



Bioerosion and encrustation in Late Triassic reef corals from Iran

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Abstract

Hard substrate communities can impact coral reef growth by adding or removing calcium carbonate when they act as encrusters or bioeroders, respectively. Although such sclerobiont communities are known across the Phanerozoic, the Triassic saw a substantial increase in reef macrobioerosion. This study provides the first quantitative assessment of sclerobionts in a Late Triassic (Norian) reef coral community (from the Nayband Formation in central Iran) and establishes some post-Paleozoic trends in reef bioerosion. Sclerobionts were common on the dominant coral *Pamiroseris rectilamellosa* and covered between 0 and 26.4% of total coral surface area among the 145 colonies investigated. Encrustation was significantly more prevalent (1.78% of total area) than bioerosion (0.36% of total area). The underside of corals was 3.5 times more affected by sclerobionts than the upper surfaces. This suggests that the sclerobionts preferentially colonized dead parts of the corals. The main encrusting taxa were polychaete worms (76.2%), followed by bivalves (11.9%). The main bioeroders were Polychaeta (51.4%), Porifera (22.2%), and Bivalvia (20.7%). The lack of a correlation between encrustation and bioerosion intensity suggests that the number of sclerobionts is not simply a function of exposure time before final burial. Our review of the published literature suggests a declining trend in the relative importance of bivalves, polychaetes and cirripeds in reefs, whereas sponges increased in importance from the Triassic until today.

Keywords Sclerobiont · Bioerosion · Encrustation · Triassic

Introduction

Sclerobiont communities consist of various groups living on hard substrates and comprise encrusting and bioeroding organisms. Bioeroders break down the hard substrate, whereas encrusters build a thick layer on the surface (Glynn and Manzello 2015). Macro-bioerosion first occurred in the Ediacaran (Buatois et al. 2020) but it had no substantial impact on reef growth prior to the Triassic (Kiessling 2002). In the Ordovician, sclerobionts first radiated in an event called the “Ordovician Bioerosion Revolution” (Wilson and Palmer 2006; Buatois et al. 2020), after which both encrustation and bioerosion became more frequent (Bardhan and Chattopadhyay 2003). Through the Silurian and the Devonian, the number of ichnogenera doubled and trace fossils

such as *Entobia* and *Rogerella* first appeared. The rise of predators during the Mesozoic Marine Revolution (Vermeij 1977) put benthic organisms under evolutionary pressure to enhance their defense mechanisms, resulting in improved armor and hiding techniques.

The Triassic marks a turning point for bioerosion and encrustation. Macroborings became more common, although the overall abundance of borings was still low to moderate compared to modern reefs (Wood 1998). Endoliths began to radiate (Wood 2011) but typical boring traces were limited to *Rogerella*, *Trypanites*, *Entobia* and *Gastrocheanolites*, which are still the prevalent ichnogenera today (Knaust 2017). Encrusting taxa expanded as well, resulting in a greater importance of encrusting sponges, foraminifera (Bernecker 2005) and polychaetes (Senowbari-Daryan et al. 1993).

Bioerosion is an important driver of reef accretion and development (Hallock and Schlager 1986), as well as the production of sediment, but quantitative data are limited in both modern and fossil samples. For example, data on spatial variation in sclerobiont settlement and macrobioeroding communities are scarce (Chazottes et al. 1995;

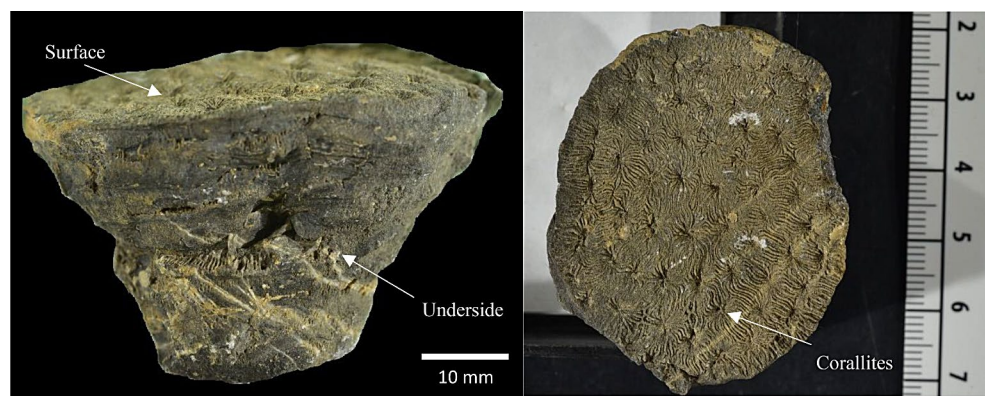
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Fig. 1 Map of Iran and the bordering countries (left); Close-up of Iran and the region of Razavi-Chorsana (right). The red dot represents the main succession of Hassan Abad village (35° 05' N, 58° 02' E). The map was created via “visme”



Fig. 2 Overview image of *Pamiroseris rectilamellosa* highlighting its massive to tabulate growth form in a side view (left) and the thamnasterioid corallite integration in the plan view (right); sample D1/12



Perry 1996, 1998; Perry and Bertling 2000; Tribollet and Golubic 2005). Most of the research was done on clionid sponges (Neumann 1966; Macgeachy 1977; Cerrano et al. 2001; Bautista-Guerrero et al. 2006; Custódio et al. 2007; Carballo et al. 2008) with lesser emphasis on barnacles, worms and bivalves (Macgeachy and Stearn 1976; Hutchings 1986). Detailed description of modern-type bioeroding communities have been reported from the Miocene (Perry 1996), Oligocene (Pleydell and Jones 1988) and the Jurassic (Fürsich et al. 1994; Bertling 2000).

Here, we are extending current knowledge by describing in detail a modern-type bioeroding community from a Triassic reef coral assemblage.

We provide a quantitative account of Late Triassic (Norian) sclerobionts on reef corals to (1) demonstrate that bioerosion/encrustation was already significant in Late Triassic reefs and (2) draw a comparison between current sclerobiont assemblages and those from the Triassic period.

