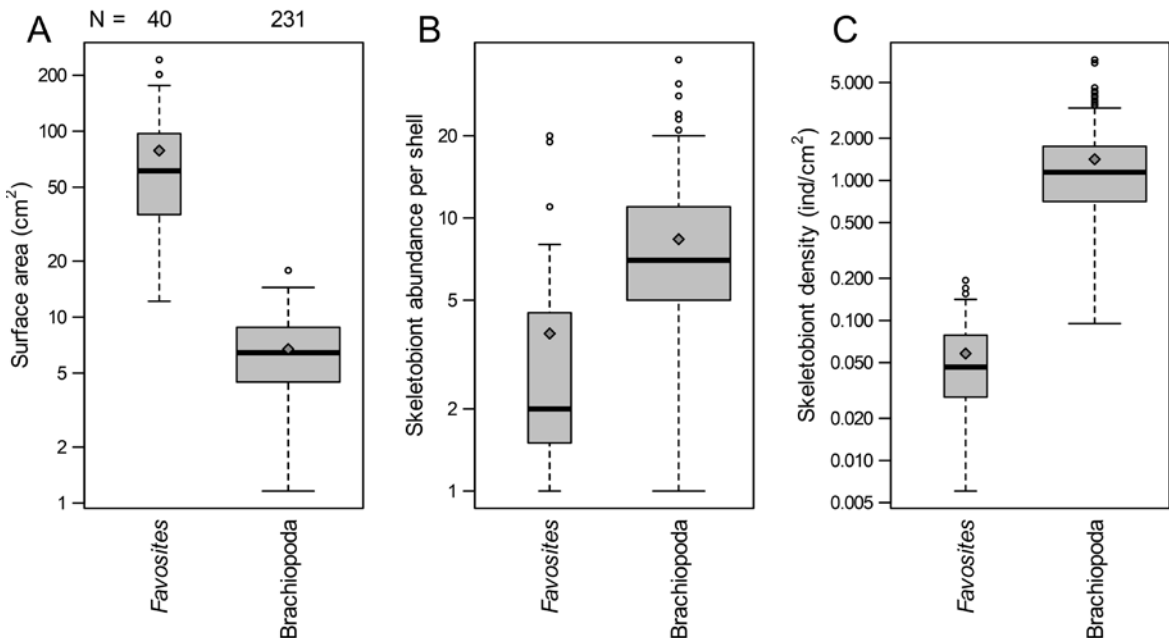
## DISCUSSION

### Diversity of *Favosites*-hosted skeletobionts

The skeletobiont assemblage colonising the favositid tabulate corals from Madène el Mrakib is characterised by a low abundance but high diversity of skeletobionts (Berger-Parker dominance index = 0.20). Obviously, as in other fossil hard-substrate assem-



Text-fig. 10. Relative abundance of skeletobiont taxa found on coral and brachiopod hosts. Indeterminate skeletobionts and taxa representing less than 2% of specimens in both assemblages are not shown.



Text-fig. 11. Variation in surface area (A), skeletobiont abundance per host (B), and skeletobiont density (C) in colonised specimens of *Favosites* d'Orbigny, 1850 and associated brachiopods. Data for brachiopods are based on random samples of colonised specimens representing the five most abundant taxa. Thick horizontal lines denote medians, diamond points – means. N: the number of measured colonised specimens per taxon. All differences are significant (Wilcoxon test;  $p < 0.001$  in all three cases). Note the logarithmic scale on all graphs.

blages, the number of encruster taxa is biased by the presence of exclusively skeletonized organisms, and thus originally it could have been much higher. The assemblage is dominated by a few groups, namely bryozoans, microconchids, and auloporids, the abundance of which significantly exceeds that of the other skeletobionts. Although the total skeletobiont richness (18 taxa) is lower than that present on the associated brachiopods (26 taxa, Zatoń *et al.* 2022a), likely due to the differences in sample size, it is still higher than that noted in many other Middle Devonian skeletobiont assemblages from Laurussia and the South China craton. For example, with respect to its richness, it may rival the rugose-hosted assemblage from New York, USA (Baird and Brett 1983), and is higher than the rugose-hosted assemblages from the Holy Cross Mountains, Poland (Zatoń and Wrzołek 2020) and brachiopod-hosted assemblages from New York, USA (Bordeaux and Brett 1990), Iowa, USA (Webb and Schneider 2013), Alberta, Canada (Barclay *et al.* 2013), and South China (Chang *et al.* 2021). Such a high diversity of skeletobionts noted on the Moroccan favositids and co-occurring brachiopods may have resulted from suitable normal-marine conditions devoid of any distinct palaeoenvironmental changes, and the availability of the vast amount of hard substrates exposed for colonising and developing organisms.

