A history of sponge erosion: from past myths and hypotheses to recent approaches

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Abstract. Bioeroding sponges have historically been mystical beasts of the sea. Originally, they were classified as half cnidarian, half sponge. It required much time and scientific convincing to confirm their status as active bioeroders. The scientists Hancock and Nasonov were pioneers of their time. They recognised and defended the main concepts: the endolithic organisms are sponges, they produce the cavities they inhabit, and their activities are likely to involve chemical and mechanical processes. However, this viewpoint was often scathingly challenged, and the notion of actively bioeroding sponges was hotly disputed. Once the concept was firmly established in the mid 1900s, related research experienced a significant leap. Notably studies by Pomponi and Hatch on the ultrastructure of etching cells and their associated biochemical properties left no room for doubt: The enzymes carbonic anhydrase and acid phosphatase are associated with sponge bioerosion, providing means for mineral dissolution and digestion of organic components, thus enabling the removal of the so-called sponge chips. However, the exact etching agent remained undetected, and since 1980 research on this phenomenon significantly slowed down. Further studies predominantly focused on environmental control of bioerosion and the taxonomic value of sponge erosion traces. A recent study with electrochemical liquid ion exchange microsensors revisited the question of how sponge bioerosion is achieved and whether acid is involved. This study is presented here to conclude the summary of current knowledge in this context. Microgradients of pH and calcium ions in the tissues of *Cliona celata* and the non-eroding sponge *Halichondria panicea* from the North Sea were compared. The pH slightly decreased with distance into the tissue of *C. celata*, whereas after an initial drop it remained stable in *H. panicea*. Calcium concentrations in *C. celata* increased slightly more with tissue depth than in *H. panicea*. *C. celata* bioerosion may be periodic (few hours cycle) as evidenced by oscillating pH values at the sponge-substrate interface, which may explain micro-terracing in sponge scars. Nevertheless, measured pH changes were too weak to prove beyond doubt that sponge bioerosion employs acid, and further studies will be necessary to confirm present preliminary findings.

Keywords. Bioerosion, mechanism, history, mechanical, chemical, microsensors, *Cliona celata*

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Introduction

Historically, sponges have thoroughly puzzled the observer, e.g., with the question whether they are plants or animals (e.g., Dujardin 1838a; Priest 1881a). Within the Porifera, the bioeroding sponges posed an even larger riddle: Were they cnidarians or sponges (e.g., Grant 1826), squatting in vacated worm borings (e.g., Bowerbank 1866) or did they make their own 'digs' (e.g., Hancock 1849a)? If they were actively eroding, did they use chemicals or minute tools facilitating mechanical erosion? If assuming a combination of chemical and mechanical erosion (e.g., Nasonov 1883), what is the compound they employ for substrate dissolution and is it secreted over the entire surface of the sponge or only very locally? All these questions created a multitude of hypotheses that were repeatedly contested, supported, contradicted, defended and re-erected, yet some issues still remain unsolved.

Parts of the available knowledge were previously summarised by Bianconi (1841: 455-463), Topsent (1888: 3-18), Vosmaer (1933: 309-315), Hartman (1958: 89-90), Warburton (1958: 555-556), Cobb (1969: 783-784), Rützler and Rieger (1973: 144-145) and Pomponi (1980: 302-315). Of these, Vosmaer's account is the most detailed and complete. After 1980 the interest in the mechanisms of sponge bioerosion markedly decreased and only recently received renewed attention (e.g., Zundelevich et al. 2007).

As the historical development of the ideas is enlightening and the ensuing debates often enjoyable, a review on contrasting viewpoints on the mechanisms of sponge bioerosion was compiled for the present publication, providing some quotes and original illustrations, and in consequence giving a significantly more complete account than previous authors. This review on sponge bioerosion will conclude with a recent study that employed a modern, frontier technique: pH and calcium liquid ion exchange microsensors. Following one of the historical and yet unsolved questions, the microsensors were used to test whether chemical dissolution in bioeroding sponges involves acid secretion. *Cliona celata* Grant, 1826 was compared to the non-eroding *Halichondria panicea* (Pallas, 1766) in the effort to detect increased acid concentration and calcium carbonate dissolution when approaching the sponge-substrate interface in bioeroding sponges.

Material and methods

The first part of this publication is a review of available knowledge on the mechanisms of sponge bioerosion that is based on literature reaching back to 1802. In this context the Systema Porifera (Hooper and van Soest 2002) and two bibliographies on sponges and marine bioeroders (Vosmaer 1928; Clapp and Kenk 1963) were of significant help for accessing full citation records of historic references. Passages will be cited, which were translated by the present author if they were not in English. Figures of publications that are older than 100 years were adapted and used for the present purpose. Photographs of historic authors were provided by museums or galleries. Missing information on biographies of historic scientists was obtained at the websites of the Oxford Dictionary of National Biography and Wikipedia (see

references). New images of sponge bioerosion traces were obtained at The Carl von Ossietzky University Oldenburg with a Leica phase-contrast microscope together with a ColorView digital camera and the software AnalySIS 3.2, viewing slide preparations of sponges obtained 1995-1997 at Orpheus Island, Palm Island Group, central Great Barrier Reef, Australia (Schönberg 2000) and from Topsent material obtained from the Paris National Museum of Natural History.

This publication additionally contains results of one original, previously unpublished study that was conducted at the Max Planck Institute for Marine Microbiology in Bremen, Germany. Calcium and pH microprofiles were measured within the tissue of *Cliona celata* Grant, 1826 and *Halichondria panicea* (Pallas, 1766) to test whether (i) calcium and pH environments differ between bioeroding and non-eroding sponges, (ii) sponges use acid for bioerosion, (iii) increased calcium concentrations resulting from sponge bioerosion can be detected in the tissue, and (iv) whether changes in pH and calcium concentrations are gradual or sudden (latter suggesting localised application of etching agent). A recent technology was employed to pursue these questions: electrochemical liquid ion exchange microsensors (LIX; Kühl and Revsbech 2001). The idea behind this study was that microsensor tips with a diameter of 3-10 µm might be fine enough to reach the area of bioerosion without significant damage to the sponge.