Materials and methods

Geological setting

Corals from the Nayband Formation in central-eastern Iran (Fig. 1), collected by the late Baba Senowbari-Daryan in 1997, were examined in this study. The corals were obtained from the Hassan-Abad area (35° 05' N, 58° 02' E) (Fig. 1). The corals represent a diverse assemblage of Late Triassic reef corals previously described in Shepherd et al. (2012). Although originally dated as Norian-Rhaetian, the presence of *Heterastridium conglobatum* in the biostromal coral assemblage (Shepherd et al. 2012) allows us to detail the stratigraphic assignment to the middle or late Norian (218–205 Myr) following Senowbari-Daryan and Link (2019). The corals were gathered from a marly unit (probably unit F in Shepherd et al. 2012) and are dominated by massive colonies. The studied material comprises 204 corals, dominated by the species *Pamiroseris rectilamellosa*, which has massive to tabular growth forms and a thamnasterioid corallite integration (Fig. 2).

Sclerobiont identification and classification

The quantitative assessment of sclerobionts was done with the Image J 1.53t software. Pictures of the corals and the sclerobionts were taken with shutter speed 1/80 seconds; exposure compensation 0LW and flash exposure compensation 0LW. The pictures were scaled, and the surface area was calculated. A grid with an area of 0.1cm² was generated to quantify the sclerobionts by the point counting method. The number of points varied depending on the size of the coral, ranging between the smallest (582 points) and the largest (4244 points) coral. Three main categories were distinguished: (i) bioerosion, (ii) encrustation and (iii) coral skeleton. Only objects beneath the points were counted. After bioerosion/encrustation quantification, the sclerobionts were identified to the finest possible label (usually genus level), and each taxon was counted.

Statistical analysis

Sclerobiont density was compared separately for encrustation and bioerosion, considering sclerobiont placement on the coral colony (surface or underside, Fig. 2). The differences between the means of the categorical independent variable (placement) were analyzed with two-way ANOVA tests. To prevent the multiple testing problem, p-values were adjusted with the Bonferroni correction.

Google Scholar was searched in August of 2023 – March 2024 using the search terms “Triassic”, “Jurassic”, “Cretaceous”, “Oligocene”, “Miocene”, “Recent”, “trace fossils”, “bioerosion” and “sclerobiont” to compile publications that contain data on sclerobionts for the past 200 million years. Only studies which analyzed encrustation and/or bioerosion on corals with a quantitative method were used. To demonstrate a difference between Triassic and Recent bioeroding intensity, a two-way ANOVA test was applied, which tested the distribution of bioerosion/encrustation abundance in time against the distribution of the traces in between the taxa and the percentages of bioeroding activity. Correlation tests are based on the Spearman rank-order correlation, because our data is not normally distributed. The encrustation and bioerosion data were squareroot-transformed to reduce the spread of the datapoints while allowing the plot of zero values. All statistical methods were performed with R-4.3.1 (R Core Team 2024)..

Results

Qualitative analysis

Among the 204 colonial corals assessed in this study, the most common genera were *Pamiroseris* (145 colonies), *Astraeomorpha* (4 colonies), *Oedalmia* (8 colonies) and *Chondorcoenia* (3 colonies). The rest of the collected samples could not be assigned to a coral genus. All *Pamiroseris* specimens in our analysis belong to the species *Pamiroseris rectilamellosa* (Winkler).

Four ichnogenera of bioerosion traces could be identified: *Rogerella*, *Entobia*, *Trypanites* and *Gastrochaenolites*. Encrustation traces were classified as sponges, bivalves, polychaetes, bryozoans and scleractinian corals.

Rogerella appeared as a slit-like boring with an ovate aperture. It was mostly smaller than 0.3 cm in diameter, usually around 0.1 cm to 0.2 cm. The depth could not be estimated (Fig. 3a and b).

Trypanites was categorized by a round aperture with a diameter greater than 0.2 cm (Fig. 3c). It appeared mostly as a deep cylindrical boring, although the exact depth could not be estimated. The borings were commonly associated with encrusting polychaetes and surficial tunnel-like borings (Figs. 4d and e and 5a, b and c).

A round, surficial boring with a diameter not exceeding 0.2 cm was categorized as *Entobia*. The opening measured usually about 0.1 cm. An accumulation of openings in proximity could be found (Fig. 3f).

Gastrochaenolites appeared as an ovate-round boring not greater than 0.3 cm in diameter. The formed chamber could not be investigated most of the time. It was distinguished from the other trace fossils by its depth since most of the time *Gastrochaenolites* appeared deeper than *Trypanites* or *Entobia*. If the chamber was visible, it could be investigated as club-shaped with an aperture narrower than the chamber itself (Figs. 3d, g and h and 6a and b).