Interestingly, for both favositid and brachiopod hosts from Madène el Mrakib, the bryozoans are the dominant group and tentaculitoids (especially microconchids) are very common as well. However, the other most abundant skeletobionts present on the brachiopods, such as foraminifers and ascodictyids, have not been found on the inspected favositids. In turn, the favositids display *Trypanites* isp. borings, which have not been observed on the brachiopods, but are found on rugose corals from the nearby locality of Aferdou el Mrakib (Zatoń *et al.* 2023a). Such host-specific differences in the composition of the skeletobiont assemblages from the same environment may suggest a role of substrate specificity in shaping the skeletobiont community structure, underlining the importance of inspecting different types of hard substrates before any wider comparisons are made (see also Zatoń *et al.* 2022b). The composition of the skeletobiont assemblage inhabiting the favositids generally falls within the taxonomic variability reported previously for the co-occurring brachiopod-hosted assemblages, as well as within the skeletobiont composition characteristic for the Mader Basin in general (Zatoń *et al.* 2023a). However, the mean skeletobiont abundance (Text-fig. 11B) and richness (see Zatoń *et al.* 2022a) observed for the brachiopods are higher

than those noted for the favositids. The same concerns the density of skeletobionts (Text-fig. 11C). This pattern may suggest that the brachiopods were a preferable substrate for skeletobiont larvae, which may be related to both the abundance of brachiopods and microhabitat type provided by the brachiopod shells. Although smaller in individual size, the large quantity of shells spread on the seafloor provided an abundant source of hard substrate for colonising larvae. Except for the strophomenid *Schizophoria* sp. having punctate shells (e.g., Halamski 2012) which potentially could have been deterrent for endoskeletobionts (see Curry 1983), the rest of the brachiopod shells were devoid of any soft tissue and thus could have been colonised both during the life of the hosts and *post mortem* until their final burial. Some surfaces of the living favositid colonies, were, in turn, at least in part occupied by closely spaced polyps. Thus, the colonies were only partly available for colonisation, and the only suitable side for the larvae settlement, at least during the host's life, was the lower side, which was often directed toward the sediment surface and formed a microhabitat favourable for cryptic species. Another possible mechanism are the antifouling properties of corals, either by avoidance (passive) or active defence (Wahl 1989), certainly stronger and more effective in corals than in brachiopods. Moreover, the death of the favositid colonies might have been caused by abrupt sediment influx events covering the upper colony surface, making it unavailable for skeletobionts.

### Colonisation patterns

A characteristic feature of the investigated favositids is a distinct polarization of the colonisation patterns depending upon the substrate orientation. The tendency of various Palaeozoic skeletobionts for colonisation of a particular side of their hosts has already been noticed for various organisms, such as alveolitids and chaetetids (e.g., Struve 1980; Suchy and West 1988; Copper 1996; Zatoń *et al.* 2018), stromatoporoids (e.g., Kershaw 1980; Segars and Liddell 1988; Vinn 2012; Vinn and Wilson 2012a, b) or peculiar, mushroom-like rugose corals (Zatoń *et al.* 2020). For the studied favositids, the majority of the encrusters settled on the lower sides of the colonies (Text-fig. 8). Such a colonisation pattern could have resulted from various factors, including cryptic preferences of some skeletobionts (i.e., coelobionts or cryptobionts, e.g., Kobluk 1981, 1988; Wilson 1986; Vinn 2012; Vinn and Wilson 2012a, b; Berkowski *et al.* 2019; Vinn *et al.* 2024), seeking low-light niches or refuges