Live samples of *C. celata* and *H. panicea* were taken at Helgoland Island, North Sea by dredging (material service of the Research Station, M. Krüß). Contained in buckets they were transported to Bremen together with water from the sample site. At the Bremen Max Planck Institute for Marine Microbiology, sample material was transferred into a 200 l holding tank and supplemented with artificial seawater mixed to the salinity at the sample site (Meersalz HW Professional, Wiegandt GmbH, Krefeld, Germany). The holding tank was cooled down and maintained at sample site ambient temperatures, the pH was automatically regulated with a CO_2 reactor. Taxonomic identity of the sponges was confirmed by viewing spicule preparations under a Leica phase-contrast microscope with ocular graticule.

LIX microsensors for pH and calcium were hand-made and used within 1-3 days of adding the membranes (Kühl and Revsbech 2001). Each sensor was calibrated and checked with standard solutions before and after each series of measurements and each time data irregularities occurred that might have signified a broken sensor tip. Data acquisition and experimental setup followed the description given in Schönberg et al. (2004), i.e., data were monitored with a voltmeter and recorded with a strip chart recorder and on computer. Sponges were taken from their holding tank one at a time and placed into a 12 x 12 x 22 cm flow chamber for measurements. The flow chamber was connected to a reservoir of 10 l of water for circulation by pump. Flow rates were kept constant. The whole system was temperature-controlled and aerated with a bubble-stone (see fig. 2 in Schönberg et al. 2004).

Microsensors were placed and moved with the aid of a manually-adjusted micromanipulator. Sensors were driven into *C. celata* through papillae emerging from the substrate (Fig. 1) and near oscula in *H. panicea*. Position and progress

were monitored with a modified microscope. Microsensors were positioned on the surface of a given sponge, brought to 2 mm above the sponge and then driven towards the sponge and into the tissue, usually in 100 µm increments. At each step three voltammetric measurements were taken at steady state, of which the means were used. Measurements for *H. panicea* were terminated after 2 mm, for *C. celata* when the background was reached, i.e., the calcium carbonate substrate (Fig. 1; as evidenced either by feeling the resistance when using the micromanipulator or by a jump in data signals monitored on a strip chart recorder, see also Schönberg et al. 2004). Finally, voltammetric values were converted to pH and calcium concentrations using the calibrations for each individual sensor.

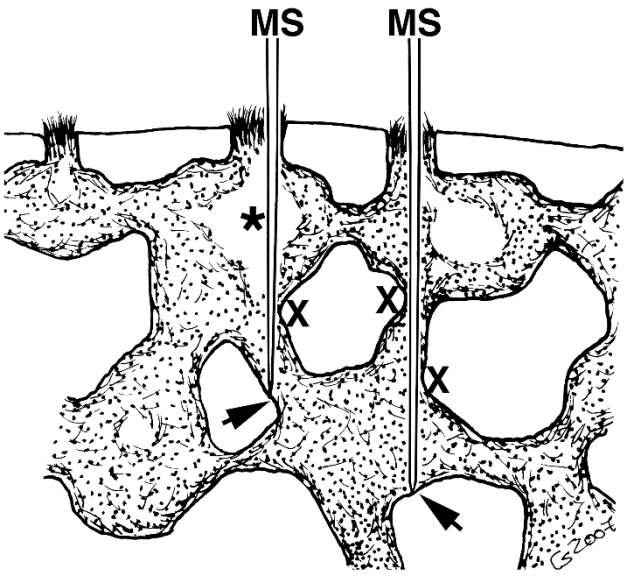


Fig. 1 Application of microsensors in the tissue of *Cliona celata* (in schematic cross-section). Microsensors (MS) were driven into the sponge through the papillae and lowered until they met with resistance from the calcium carbonate substrate (arrows). The measured profiles were probably influenced by heterogeneities in the sponge morphology (* = water in the canal system, likely to reflect external conditions) and the occasional proximity to remaining substrate material (X = conditions may resemble those at the ends of the profiles)

These measurements were repeated three times in a given sponge and conducted with three sponge individuals for *C. celata* and *H. panicea* each. As the initial sample series of *C. celata* did not provide the expected strong evidence in support of the present hypotheses, measurements were repeated with three fresh specimens of *C. celata*, again sampled at Helgoland Island. For a small number of *C. celata* individuals, measurements over longer periods were attempted, i.e., sensors were carefully driven into the sponges until the background (substrate) was reached and remained in place for at least 20 h to ascertain whether sponge erosion followed temporal patterns. Of these data series, four for pH and one for calcium are available.

Literature review

Early 1800s: What is this endolithic organism?

Bosc (1802a: 147-148) was probably the first scientist to describe a bioeroding sponge. In contrast to some of the later authors he immediately recognised it as a sponge. The entire description reads as follows: *'Éponge pézize, Spongia peziza. Jaune; les rameaux sortant des cavités des pierres, sous la forme d'un petit champignon. Voyez la fig. 8 pl. 30 qui la représente de grandeur naturelle. Cette espèce ne se trouve que dans les cavités des pierres et des bois, qui sont dans le mer; elle en remplit l'intérieur, et sort, par leurs orifices, sous la forme d'une petite pézize de couleur jaune. Les graves, que l'où jette dans le mer, à Charleston, observe Bosc, à qui on doit la connaissance de cette espèce, en sont quelquefois si couverts qu'ils ont l'air d'un lichen tuberculeux.'* (Translation: 'Cup fungus sponge [cup fungus gen. *Peziza*], *Spongia peziza*. Yellow; the branches exit from cavities in stones in form of a small mushroom. See fig. 8, pl. 30 that represents the natural size. This species can only be found in cavities of stones and timber that are in the sea [timber: erroneous observation]; it fills the interior and exits through pores in the form of a small cup fungus of yellow colour. The gravel that extends into the sea at Charleston is sometimes so covered [in it] that it has the appearance of a tuberculate lichen, observes Bosc to whom the recognition of this species is due.') Bosc did not try to explain how this sponge came to live in a stone. Judging from the sample site, the colour and the form of the erosion (resembling *Entobia megastoma* (Fischer, 1868); see Fig. 2), we can assume that he described a member of the *Cliona celata* species complex. He should thus receive part of the credit for discovering bioeroding sponges. However, as the description was published in a little-known journal and is very short and vague, it has all but been forgotten.