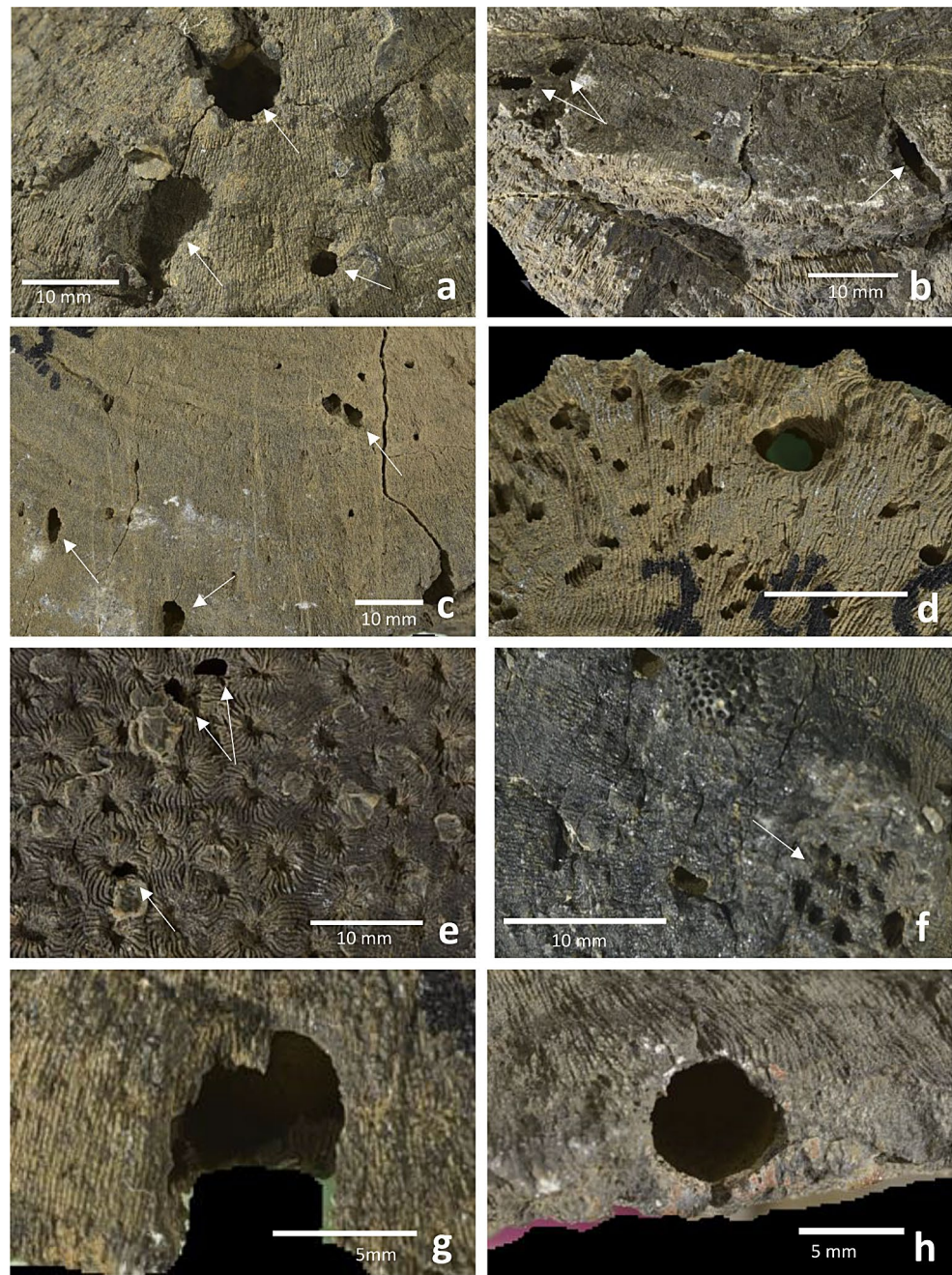
For encrustation, the main reef inhabiting organisms were identified. These consist of sponges, bivalves, polychaetes, bryozoans and solitary scleractinian corals.

Encrusting calcisponges were only found on one specimen and they appeared as round/oval structures up to 0.1 cm to 0.6 cm in diameter and 0.1 cm to 0.3 cm in height. They had a porous texture with a widespread distribution, partly overgrowing each other (Fig. 4a).

Bivalves have been recognized by the residue or imprints of the shell or a circular recess with raised edges (Fig. 4b and c). They resemble *Placunopsis*, which is in need of taxonomic revision (Todd and Palmer 2002).

Serpulids and sabellids mostly left surficial tunnel-like structures (*Glomerula*) or filiform imprints on the coral, where the fossilized serpulid/sabellid detached from the

Fig. 3 Boring traces on *Pamiroseris recti-lamellosa* **a** (underside) bottom left arrow *Rogerella* boring, bottom right arrow *Trypanites* boring, upper arrow *Gastrochaenolites* boring; **b** (underside) right arrow *Rogerella* boring, left arrows *Trypanites* borings; **c** (underside) *Trypanites* borings; **d** (underside) *Trypanites* borings and *Gastrochaenolites* boring in the upper right corner; **e** (surface) upper arrows *Trypanites* borings, bottom arrow residues of encrusting bivalves; **f** (underside) bottom right corner *Entobia* borings; **g** (underside) *Gastrochaenolites* boring; **h** (underside) *Gastrochaenolites* boring



hardground (Fig. 4d and e). Small circular bryozoan colonies up to 0.3 cm in diameter and 0.4 cm of maximum height have a dotted texture (Fig. 4f).