from predators and environmental stress (e.g., Taylor and Wilson 2003). In other instances, the lower side of a colony was the only space available for colonisation, as the upper side was covered by the soft tissue of the host organism. For example, Copper (1996) proposed that the lack of davidsoniid brachiopods on the upper surfaces of alveolitid tabulates resulted from the activity of polyps and their cnidae, discouraging the colonisation of larvae. It was also suggested that during life the upper surface of the mushroom-shaped Silurian coral *Schlotheimophyllum patellatum* (Schlotheim, 1820) was entirely covered by the soft tissue, with tentacles and nematocysts preventing its colonisation by skeletobionts (Zatoń *et al.* 2020). The upper sides of the stromatoporoids are also considered to have been covered by soft tissue during their life (Kershaw 1980; Segars and Liddell 1988). These constraints complicate the recognition of obligate cryptic (or coelobiontic) skeletobionts. This is well-exemplified by the microconchids, which overwhelmingly encrusted the lower sides of the investigated favositids and were previously reported as colonising the cryptic undersides of alveolitid tabulates (Zatoń *et al.* 2018), *Schlotheimophyllum rugosans* (Zatoń *et al.* 2020) and stromatoporoids (e.g., Kershaw 1980; Vinn 2012). However, they were also found dominating the upper, exposed surfaces of other stromatoporoids from Gotland (Segars and Liddell 1988), Estonia (Vinn and Wilson 2012a, b), and the USA (Lebold 2000). The controls on the polarization in the skeletobiont colonisation patterns observed on different hosts are, therefore, not straightforward to identify and may have included a complex interplay of environmental (sedimentation rate, substrate topography and consistency) and biological (skeletobiont population dynamics, microhabitat preference and host growth, host's antifouling mechanisms) factors (e.g., Kershaw 1980; Segars and Liddell 1988; Gibson and Broadhead 1989; Wahl 1989; Kershaw *et al.* 2018; Zatoń *et al.* 2018, 2020), the combination of which might have been unique in a particular palaeoenvironment.

The lack of skeletobionts preserved on or very close to the initial part of the colonies may potentially indicate that the favositids were colonised while they were still attached to (or embedded within) the substrate. During their growth and even for some time after the death of the corals, the colonies could have, at least periodically, been colonised. Taking into account the low mean density of skeletobionts on these hosts, it seems that they were not the main target substrate for colonising larvae, most probably due to the presence of polyps in different parts of the colony. However, as evidenced by the positive and sta-

tistically significant correlation between the colony size and skeletobiont abundance and richness (Text-fig. 6B, C), the favositids could have been more or less continuously colonised during their growth, so that the larger colonies hosted more abundant and diverse skeletobiont assemblages. Although favositids could have been colonised *post mortem*, the presence of the embedded rugose coral indicates that some colonies were certainly colonised during their life.

In the investigated favositids, the calices occur on the upper side of the colonies; however, they may also be present on the lateral sides and undersides of the colonies. Anyhow, a distinct dominance of skeletobionts on the lower side of the colonies suggests that those parts were more often polyp-free and thus available for larvae settlement. Nevertheless, the space between the sea bottom and the favositid's underside could have been filled by sediment, significantly limiting or completely preventing colonisation. The studied favositids exhibit predominantly bulbous growth forms with distinctly convex bases, which are typically interpreted as an adaptation to an increased sedimentation rate, as the colony had to grow vertically to keep up with the accumulating sediment. This is opposed to expanding laterally to form a flat-based dome, which, if possible, would be favourable for the corals living in soft-bottom conditions, as a type of the snow-shoe survival strategy (Philcox 1971; Gibson and Broadhead 1989). This limiting factor may explain the generally low abundance of skeletobionts on the favositids, and can also be responsible for similar colonisation patterns observed on Silurian stromatoporoids and some rugose corals (see also Kershaw 1980; Kershaw *et al.* 2018; Zatoń *et al.* 2020). However, the lack of clear growth interruption surfaces and rejuvenations in the colonies studied here may indicate that, unlike the favositids from a shallower setting of the nearby Aferdou el Mrakib reef (see Król *et al.* 2018; Jakubowicz *et al.* 2019), the colonies from Madène el Mrakib were not affected by any serious high-energy sedimentary events. It is also possible that the favositids from the latter locality were able to actively remove sediment blankets, as the genus *Favosites* is generally regarded as well-adapted to conditions related to increased sedimentation rates (e.g., Seilacher and Thomas 2012; Król *et al.* 2018). The episodic occurrence of stronger currents may be supported by the presence of the circumrotatory mode of growth in some rare, spherical specimens (Text-fig. 2E, F) which, due to their small size, could have been rolled on the bottom (e.g., Zapalski *et al.* 2022). This is consistent with the depositional environment of Madène el Mrakib, in-



terpreted as an offshore, low-energy setting situated between the storm and normal wave bases, characterised by rather low to medium turbidity and low water turbulence (see Zatoń *et al.* 2022a).