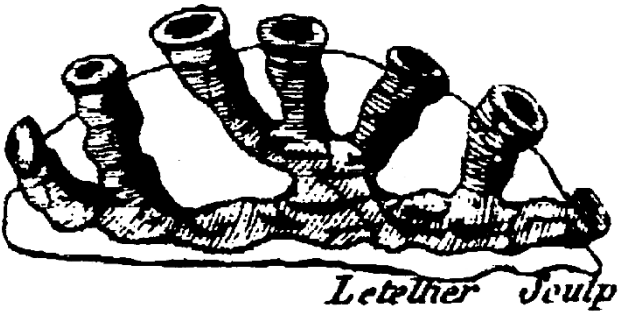


Fig. 2 *Spongia peziza* (Bosc, 1802:pl. 30, fig. 8) (= *Cliona celata*?). The first known drawing of a bioeroding sponge, slightly modified to remove spots

Only four years later fossil traces of sponge erosion were noted by Parkinson (1808: 76 and pl. 8), who assumed organisms similar to cnidarians to be the tracemakers: *'That the formation of these bodies has been the work of some animal, of a nature similar to the polypes, by which the known zoophytes are formed, cannot, I think, be doubted. But in what genus in the order of zoophytes can they be admitted?'*

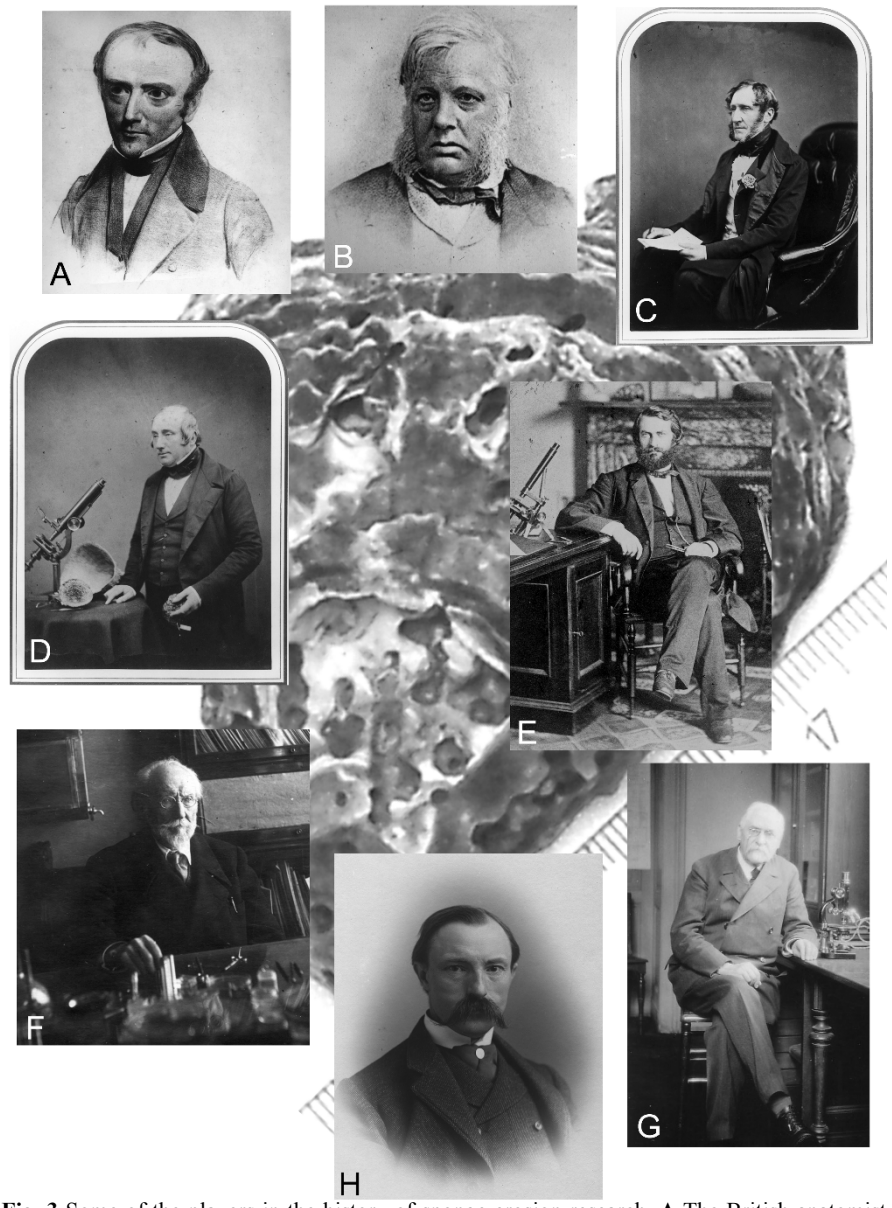


Fig. 3 Some of the players in the history of sponge erosion research. **A** The British anatomist Robert Edmont Grant (1793-1874). Photograph provided by C. Valentine, courtesy Porifera Section, Natural History Museum, London. **B** The British zoologist Albany Hancock (1806-1873). Photograph taken by R. B. Bowman, provided by J. Holmes, courtesy of the Natural History Society of Northumbria, Hancock Museum (archive no. NEWHM:1996.H54). **C** The British naturalist John Hogg (1800-1869). **D** The British naturalist and palaeontologist James Scott Bowerbank (1797-1877), well-known for his sponge monographs. C and D © National Portrait Gallery, London [archive nos. P120(50) and P120(1), respectively], provided by H. Trompeteler. **E** American naturalist Prof. Joseph Leidy (1823-1891). Photograph taken 1863. Courtesy of E.

Despite these earlier records, the credit for discovering and naming bioeroding sponges has traditionally been given to Grant (1826: 79; Fig. 3A), who found some *'pulpy matter'* and *'fleshy mass'* that inhabited excavations within a common oyster. He created the new genus *Cliona* in reference to its *'high degree of contractile power'*. Similar to Parkinson (1808), he believed *C. celata* to be *'zoophyte'*, and to be an intermediate form between cnidarians and sponges. In the same year Osler (1826: 364) mentioned *'a fibrous yellow pulp, filling a number of irregular cells, which open freely into each other, and eventually occupy and destroy the whole shell.'* He recognised it as *'a kind of sponge'*. This view was shared by Dujardin (1838a and b) and Michelin (1846), but other authors understood *Cliona* as an alcyonarian, even though they knew sponges (e.g., de Blainville 1834). The latter was puzzling over sponge erosion traces and obtained advice from Nardo (1839) before he formed his opinion. Bianconi (1841: 458) summarised this by stating: *'... e per conseguenza che non trattavasi qui di un alcionario, ma di un vero spongiale.'* (Translation: '…and consequently this was not a matter of an alcyonarian, but of a true sponge.'). Hancock (1848, 1849a and b, 1867) firmly established that the genus *Cliona* should be understood as a sponge.