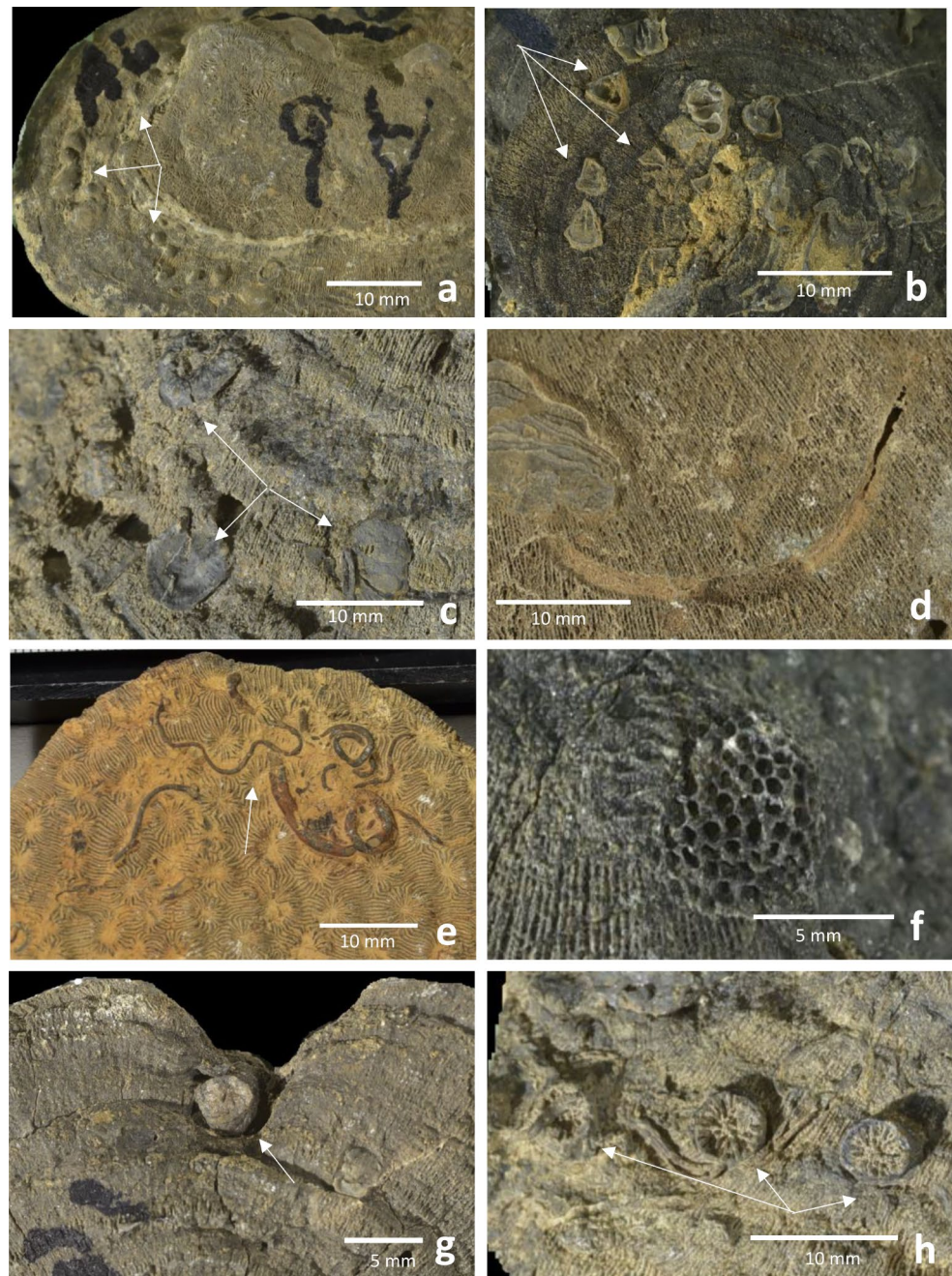
Solitary scleractinian corals were sometimes found on the underside of *Pamiroseris*. Corals are mostly well preserved, with clearly visible septa. The corallites ranged from 0.3 to 1 cm in diameter and 0.3–0.7 cm in height (Fig. 4g and h).

Quantitative analysis

Out of the 204 analyzed corals, 51 (25%) were affected by bioerosion or encrustation on the surface of the coral. The underside of the corals showed traces in 177 specimens (87%) (Fig. 7; Table 1).

Bioerosion on the underside was mostly performed by polychaetes (38.6%) and bivalves (27.9%) whereas sponges had an abundance of 24.5% and barnacles of 8% (Fig. 8). On the surface, *Trypanites* borings were most abundant (81.7%) whereas almost no other trace fossils could be detected. The

Fig. 4 Encrusters on *Pamiroseris rectilamellosa* **a** (underside) encrusting calcisponges; **b** (underside) encrusting bivalves; **c** (underside) encrusting bivalves; **d** (underside) encrusting polychaetes, **e** (surface) encrusting polychaetes; **f** (underside) encrusting bryozoan; **g** (underside) encrusting coral; **h** (underside) juvenile solitary corals



underside was more affected than the surface. *Entobia*, *Gastrochaenolites* and *Trypanites* borings differ significantly in the distribution between surface and underside since the underside was more intensively affected in each trace fossil (Fig. 8).

The encrusting taxa on the corals' underside are dominated by polychaetes, followed by solitary corals and bivalves. Bryozoans and sponges are rare (Fig. 9). Again, the underside is more affected than the surface of the colonial corals. On the surface, bivalves are the main encrusters, followed by sponges and bryozoans (Fig. 9). Only encrusting

polychaetes differ significantly in their distribution, which means they encrust the underside to a greater extent than the surface (Fig. 9). In all other encrusting groups, the difference was not as significant.

There is no correlation between encrustation and bioerosion density on the corals' underside (Fig. 10).

Bioerosion through time

To assess trends in relative bioerosion intensity through the geological record, we analyzed the results of six published

Fig. 5 **a** Cross section of a *Trypanites* boring; **b** 3D model of *Trypanites* aperture; **c** 3D model of *Trypanites* boring in CT-scan

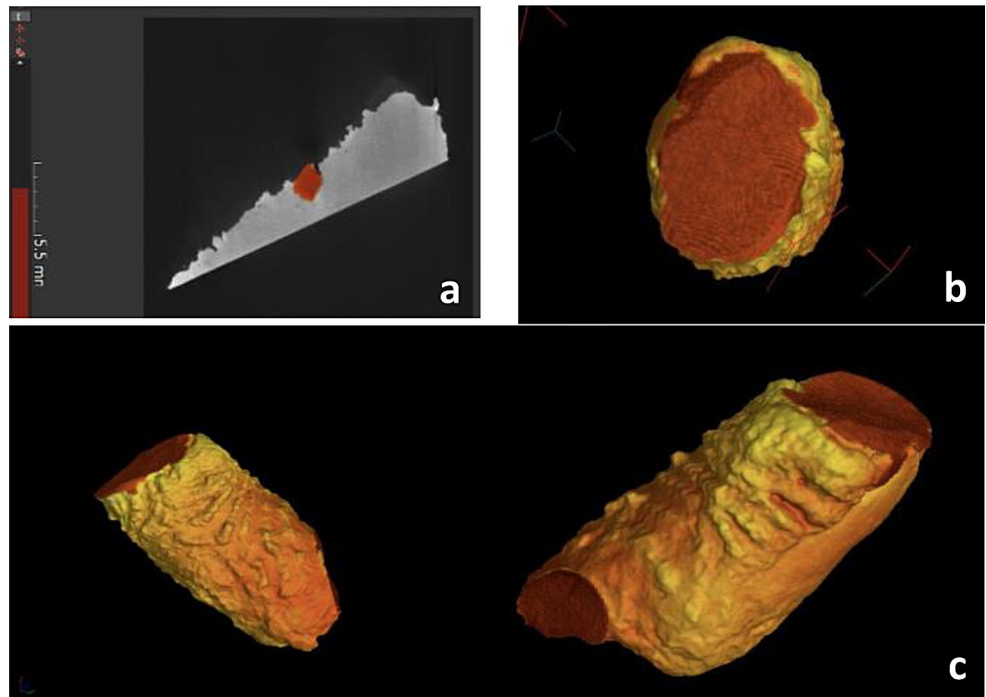


Fig. 6 **a** (underside) Fossil of a boring bivalve on *Pamiroseris recti-lamellosa*; **b** (underside) *Gastrochaenolites* boring on *Pamiroseris recti-lamellosa*