The majority of the studied skeletobionts are tiny encrusters, which likely first colonised the polyp-free, lower and lateral sides of the favositid colonies. The much lower abundance of skeletobionts on the upper sides implies that these exposed areas might have been permanently, or nearly so, covered by the coral soft tissues. Thus, those skeletobionts which occur on these exposed sides likely colonised them after death of the host corals, or colonised only small spots which were devoid of living polyps – small lesions of soft tissue commonly occur in modern scleractinian corals (Work *et al.* 2014; Hawthorn *et al.* 2023) and may provide available substrate for epizoan recruits. Interestingly, crinoids are also more numerous on the lower and lateral sides. It is known that crinoids were able to grow downward when encrusting cavity roofs (Jakubowicz *et al.* 2014; Berkowski *et al.* 2019) or overhangs produced by some rugose corals (Zatoń and Wrzolek 2020). Crinoids could have also settled on the dead, overturned colonies. Two skeletobiont groups, the auloporids and stromatoporoids, are more abundant on the exposed sides of the corals. Interestingly, auloporids also dominate the upper sides of alveolitids from the Holy Cross Mountains, Poland (Zatoń *et al.* 2018), whereas stromatoporoids occur exclusively on the tops of *Schlotheimophyllum* corals from Gotland (Zatoń *et al.* 2020). However, as proposed also for the favositids from the Aferdou el Mrakib reef, stromatoporoids likely encrusted these tabulates after their death, as the hosts do not display any signs of growth disturbance (see Król *et al.* 2018).

The dominance of the auloporids on the exposed sides of the alveolitids from Poland could have been caused by the light requirements of these possibly photosymbiotic tabulates (see Zapalski 2014) in an otherwise light-depleted, mesophotic ecosystem (Zatoń *et al.* 2018). However, in the present case, the favositids lived in a shallower, apparently well-illuminated environment, as implied by the presence of the encrusting alga *Rothpletzella* sp. (see Kaufmann 1998; Zatoń *et al.* 2022a). Thus, the auloporids may well have inhabited both the lower and upper sides of the host corals, as indicated by the rather small difference in their abundance between both sides (Text-fig. 8). On the other hand, auloporids are known to selectively choose substrate (Zapalski 2005; Mistiaen *et al.* 2012), so that subtle differences in the substrate texture might have also played a role in their preferential settlement. The *Aulopora* sp. from Madène

el Mrakib belong, however, to a species with quite large corallites which, potentially, could have to some extent invaded the upper sides of the favositids still covered with polyps.

In summary, although the majority of the skeletobiont taxa more often colonised the lower sides of the favositid colonies, they also include individuals present on the upper, exposed surfaces. Among the abundant taxa, there is no group which would be present exclusively on the lower sides, indicating that none of them were obligate cryptobionts. This interpretation is further supported by the associated brachiopods, both valves of which were colonised by the same groups of skeletobionts (Zatoń *et al.* 2022a). The observed colonisation pattern supports the earlier consideration of Kobluk (1988) that obligate cryptobionts became particularly prominent during the Mesozoic, when the predation pressure increased (Palmer and Fürsich 1974; Palmer 1982).