He elaborated (Hancock 1849a: 322; Fig. 3B): *'I have examined with much care the papillae of* Cliona *when just removed from the sea, but have not succeeded in detecting any polypes. The propriety, nevertheless, of retaining it as a distinct genus would appear evident; for though it undoubtedly possesses many characters in common with* Halichondria*, yet* Cliona *differs widely from it in its habits, and particularly in its contractile power, a quality surely of great importance...'*. Hogg (1851: 192-193; Fig. 3C) again disputed that the organisms in question are really sponges: *'...these perforating 'sponges' do not seem to be true sponges – merely species of* Cliona *– a genus, according to the accurate accounts of Dr. Grant, Dr. Johnston, De Blainville, &c., belonging to the class Zoophytes, and which is described by them as a polype furnished with about eight short tentaculata.'* But due to the minute studies of Hancock (1849a; see above), Hogg failed to find acceptance.

Grant (1826) remains the accepted founder of the group despite Bosc's (1802a) earlier account of *Spongia peziza* and Nardo's (1839) and Bianconi's (1841) insistence it should be called *Vioa*, because Grant did not recognise his *Cliona* as

Mathias, © Academy of Natural Sciences, Ewell Sale Stewart Library (archive details: coll. 9, Leidy seated at desk). **F** The Russian-Soviet researcher Prof. Nicolai Victorovich Nasonov (1855-1939) at the age of 80 years. Photograph taken 1934, provided by C. Eckert, courtesy of the Historical Image and Script Collections at the Museum für Naturkunde, Humboldt University Berlin (MfN HUB, HBSB, Zool. Mus., B I/1787). **G** French spongiologist Prof. Emile Topsent (1862-1951) who contributed significantly to sponge taxonomy and systematics. Photograph provided by C. Valentine, courtesy Porifera Section, Natural History Museum, London. **H** Dutch spongiologist and taxonomist Prof. Gualtherus Carel Jacob Vosmaer (1854-1916), best known for his Bay of Naples monograph (Vosmaer 1933). Photograph by Vanderstok, Leiden, provided by C. Eckert, courtesy of the Historical Image and Script Collections at the Museum für Naturkunde, Humboldt University Berlin (MfN HUB, HBSB, Zool. Mus., B I/2078). In the background an oyster shell from Houlgate, Côte Fleurie, Normandie, France, riddled with bioerosion traces produced by *Cliona celata*. Scale in cm

a sponge. Since the description of *Cliona celata* a wave of nominations of new species of bioeroding sponges was triggered and this curious group of poriferans attracted the interest of many scientists. This quickly led to the next question: if the sponges are found inside substrates harder than their own tissue, do they actively erode?

Mid to late 1800s: Does the sponge make the hole it occupies or is it a squatter?

In the mid 1800s the intense discussion erupted: does the sponge itself produce cavities or does it invade spaces created by other organisms (e.g., Ehrenberg 1834: 62): *'Ostreas perforans. An perforatas occupans?'* (Translation: Perforating in oysters. Or occupying perforations?) Several authors assumed at an early stage that the sponges were able to erode, e.g., Osler (1826), Nardo (1839), Bianconi (1841) and Lereboullet (1841: 131): *'Il est probable que les galeries tapissées par l'Éponge ont été creusées par cette substance animale elle-même'*. (Translation: 'It is likely that the chambers that are coated with the sponge were eroded by the animal substance itself.')

Others claimed that the sponges invaded spaces created by various other eroding organisms, especially by worms. Grant (1826: 78 and 81) set precedence by reasoning that the cavities were *'perforated by some marine worms'* and only inhabited by the sponge as a nestler. But he allowed that perhaps *'the sharp siliceous specula, and constant currents of its papillae'* in the organism provided some means *'in forming or enlarging the inhabitation of this zoophyte'*. Duvernoy (1839: 685) could not imagine how the sponges should be able to erode by themselves: *'Ici les moyens mécanique sont évidemment nuls. Il n'y a que les moyens chimiques qui puissent être mis en jeu par un organisme privé de toute espèce de force motrice apparente.'* (Translation: 'Here, the mechanic means are obviously nil. Only chemical means can be employed by an organism entirely withdrawn from any species by an obvious driving force.') Dujardin (1838b: 5) thought the cavities were made by sabellids: *'...occupant dans les pierres calcaires, des trous qu'elle n'a pas creusés, mais qui sont dus à une Sabelle trouvée souvent dans les mêmes pierres...'* (Translation: '... occupies calcareous stones and holes that it did not erode, but which are due to a sabellid often found in the same stones...').

Bowerbank (1866: 215-217; Fig. 3D) passionately held the view that the sponges nestled in excavations left by annelids and explained in detail: '*...lithodomus Annelids which probably excavated the tortuous passages which have subsequently been taken possession of by the sponge.* [...] *There is no British sponge regarding which there has existed a greater diversity of opinion than the present subject of investigation, and this is, perhaps, in a great measure due to the singularity of its habit, in selection the perforations of lithodomus annelids, and other marine animals as its habitation, and very few oyster or other shells in which such perforations exist, are free from this parasitical sponge, but it does not confine itself to the sinuous canals thus formed; if they happen to open into the bases of large parasitic Balani attached to the shell, the whole of the interiour of the Balani become coated with the sponge, and in the excavated stones of Tenby it frequently entirely fills the smaller*

cavities, or completely coats the larger one made by the lithodomus molluscs so abundant in the surfaces of the limestone rocks between high and low-water marks in those districts.'

