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Hidden from plain sight: Sclerosponges as environmental archives of ocean conditions from the surface to the mesophotic zone

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Sclerosponges dwell in an underexplored region of reefs. Their massive basal skeleton offers an opportunity as a unique, but underappreciated, paleoenvironmental archive. Here, we give an overview of the paleoclimate potential of sclerosponges and highlight current and future research areas.

Sclerosponges: Dwellers of caves, overhangs and mesophotic zones

Tropical shallow-water coral reefs are colorful, bright environments in which light drives the growth of a plethora of corals and other organisms. Off the well-lit parts of the reef, however, the light gets gradually dimmer and different organisms appear. Caves, overhangs, and the twilight environment of the mesophotic zone represent the refuge for a group that, in evolutionary terms, are the most ancient animals that form a massive calcareous skeleton (Fig. 1a). These organisms are coralline sponges or sclerosponges which were thought to be extinct until their rediscovery in cryptic habitats in the early 20th century.

While their ancient relatives contributed significantly to reef-building during the Paleozoic and Mesozoic, in today's oceans, sclerosponges are important contributors to nutrient cycling, and their massive skeletons cement and stabilize reef structures. The depth distribution of approximately one dozen sclerosponge species spans from surface waters to over 600 m deep, and they are found in the tropical and subtropical regions of the Atlantic, Pacific and Indian oceans (Vacelet et al. 2010). Although leading a life in shaded environments, sclerosponges are important for the movement of elements between living things and the ocean water.

Sclerosponges as paleoclimate archives

Research on sclerosponges dates back to the early 20th century when Joseph Jason Lister (1857–1927) and Randolph Kirkpatrick (1863–1950) investigated "pharetronid sponges" and rediscovered "living fossils" (e.g. *Astrosclera willeyana* Lister, 1900 from the Pacific; Fig. 1b). It was only in 1976 that Veizer and Wendt published the first geochemical analysis of the basal skeleton of *A. willeyana* (Fig. 1b), *Ceratoporella nicholsoni*, and *Petrobiona massiliana*. Together with *Acanthochaetetes wellsi* (Fig. 2), they are currently still the most investigated sclerosponge species.

Since the first geochemical investigations in the 70s, sclerosponges have been successfully used for paleo reconstructions. Their first application as an environmental archive was presented in 1986 by Druffel and Benavides, who used sclerosponges from the Caribbean to fingerprint oceanic anthropogenic CO_2 increases through $\delta^{13}C$ analysis. The observed decrease of ^{13}C, the ^{13}C-Suess effect, results from fossil fuel burning. This effect was later also found in Pacific sclerosponges (Böhm et al. 1996). Radiocarbon analyses revealed the bomb curve; a peak in $\Delta^{14}C$ due to above-ground thermonuclear testing starting in 1955 (Benavides & Druffel 1986). Instrumental advances in geochemistry allowed an increase in the spatial analytical resolution from mm- to µm-scale, which is equivalent to bimonthly resolution in sclerosponge skeletons (Swart et al. 2002). Besides their application to trace atmospheric chemistry, they can be used to reconstruct seawater temperature and $\delta^{18}O$ values by analyzing their trace metal and stable isotope composition. While Wörheide (1998) reconstructed relative temperature changes using $\delta^{18}O$ values, Rosenheim and coworkers (2004) provided the first absolute temperatures through an empirically calibrated Sr/Ca-temperature relationship, with the longest record from a single sponge being ≈ 600 years (Waite et al. 2020).

To achieve any paleoclimate record, a chronology of the skeleton is necessary, and the sclerosponge needs to be dated. Unlike corals or bivalves, sclerosponges lack the presence of an internal annual banding that would allow dating through sclerochronological means, such as with tree-ring chronologies. Dating and growth-rate estimates of sponges have so far been conducted by in situ staining with fluorescent dyes (Fig. 2), $\delta^{13}C$-Suess effect values, the identification of the leaded fuel combustion-Pb peak in 1971, and $\Delta^{14}C$ or U/Th radiometric dating (e.g. Benavides & Druffel 1986; Swart et al. 2002; Wörheide 1998). These methods are currently the only way to determine their age. Compared to tropical corals, coralline sponges are