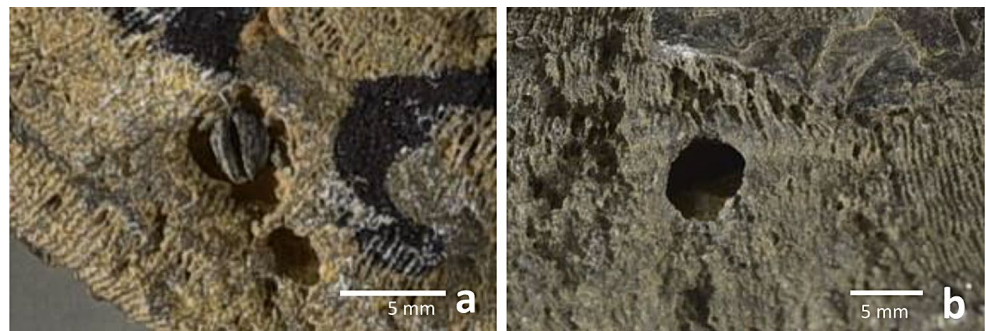


Fig. 7 Venn-Diagrams showing the number of reef corals affected by bioerosion and encrustation on the surface (left) and bioerosion and encrustation on the underside (right)

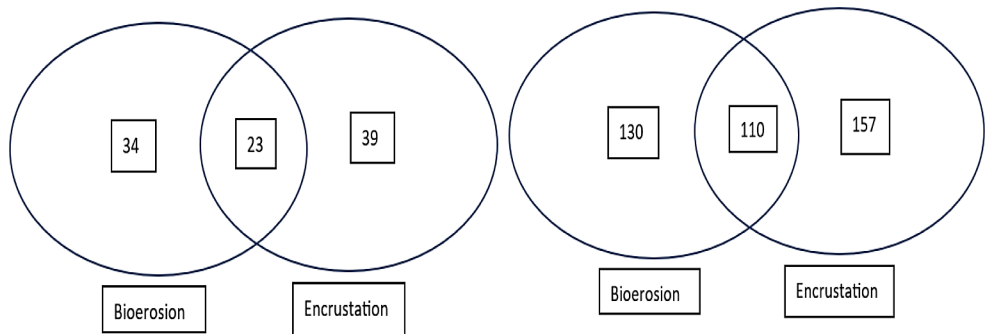


Table 1 Bioerosion and encrustation data of both the underside and the surface of *Pamiroseris rectilamellosa*; avg=average

	Affected specimens	% specimens	Point counting (Arithmetic Avg)	% point counting	Weighted average
Bioerosion surface	34	16.6	0.0057	0.57	0.0009
Encrustation surface	39	19.11	0.0197	1.97	0.0058
Bioerosion underside	130	63.72	0.0075	0.75	0.0065
Encrustation underside	157	76.96	0.0315	3.15	0.0301

Fig. 8 Comparison of bioerosion activity on the surface and the underside of the corals. Asterisks show the statistical significance ($***p < 0.001$, $**p < 0.01$, $*p < 0.5$) of differences between bioeroding activity on the coral's side and in between taxa