Waller (1871: 269) was utterly mystified how people could believe in bioeroding sponges: *'The errors and the dreams of science have been numerous. We have had the flints on the upper chalk formation attempted to be accounted for as the coprolites of whales; the 16th and 17th century gives us the wonderful story of the goose which developed from barnacles, and now we have a 'burrowing or boring sponge.'* […] *It is extraordinary how completely it has been accepted, and how widely disseminated.'* Waller (1871, 1881) agreed with Bowerbank and insisted that bioeroding sponges are nestlers. He pointed out encrusting sponges that live in a similar situation, but do not erode, claiming that it is extremely unlikely that only *Cliona* should be able to dissolve carbonate materials. Regrettably he overlooked that he had already minutely studied more than one species of bioeroding sponges, not noticing the difference between the spicules: *C. celata* with subterminal tylostyles (Waller 1871) and an *Aka* with smooth oxeas (Waller 1881). He observed the surprising accuracy of the scalloped, excavated walls, marvelled at the precision of the erosion scars and noted that *'a thin membrane* [of sponge tissue] *overlies the work described, having upon it its spicules'* and accurately portrayed the papillar spicule palisades (Waller 1881: 257; Fig 4).

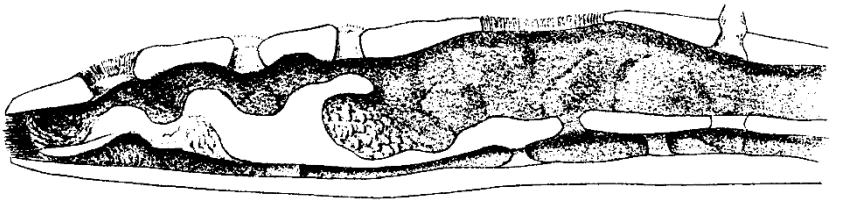


Fig. 4 Sponge traces *Entobia* of *Cliona celata* as observed by Waller (1871: pl. 20, fig. 1). Despite accurately representing the morphology of the erosion and the arrangement of the sponge tissue in the cavities, Waller believed the chambers to be the product of worms

Nevertheless, he was unable to see spicules arranged in a way that would suggest mechanical erosion. Waller considered and rejected three possible pathways of erosion:

1. Acid – he regarded the necessary self-protection of the sponge as unlikely.
2. Wear by soft tissue – the observed sharp edges of the sponge scars did not quite agree with this hypothesis.
3. Wear by hard tissue – he found that the spicules were arranged in parallel to the substrate, and he could not find linear or angular traces of scraping that would reflect the grinding of hard materials.

Waller also thought this ineffective (1871: 272): *'To my mind this process would be as effectual as mining the tunnel of Mont Cenis with darning needles.'* In the same publication (1871: 269) he lectured: *'There is nothing more commonly witnessed in*

historical literature, or in the records of science than the persistence of error. This is especially the case if it contains something of the romantic or of the marvellous. A writer of credit puts forward a statement; he may, or he may not, give an authority for it: let it be accepted without dispute, it gets copied by one writer after another and passes as an established feat. At length an inquisitive eye, by chance perhaps, happens to refer to the authorities, and it is found, either that they are inconclusive, or, as it has often happened, absolutely disprove the statement which has long been accredited. In fact, though it is not flattering, man has much of a sheep in his composition, and likes to follow a bell-weather.' Overall, Waller blamed annelid larvae and rejected the concept of bioerosion by sponges (1881: 265): *'It is my hope that the subject may now be definitely settled, for, in friendly warfare, both victor and vanquished are gainers equally in the contest, when the struggle is not for victory but for truth.'*

Hancock (1848, 1849a, b, 1867) was just as unsure about the exact means of erosion as were the above authors, but presented observations that clearly supported that the sponges were able to actively erode calcium carbonate. He hotly and sometimes scathingly defended their excavating powers against the views of other scientists. His arguments were (1849a, 1867):

1. Healthy sponges always fill the entire excavation.
2. Their traces were observed in different materials and geological periods.
3. Observations involved different growth stages and a variety of sponge species that share common, but complicated, partly species-specific erosion traces (sponge scars = 'shagreen', globular and connected cavities = 'lobes' (Fig. 5), a specific number of papillar openings).
4. Sponge erosion clearly differs from worm traces, latter are tubular and have smooth surfaces.
5. Why should sponges not be able to erode hard substrate if the ability has been accepted for other groups?
6. Sponges have chips in their tissues that they have obviously removed from the substrate.

Hancock (1867: 232) challenged: *'But here, again, we are unfortunately at issue with Dr. Bowerbank* [1866]*, who asserts that these burrows are made by 'lithodomous Annelids'* [...] *the sponge is lodged, being moulded, in fact, in worm-burrows.* [...] *It may* [...] *be asked how it is that, while* C. celata *is found in vast abundance on our coasts* [...] *the worm or annelid assumed to have made the cavities has never yet been determined.'* And (1867: 234): *'...or that the worm made the openings purposely, in strict accordance with the requirements of the sponge that in some future day might take up its abode in the deserted excavation?'* He observed that it was more likely to find bioeroding sponges in larger oyster shells than in smaller ones, the sponge sometimes conquering the oyster with gregarious growth and simultaneously weakening its own dwelling (Hancock 1849a: 323): *'...the whole system of elaborately wrought chambers becoming exposed soon gives way, and* Cliona*, Sampson-like perishes amidst the ruin produced by its own energy.'* He resolutely stated (1849a: 327): *'...it would seem impossible to arrive at any other conclusion.'*