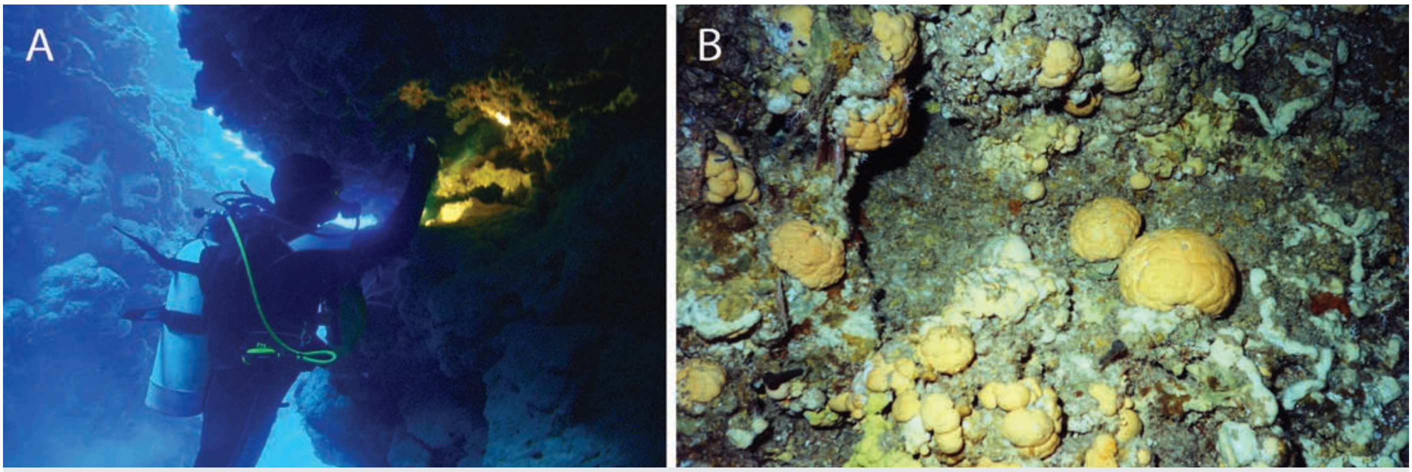

Figure 1: (A) A diver (G. Wörheide) samples sclerosponges in the Coral Sea, Australia. Photo credit: C. Vogler. **(B)** *A. willeyana* (yellow) off Saipan, Northern Mariana Islands. Photo credit: A. Grottoli.

slow-growing at less than 2 mm/year (e.g. Grottoli et al. 2010). Still, they have extraordinary longevity, reaching up to one thousand years (Vacelet et al. 2010). Hence, individuals of *C. nicholsoni* can become larger than 1 m in diameter, emphasizing their potential as a valuable high-resolution environmental archive for extended periods (Lang et al. 1975).

More recent work focused on proxy verification and reconstructing the paleoceanographic history of the Pacific using element ratios, $\delta^{13}C$ and $\delta^{18}O$ values (e.g. Asami et al. 2021; Grottoli et al. 2010, 2020). These studies found little impact of biological activity, the so-called vital effect, on skeletal $\delta^{13}C$ and $\delta^{18}O$ values, or the partitioning of Sr, and they also reported P/Ca ratios as a promising proxy of seawater P concentrations. An improved Sr/Ca temperature calibration for *C. nicholsoni* allowed for water-temperature reconstruction with a precision of <0.5°C (Waite et al. 2018), enabling Waite et al. (2020) to determine how the combination of volcanic activity and anthropogenic forcings drove Atlantic climate variability during the past 600 years.

The anthropogenic change in atmospheric CO_2 has lowered the pH of the ocean. Boron isotopes (skeletal $\delta^{11}B$), a common proxy for seawater-pH reconstruction in corals, showed that *C. nicholsoni* grows close to equilibrium with the seawater borate isotopic composition and links $\delta^{11}B$ variability on the sub-mm scale to seasonal pH changes (e.g. Sadekov et al. 2019). These results emphasize the potential of sclerosponges as a recorder of ocean acidification. Sclerosponges were also applied to trace other anthropogenic pollutions. For example, Pb/Ca ratios are used to trace environmental Pb contamination (e.g. Asami et al. 2021).