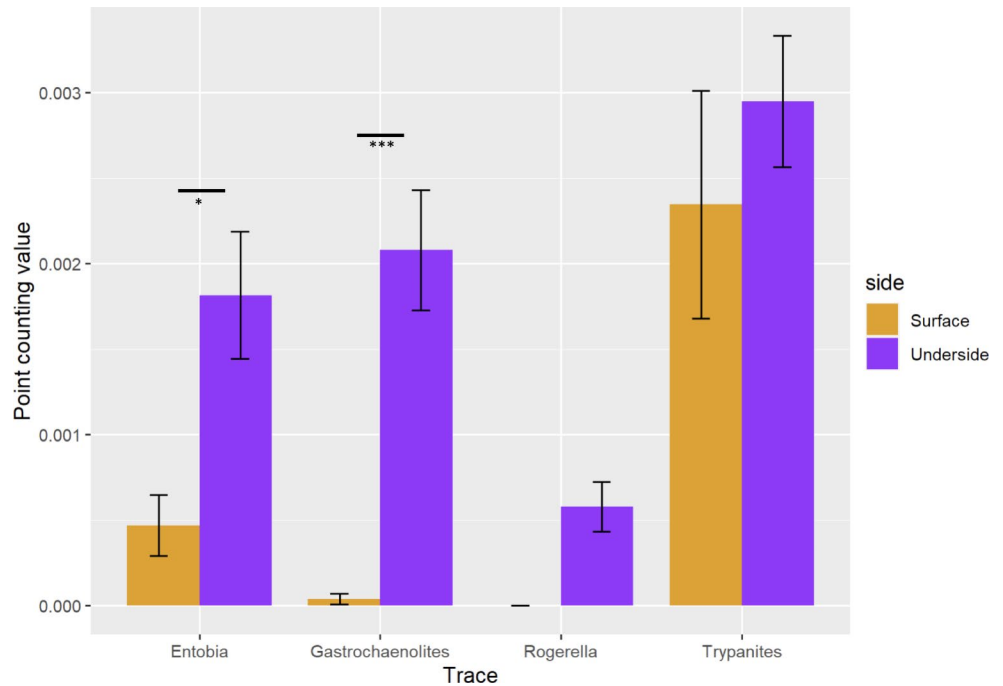
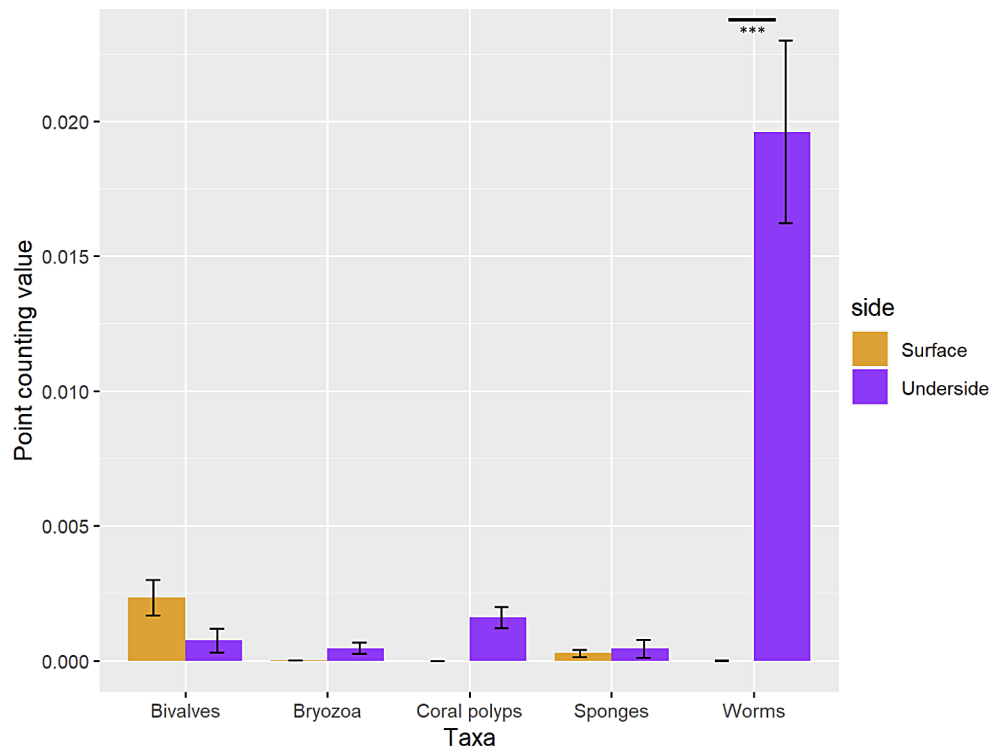


Fig. 9 Comparison of encrusting activity on the surface and the underside of the corals. Asterisks show the statistical significance ($***p < 0.001$, $**p < 0.01$, $*p < 0.5$) of differences between encrusting activity on the coral's side and in between taxa



studies (Table 2). Bioerosion of bivalves, cirripeds, and polychaetes decreased over time, whereas sponge bioerosion increased over time (Fig. 11). The rank-order of bioerosion traces has significantly changed since the Triassic. For example, worms were significantly more common than cirripeds in the Triassic, whereas today sponges are dominant compared to cirripeds. Including more datasets from the Jurassic and Triassic does not show a difference in the rank

order of bioerosional active taxa (Table 2, Fig. 12). This temporal data show a gap from 191 Ma to 23 Ma, which is a result of our strict selection of criteria. There are several bioerosion studies e.g. (Bertling 1999; Scasso and Kiessling 2002), which do not report the required quantitative data to be included.

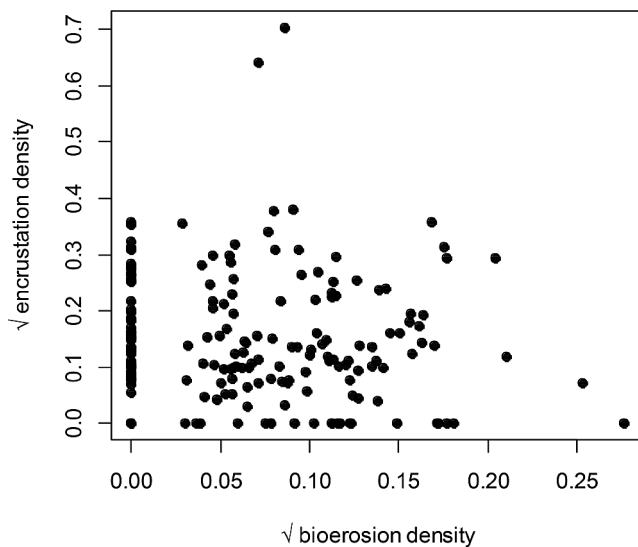


Fig. 10 Scatterplot of the proportion of encrustation and bioerosion intensity on the corals' underside. There is no significant correlation (spearman rho 0.076, p-value 0.28)

Discussion

Bioerosion intensity in the Triassic

Our results support that bioerosion already had a substantial impact on reef frameworks in the Triassic (Senowbari-Daryan et al. 1993; Bertling 2000; Bromley 2004). Although sclerobionts radiated in the Ordovician Bioerosion Revolution, the impact of macro-bioerosion on reef-growth was negligible before the Triassic (Kiesling 2002). The increase in abundance and diversity of ichnotaxa in the Mesozoic becomes apparent against a Permian baseline. The rising bioerosion intensity, from a low state in the Permian to an increasing importance in the Triassic, reflects the general trend of an increase in the significance of bioerosion throughout the Mesozoic (Schmidt-Neto et al. 2018; Luo et al. 2020). The Triassic increase in macro-bioerosion may be explained by the onset of the Mesozoic Marine Revolution

(Vermeij 1977; Benton and Wu 2022). An arms race between predators and prey began in the Triassic and lasted until the Cretaceous (Bardhan and Chattopadhyay 2003). The prey, in this context the coral bioeroders maximized their protection by drilling into hard substrates. Besides predation pressure, nutrient levels are an important determinant of bioerosion intensity (Highsmith 1980; Wizemann et al. 2018). In our case locally enhanced nutrient levels are suggested by the siliciclastic input, evidenced by the marly substrate in which the corals were recorded. Another control is exposure time, that is, the time the dead (part of the) skeleton was exposed to larval settling. The overall abundance of sclerobionts was likely related to exposure time in our material suggesting low sedimentation rates. In the Jurassic, bioerosional and encrustational taxa became even more abundant. This might be due to the Jurassic heyday of the Mesozoic Marine Revolution (Bardhan and Chattopadhyay 2003) and, a calcite sea ocean chemistry, which favors the proliferation of calcite hardgrounds and their preservations (Taylor and Wilson 2002, 2003), respectively. Our results suggest that bryozoans and scleractinians were already important encrusters in the Triassic, due to an increase in the diversity of encrusting communities in the mid-late Mesozoic (Taylor and Wilson 2003). Macro-bioerosion increased throughout the whole Cenozoic until the Recent (Perrin 2002).