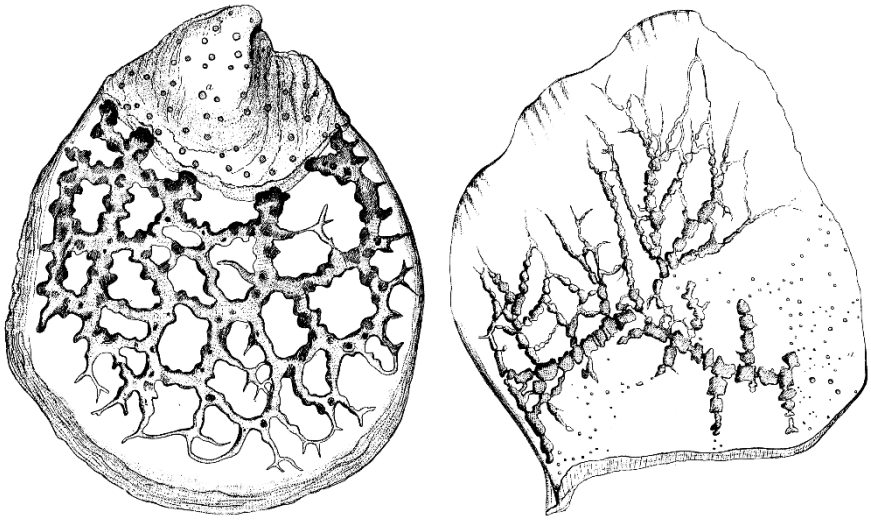


Fig. 5 Sponge traces *Entobia* of *Cliona celata* (left) and *Cliona corallinoides* (= *Pione vastifica*; right) according to Hancock (1849a: pl. 13, fig. 3 and pl. 15, fig. 1). He recognised that even though sponge traces differ between species, the underlying principles are the same

Schmidt (1862: 77) shared Hancock's opinion but reserved the possibility that the sponges may also benefit from existing pores: *'Daß die Vioen sich vorzugsweise selbst ihre Wohnhöhlen bilden, ist bei manchen Arten schon aus der regelmäßigen Stellung der Ausströmungslöcher in Reihen ersichtlich. Jedoch scheinen manche Arten auch schon vorhandene Bohrlöcher zu benutzen,...'*. (Translation: 'That the vioas preferentially make their own dwelling cavities is visible in some species that have a regular arrangement of the exhalant pores in rows. However, some species also appear to utilise already existing erosion cavities,...')

After first supporting Bowerbank's view, Priest (1881a, b: 270-271) convinced himself of the sponges' activities: *'Even though Dr. Bowerbank himself tells us that very few oyster, or other shells in which the perforations exist, are free from this Sponge, and yet he is trying hard to prove that it is only as a parasite that it exists in them. It seems strange to me that, if such is the case, the same species or class of Sponge should almost always be found to occupy those cavities.* […] *As I said before, I certainly agreed with Dr. Bowerbank until I came across shells where the cavities ramified right and left into such fine processes, and those cavities being filled with the Sponge I could not at all make the burrowing of Annelids agree with them'*. He may also be the first to provide evidence for variability in the diameters of sponge scars (Fig. 6). Hyatt's (1882: 83) views were very similar. He explicitly pointed out the differences between sponge and worm erosion traces and argued: *'*[…] *large annelids* […] *are, from the character of their jaws, incapable of cutting such depressions, and moreover, from their size, unable even to enter the burrows.'*

Leidy (1856; Fig. 3E) also believed that the sponges were capable of bioerosion. He summarised some of the opposing views, but did not make clear whose opinion he shared (Leidy 1889). In the end, Hancock won through and was supported by

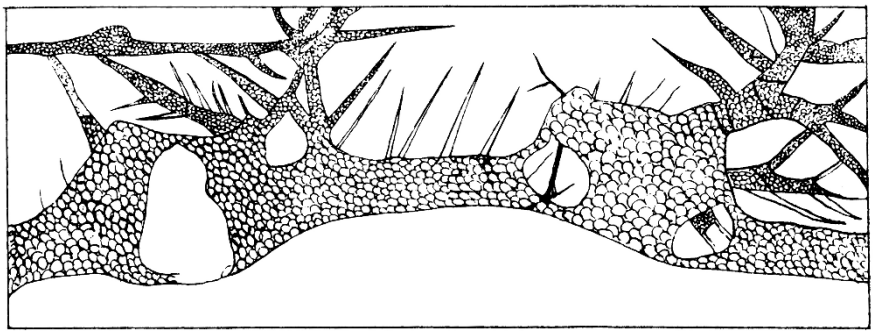


Fig. 6 Erosion traces of an unknown sponge (trace: *Entobia*) in a *Haliotis* shell (Priest 1881a: pl. 17, fig. 6). The author fairly accurately represented main chambers with pitting by sponge scars, connecting canals and very fine pioneering canals. It is interesting to note that even at this early stage, Priest recognised the different diameters of sponge scars in central areas of the erosion (larger) and in pioneering areas (smaller)

later studies. Nasonov's (1881, 1883; Fig. 3F) outstanding, detailed and accurate observations on the settling of clionaid larvae described very clearly that cell extensions were in contact with circular fissures and that they removed ellipsoidal bodies from the substrate that were expelled by the sponge (Fig. 7). Topsent's (Fig. 3G) excellent PhD thesis (1888) added to this evidence and pictured sponge chips more accurately than Nasonov. Topsent recognised that chips removed from surfaces already scalloped by sponge erosion have concave facettes on their upper surfaces (Fig. 8A). He also noted the difference in the sponge scars of the main erosion chambers and pioneer areas (Fig. 8B).

By the end of the 19th century it was largely established that the sponges were actively eroding calcium carbonate substrates (e.g., Hinde 1883; Nasonov 1883; Topsent 1888; Keller 1891; Topsent 1900). However, this decision increasingly

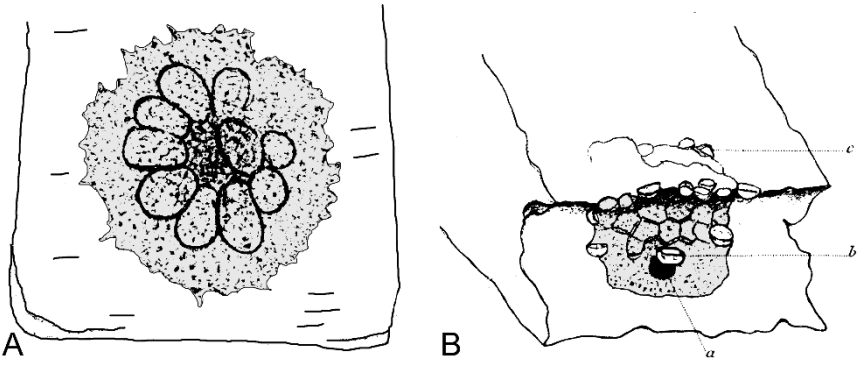


Fig. 7 Initial erosion traces of *Clione stationis* (Nasonov, 1883: pl. 18, figs. 4-5) (= *Pione vastifica*), the figure was manually enhanced. **A** A larva shortly after settling on a transparent calcium carbonate fragment. It can be clearly seen that at this early stage of development fissures for the removal of sponge chips are already cut. **B** Similar situation with a sponge scar (a) from which a sponge chip is being removed (b). On the upper surface sponge tissue can be seen through the transparent material, showing filipods and threads (c) that reach into freshly cut fissures. At this stage the sponge does not yet have spicules