### ***Chaetosalpinx* endobionts – where are they?**

Palaeozoic corals have often been reported to host endosymbionts, usually of unknown taxonomic affinity (e.g., Oekentorp 1969; Stel 1976; Zapalski 2007; Mõtus and Vinn 2009; Borisenko *et al.* 2022). Among a wide array of hosts, representatives of the genus *Favosites* and related taxa were the most commonly infested, especially in the Early/Middle Devonian (e.g., Stasińska 1958; Oekentorp 1969), as the peak of their diversity took place in the Middle Devonian (Tapanila 2005). While in some environmental settings, such endosymbionts occur commonly (e.g., Sokolov 1962; Plusquellec 1968), in others they are absent. These endosymbionts can also be massively present in some taxa, while absent in others (Tapanila 2005). Such endosymbionts, or rather bioclastration traces produced by them, are commonly attributed to cecidotaxa (see e.g., Bertling *et al.* 2022, Wisshak *et al.* 2023) such as *Chaetosalpinx*, *Helicosalpinx* Oekentorp, 1969 or *Actinosalpinx* Sokolov, 1962 (e.g., Tapanila 2005; Zapalski 2007). Especially the elongate and circular in outline *Chaetosalpinx* traces are very common within the colonies of favositids. For example, Zapalski (2009) noticed abundant *Chaetosalpinx* in Emsian–Eifelian favositids from the Holy Cross Mountains, Poland, and found that their number increased during the coral astogeny. He counted over 400 traces in a single colony of *Favosites* and proposed that such a high infestation intensity may indicate insufficient protection of the host by cnidae and its insufficient immune system response.

Thus, in an environmental setting similar to the one described in this paper, the favositid corals would be expected to host a number of endosymbionts, also given their taxonomic affinity and anatomical features, such as cerioid coralla and small corallites (Tapanila 2005). However, among the more than 80 sectioned *Favosites* colonies from Madène el Mrakib, no *Chaetosalpinx* or related endobionts have been found. We may only speculate about the potential causes of their absence. As these structures are in fact bioclaustrations, their absence is not a result of a taphonomic bias. Of importance may have been the absence of invasive forms of endosymbionts at the time of the coral growth, limited larval survival, development of the community in high-latitude settings (e.g., Jakubowicz *et al.* 2019), suppressive for particular endosymbionts, or the coral's antifouling properties that prevented the larval settlement. Last, but not least, the immune system of the host could prevent the parasite settlement.

## CONCLUSIONS

Favositid tabulate corals are a common constituent of the Middle Devonian soft-substrate benthic communities preserved in the Madène el Mrakib section, Mader Basin, Morocco. They are predominantly represented by the species *Favosites goldfussi* d'Orbigny, 1850, which inhabited offshore, low-energy palaeoenvironments situated between the storm and normal wave bases. Any serious high-energy sedimentary events may be excluded as the favositids are devoid of clear growth interruption surfaces and rejuvenations. However, episodic stronger currents may have occurred as evidenced by the presence of the circumrotatory mode of growth in some rare, spherical specimens.

Compared to the associated brachiopods, the favositid colonies were infrequently colonised by encrusting and boring organisms. However, a total of 18 taxa (including two boring ichnotaxa) of skeletobionts have been recognized, making the assemblage less diverse than the one described on the co-occurring brachiopods, but more diverse than many coeval, coral- and brachiopod-hosted skeletobiont assemblages known from Laurussia and the South China craton. Although the assemblage lacks some taxa present on the brachiopods, its diversity and composition are similar to those of the other skeletobiont assemblages known from the Mader Basin. However, the lower mean abundance and density of skeletobionts noted on the favositids indicate that, in

contrast to the brachiopod shells, the corals were not a preferred substrate for colonisation.

The assemblage is dominated by bryozoans, microconchids, and auloporids. The skeletobionts occur on both the upper (exposed) and lower sides of the favositid colonies, but the majority of individuals occurs on the latter. Only auloporids and stromatoporoids occur more often on the upper surfaces. The lack of any skeletobiont group present exclusively on the lower sides indicates that none of the abundant taxa were obligate cryptobionts. Such a pattern may indicate that the favositids were colonised during life, so that the skeletobiont larvae settled first on those parts of the colony which were devoid of the host's soft tissues. A much lower abundance of skeletobionts on the upper colony surfaces may, in turn, indicate that they were mostly covered with the coral polyps. Thus, these areas were either colonised *post mortem* or the larvae settled on those parts of the living host which were devoid of soft tissue. Some auloporids, due to their larger corallites, could have potentially overgrown the host's polyps.

The complete lack of any *Chaetosalpinx* parasitic endobionts, usually infesting favositid colonies in large numbers, could have resulted from the general absence of these endobionts at the sites of the corals' growth or, alternatively, from limited survival of the larvae or an efficient immune system of the hosts, preventing their settlement.

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