Composition of sclerobiont-assemblages

Polychaete worms were dominant bioeroders and significantly dominated sponges and barnacles in our materials. Encrustation-wise, polychaetes were most common, followed by coral polyps, bryozoans, and sponges. Our results support research about worm-dominated bioerosion in the Triassic (Perry and Bertling 2000; Knaust et al. 2007, 2021; Glynn and Manzello 2015). The co-occurrence of serpulids and calciferous sabellids (i.e. *Glomerula*) in this study is similar to the encrustation of hard substrates in the Middle Jurassic of Europe (Słowiński et al. 2022) and Israel (Vinn

Table 2 Macrobioerosion data for the comparison of bioeroding taxa throughout the geological record

Time	Location	Reference	Sponges	Bivalves	Worms	Cirripeds
Norian	Nayband, Iran	(Bertling 2000)		27.3	57	15.6
Rhaetian	Adnet, Austria	(Bertling 2000)	11.1	25.2	60.3	3.3
Rhaetian	Feichtenstein, Austria	(Bertling 2000)		40.3	59.6	
Carixian	Moulay Idriss, Morocco	(Bertling 2000)	2.5	46.2	31.1	20.2
Domerian	Beni Tadjit, Morocco	(Bertling 2000)	3.3	11	50.6	35.2
Miocene	Mallorca	(Perry 1996)	75	23	2	0
Pleistocene	Falmouth Formation, Jamaica	(Perry 2000)	64.7	8.2	25.8	0
Holocene	Gulf of Eilat, Red Sea	(Klein and Loya 1991)	10.8	19.4	42	0
Recent	Gulf of Eilat, Red Sea	(Klein and Loya 1991)	32.1	19.8	35.3	0
Recent	Gulf of Eilat, Red Sea	(Klein and Loya 1991)	15.6	18.5	47.4	0
Recent	Discovery Bay Jamaica	(Perry 1998)	81.5	2.5	15.9	0.1
Recent	South China Sea	(Chen et al. 2013)	38.3	48	5.6	8

Fig. 11 Comparison between Triassic and Recent bioerosion data. The remaining 0.5% in the Triassic data set were not identifiable

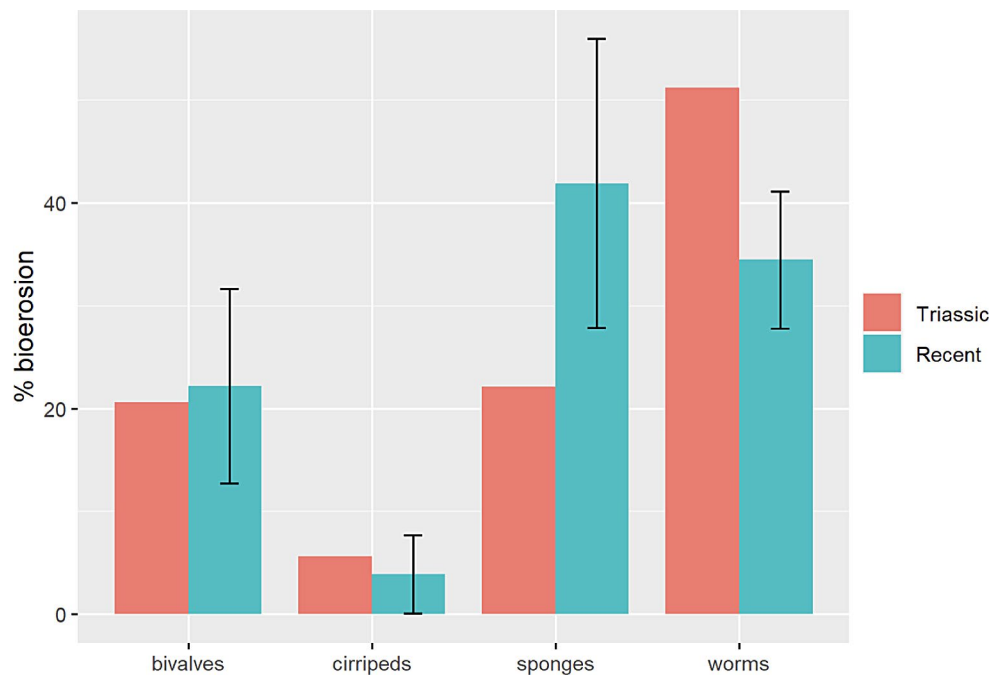
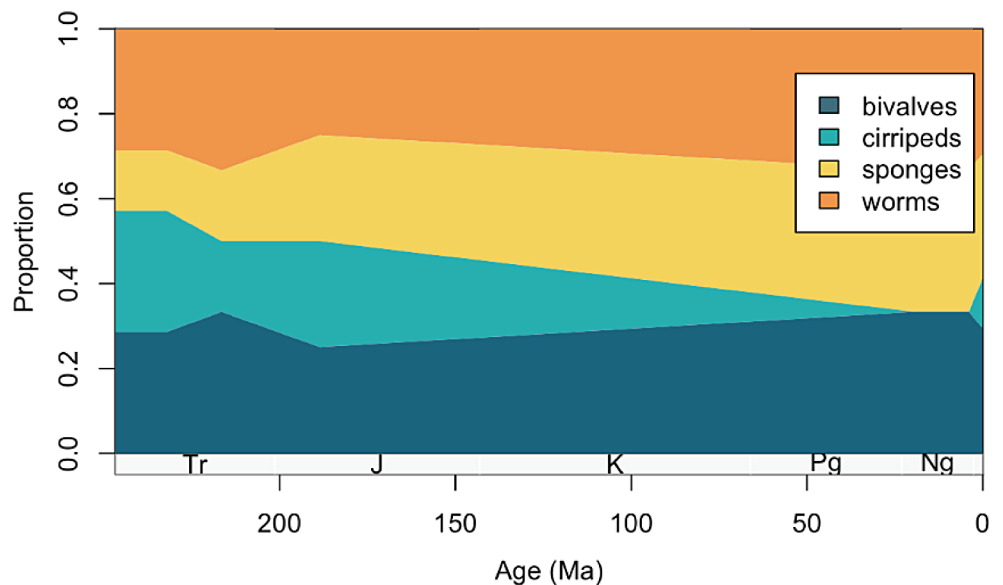