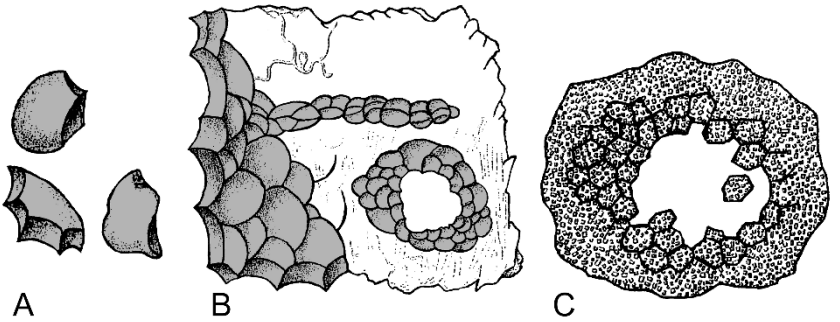


Fig. 8 Sponge erosion as illustrated by Topsent (1888: pl. 3, fig. 13 and pl. 4, figs. 1, 3), the figure was manually enhanced. **A** Sponge chips (grey) figured with smooth, convex basal sides and concave-facetted sides nearer the sponge tissue. **B**-**C** Sponge scars (grey) in calcium carbonate substrate (B) and conchiolin (C). B Note the difference in diameter in established areas of erosion (left) and pioneering regions (extending towards right and circular area)

provoked the question: how? Nasonov (1887: 362) suggested that different species may have different ways to erode and noted with sorrow: *'Malgré l'intérêt que présente cette particularité au point de vue scientifique comme au point de vue pratique biologique, elle n'a pas étudié avec tous le soin désirable'*. (Translation: 'Despite the interest of this peculiarity, both in scientific and practical biological context, it has not been studied with the desired care.') But more research was about to be published.

Mid 1800s to early 2000s: How does the sponge make the hole?

Accepting that sponges are able to erode, it still could not be explained how they achieve this. Several possibilities were hotly discussed: mechanical erosion by scraping of spicules or other particles, by wear with the soft tissue, including the removal of fragments by traction, erosion with water jets created by the pumping, chemical erosion through the action of acid or other agents and any combination of the above. Early opinions tended to favour mechanical erosion and occasionally mused over possibilities of additional means. Bate (1849: 74) proposed: *'Cliona first obtains a footing in some crevice, where it developes itself so as to penetrate the whole fabric, destroying the shell or pebble by simply fulfilling the condition of its existence, which is by pouring its currents in a given direction, until a passage be broken through by the corroding power of the carbonic acid in those currents.'* Hancock (1848: 243) supported mechanical erosion: *'...there can be no doubt that* [the cavities] *are the work of this creature, most probably aided by its siliceous spicula, which penetrating the surface* [have] *the character of rasping-paper.* […] *The excavations* [...] *can only be effected by the surface of the sponge, aided either by minute mechanical instruments in connexion with it, or by a solvent'*. He discounted the possibility that water jets are used to dig into the substrate. If a chemical was used, he reasoned it should be exuded from the entire surface of *'this humble animal'* with its *'extreme simplicity of the organic structure'* (Hancock 1849a: 328). But he did not think it could be acid, doubting that the sharp-edged, replicate structures of the sponge scars could have been the product of etching. He

reflected that the occurrence of particles (sponge chips) in the tissue was evidence for mechanical means of erosion, the tool being either the sponge spicules or large acid-resistant crystals he noticed on preparations (Hancock 1849a, 1867). However, Nasonov (1881, 1883) found sponge erosion to proceed before sponge spicules were formed. The hypothesis of mechanical erosion with crystals was also supported by Fischer (1868), but the structures represented an artefact: According to Waller (1871: 273), Hancock observed *'only disintegrated cells of carbonate of lime'* (remains of sponge chips?). It is more likely, however, that the structures he found were the yellow crystals that sometimes form in saturated nitric acid digestions – Leidy (1889) had thus difficulties to find them.

Letellier (1894) presented a new possibility for mechanical erosion and claimed that the sponge created traction with tissue contractions to break off small particles. Topsent (1894: 11) discussed the feasibility of this idea: *'La question est évidemment de savoir si les fragments de calcaire ou de conchyoline que détache l'Èponge pour s'enfoncer dans son support sont extirpés par simple traction ou, au contraire, découpés et façonnés.'* (Translation: 'The question is obviously to know if the fragments of limestone or conchiolin that are detached as the sponge subsides into its support are torn out by simple traction or, in contrast, cut out and formed.') He further pointed out politely that the observed minute fragments are unlikely the outcome of tearing by the entire body of tissue. Then, becoming less polite, he suggested that Letellier (1894) had based his idea on a hypothesis without any direct