In conjunction with their longevity and resistant skeleton, these recent findings concerning the geochemistry of sclerosponges pave the way for establishing them as a valuable archive of climatic, oceanographic and pollution conditions at depths beyond that recorded by scleractinian corals in warm-water reefs.

The future of paleo-sclerosponge science
The importance of the underexplored mesophotic zone makes research on local environmental archives, such as those provided by sclerosponges, urgently required. New sampling and habitat mapping opportunities using affordable underwater drones, or hybrid, remotely-operated vehicles, can increase the accessibility of coralline sponges. Technological advances in the field of omics (genomics, proteomics, metabolomics, etc.), X-ray microtomography and geochemical analytical advances like Laser Ablation Inductively Coupled Plasma Time of Flight Mass Spectrometer (LA-ICP-ToF-MS), or Nanoscale Secondary Ion Mass Spectrometry (NanoSIMS), allow for a wide range of analyses of slow-growing carbonate structures.

Figure 2: A section of *A. wellsi* from Saipan, Northern Mariana Islands. The sample shows an alizarin red stain from a growth-rate experiment. Photo credit: A. Grottoli.

Recent years have seen a huge leap forward in understanding the biomineralization of scleractinian corals to build their $CaCO_3$ skeletons. In sclerosponges, however, very little is known. Arguably, a thorough knowledge of biomineralization is required, to not only form a mechanistic understanding of the impacts of future climate change, but also as a prerequisite for the application of geochemical proxies. Since sclerosponges are among the most ancient multicellular $CaCO_3$ biomineralizers, such insights could also provide unique information about how animal skeletal formation evolved.

So far, diagenesis has only been studied in fossil sponges, but no studies have investigated the fate of the skeletal elemental and isotopic composition and structure after formation. In addition to long-term changes, several other skeletal processes require further studies, such as the extracellular backfill of the skeleton observed in *A. willeyana* (Wörheide 1998) and the chemical heterogeneity in *A. willeyana* and *C. nicholsoni* that could not be linked to environmental variations (e.g. Asami 2021).

Despite these challenges and the limited number of paleo studies, sclerosponges have enormous potential as long archives of past climates in the subsurface of the upper ocean. However, to maximize the potential of these environmental archives, the following issues are pressing areas of sclerosponge investigation: i) dating at sub-seasonal resolution; ii) lab culturing and in situ experiments on the effect of environmental changes on skeletal formation and composition; iii) investigation into possible early diagenesis; and iv) the influence of biomineralization on the geochemistry of the calcareous skeleton.

One exciting aspect of sclerosponges, which was only briefly explored, is the potential to reveal changes in the thermocline structure of the upper ocean. As the ocean warms, the depth at which the thermocline occurs should deepen. Given carefully chosen sampling locations and appropriate geochemical methods, sclerosponges can offer insight into how thermocline depth and heat penetration in the oceans have responded to rising global temperatures.

Addressing these knowledge gaps would be most effective through cross-disciplinary collaboration between paleoclimatologists, (bio)geochemists, microbiologists, geneticists, and physical oceanographers. We hope this article stimulates these collaborations to maximize the study of sclerosponges as a potentially unique climate archive.

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REFERENCES
Asami R et al. (2021) Prog in Earth Planet Sci 8: 38
Böhm F et al. (1996) Earth Planet Sci Lett 139: 291-303
Benavides LM, Druffel ERM (1986) Coral Reefs 4(4): 221-224
Druffel ERM, Benavides LM (1986) Nature 321: 58-61
Grottoli AG et al. (2010) J Geophys Res 115: 1-14
Grottoli AG et al. (2020) Geochem Geophys Geosyst 21: 1-14
Lang JC et al. (1975) J Mar Res 33: 223-231
Rosenheim BE et al. (2004) Geology 32: 145-148
Sadekov A et al. (2019) J Anal Atom Spectrom 34: 550-560
Swart PK et al. (2002) Paleoceanography 17: 1-12
Vacelet J et al. (2010) Treatise Invertebr Paleontol 4: 1-16
Veizer J, Wendt J (1976) J Archäol Sci 23: 558-573
Waite AJ et al. (2018) Chem Geol 488: 56-61
Waite AJ et al. (2020) Geophys Res Lett 47: 1-11
Wörheide G (1998) Facies 38: 1-88