Fig. 12 Polygon plot showing the distribution of bioerosing taxa from the Triassic to Recent (see Table 2)



and Wilson 2010). Although it is not typical for the Triassic since it lacks the encrustation of microconchids, which were among the most dominant triassic encrusters (Vinn and Mutvei 2009; Zatoń et al. 2013).

Our literature research suggests a trend towards high sponge bioerosion towards the Recent, whereas other bioerosional taxa decreased since the Triassic. Sponges are the dominant endolithic bioeroders in modern reefs, comprising 75–90% of the total macroboring community (Perry and Harborne 2016). This trend may be due to competition between the species. Sponges are hypothesized to be the primary long-term bioeroders on reefs today when grazers are absent (Weinstein et al. 2019), most probably because they

inherit multiple ways of reproduction, fast growth and healing abilities (Schönberg et al. 2017a).

Distribution of bioerosion and encrustation

Another notable result is the slight dominance of encrusters compared with bioeroders regardless of the coral side. Overall, however, there is no correlation between bioerosion and encrustation intensity of coral undersides. Therefore, the relative amount of sclerobionts is not simply a function of exposure time before final burial. Idiosyncratic larval settlement is the most likely explanation for the absence of a correlation, perhaps enhanced by priority effects.

The coral samples were collected from marly sediment, which indicates that these corals grew in a turbid (i.e., brown mesophotic) environment. Brown mesophotic environments are those where limited light is governed by high turbidity in the water column (Majchrzyk et al. 2022). This results in a reduced abundance of phototrophic organisms (Tribollet and Golubic 2005; Schönberg et al. 2017b). Bioerosion intensity is suspected to be low to moderate in the mesophotic zone, whereas encrustation might be positively affected (Loya et al. 2019). The lower water temperature and reduced algal food sources due to the restricted light intensity are leading to a reduced grazer abundance. Encrusters might benefit as they can settle undisturbedly in the absence of grazers (Weinstein et al. 2019, p.840). For encrustation the substrate space is the limiting resource (Taylor 2016).

Differences in upper surface and underside settlement

The much higher sclerobiont density on the underside of corals compared with their surface is probably related to defense mechanisms of the living coral. Although encrustation and bioerosion can happen during the life of the coral, these processes usually take place post-mortem because of the defense mechanisms (Wood 2011). Pre-mortem the coral is able to inhibit biofouling by the secretion of an antimicrobial mucus-layer (Shnit-Orland and Kushmaro 2009; Bythell and Wild 2011) or the usage of cnidocytes to parry macro-organisms (Watson and Hessinger 1989).

The lack of defense strategies on the underside of platy corals against fouling makes them more likely to be eroded/encrusted before the death of the entire colony (Taylor and Wilson 2003). The corals' upper side can only be encrusted/bioeroded post-mortem (Shnit-Orland and Kushmaro 2009; Wood 2011). Settlement is halted with the time of burial, wherefore the top can only be inhabited in the interval between the corals' death and its burial, indicating the exposure time of the dead coral (Wood 2011; Glynn and Manzello 2015). This might demonstrate that the 51 corals that had an affected top side, have been colonized post-mortem, whereas the other 177 bottom affected specimens could also have been colonized pre-mortem.

In the presence of adapted predators, encrusters need a safe environment for settlement, such as a cryptic habitat, characterized as a dark and shaded environment, providing shelter and protection from biological and physical disturbances. As all bottoms of corals fulfill those criteria, encrusters preferably settle on the underside (Kobluk 1988). Since bioeroders create their own cryptic habitat, the higher predation pressure cannot be responsible for the shift to a more intensive bottom settlement thus the adaptive defense strategies corals gained throughout the Marine Mesozoic

Revolution, to protect their upper side, are the relevant explanation for the imbalance.

However, the advanced defense mechanisms are only of importance if the settlement is pre-mortem. Post-mortem settlement would still be possible on the underside and surface of corals.

Another notable result is the presence of colonial corals on the underside of *Pamiroseris rectilamellosa*. To thrive on the underside of the coral, the encrusting corals must have been able to cope with low-light conditions, which suggests that those encrusting corals were azooxanthellate. Most literature is targeting proof for an azooxanthellate lifestyle in the Triassic (Stanley and Swart 1995; Frankowiak et al. 2016), such that this proof for azooxanthellate corals fills an important gap.

In conclusion, our samples represent a highly eroded and encrusted reef-environment for Triassic times. The abundance and extent of encrusters increased as they settled preferably in a safe space such as a cryptic environment. Our study can be used for assessing the impact of increased nutrient levels in recent environments, since our sclerobiont communities settled in a high-nutrient, brown mesophotic environment. Overall, research on reef assemblages needs a better overview of the bioerosional impact on different coral species in different environments to predict reef framework changes, since most modern coral reefs consist of various species. We added to this debate a quantitative analysis of bioerosion on the species *Pamiroseris rectilamellosa* in the Triassic, a critical time of low grazer abundance and similar composition of recent bioeroders, which settled in a nutrient dense, brown mesophotic environment.

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