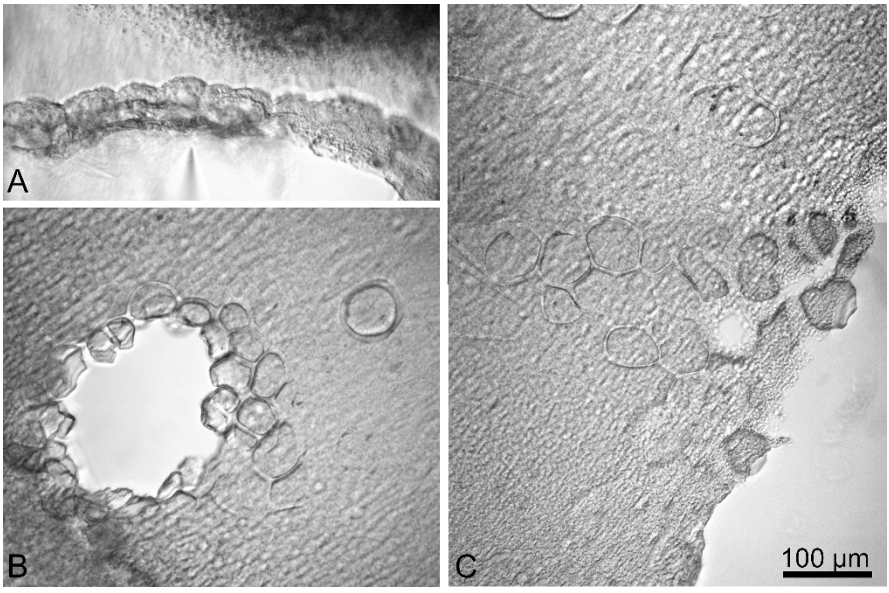


Fig. 9 Bioerosion traces in the conchiolin of a bivalve, produced by an unknown *Pione* species (Topsent sample from the Paris Museum). **A** Edge of an area, where a thick layer of conchiolin was entirely penetrated. **B** Small hole in conchiolin with partially freed chips and beginning etching grooves. Small chip diameters suggest that this is a marginal, pioneering erosion area. **C** Partial etching grooves with larger diameters in a more central area of the sample. Scale bar applies for A-C

observations supporting it. Topsent was unable to offer a better explanation, but he argued that the force needed to tear fragments out of nacre should be too large for tissue acting in parallel to its surface. Finally he firmly declared that the very specifically shaped sponge chips could not be the product of a general tearing action that would usually result in larger, more irregularly formed particles corresponding to the layering characteristics of a given shell. Also, sponge chips always have the same form, regardless of the material they stem from, calcareous material or conchiolin (Figs. 8-9).

The use of acid was repeatedly proposed, sometimes as the only means of erosion (e.g., Parfitt 1871). Several scientists tried to detect acid secretion in bioeroding sponges, but failed (Table 1). Some of them reflected that the reason might be very local application of the etching agent (Cotte 1902; Hatch 1980). Warburton (1958: 561-562) mused: *'... an acid, or some other solvent, is secreted in minute quantities by the threads of cytoplasm* […] *carving out blocks with acid dispensed from a pipette.'* Other scientists suggested that instead of acid other chemicals might be used (Pomponi 1979a; Hatch 1980; Pomponi 1980). Nasonov (1883: 300) reasoned that a combined chemical-mechanical erosion was most likely: *'Auf diese Weise übt in diesem Falle der Schwamm zugleich eine chemische und mechanische Zerstörungswirkung aus, wodurch er bedeutend viel weniger Kraft aufwendet. Anstatt jedes einzelne Kalkpartikelchen gänzlich aufzulösen, löst er eine dünne Kalkschicht auf, die der konvexen Oberfläche des Partikelchens entspricht.'* (Translation: 'In this manner the sponge simultaneously affects chemical and mechanic destruction and in consequence needs to spend significantly less energy. Instead of entirely dissolving each separate little chalk particle it etches a thin layer of chalk that matches the convex surface of the little particle.') He thought that the etching agent is probably acid.

In 1924 Nasonov described how larvae of *Clione stationis* (Nasonov, 1883) (= *Pione vastifica*) settle on oyster shells and actively penetrate the surface of the carbonate, eventually proceeding inwards, the scars then covering all internal walls of the endolithic cavities. He again concluded that sponge erosion is partially chemical as it can dissolve calcium carbonate and conchiolin. Other authors agreed (e.g., Vosmaer 1933; Fig. 3H; Old 1942), but the agent still remained unknown (e.g., Otter 1937).

Table 1 Previous attempts to ascertain the existence of acid as etching agent in bioeroding sponges

Experimental approach	Author	Year
failed to detect acid when applying sponge extracts to litmus paper	Hancock	1849a
failed to detect acid, but believed the sponge obtains it from the seawater	Parfitt	1871
failed to detect a lowered pH in the sponge culture water using indicator solutions	Cotte	1902
detected an increase in dissolved calcium carbonate	Old	1942
failed to detect a lowered pH, could not demonstrate increase in dissolved calcium carbonate, argumented that it may be applied very locally	Warburton	1958
observed flocculent material of unknown nature	Rützler and Rieger	1973

Roughly between 1970 and 1980 the most significant experimental results with regards to sponge bioerosion were generated. In 1969, Cobb provided excellent summaries and new data and urged not to forget the earlier findings of particles cut out by the sponges that indicated that part of the erosion must be mechanical by removal of these fragments (Nasonov 1881, 1883; Cotte 1902; Warburton 1958). He experimentally confirmed Nasonov's (1883, 1924) results by using explants of *Cliona celata*, a method established by Warburton (1958). Cobb (1969: 785) detected about 1 µm wide, cup-shaped fissures around unfinished sponge chips. After staining the tissue next to them and finding it to reach into the fissures, he proposed amoebocytes with *'prominent nucleus and nucleolus and numerous basophilic granules'* to be responsible for the etchings. Following Pomponi 1979b, Cobb probably chose the wrong cell type, i.e., osmiophilic cells that are closely associated with etching cells; see also Cotte (1902) for *Pione vastifica* (Hancock, 1849) and Rützler and Rieger (1973) for *Pione lampa* (de Laubenfels, 1950). Cobb (1969) concluded that one cell produced one scar. Several cells together remove the resulting chip of calcium carbonate, a chip with the characteristic shape of a smooth convex lower half and a facetted upper side. He noted that calcite and aragonite substrates with different organic content as well as conchiolin layers in bivalve shells and *Mytilus* Linnaeus, 1758 periostracum were eroded in the same manner (Figs. 8-9), but that possibly the chip-size varied with substrate. Agreeing with Cotte (1902), Warburton (1958) and Vosmaer (1933), Cobb further reasoned that the ability to dissolve mineral and organic materials suggests the secretion of acid and an additional enzyme, but he could not be more precise. Cobb (1969, 1975) was the first to coin the expression 'sponge chip' and to describe the terraced microstructure of concentric rings within *Cliona* erosion scars, which he ascribed to intermittent activity of the etching cells and which differed between substrate types.

Cobb's work was supported by the excellent studies of Rützler and Rieger (1973) on *Pione lampa*. However, whereas Cobb's (1969) data suggested that in *Cliona celata* one chip is excavated by a single cell etching along its edges, *Pione lampa* chips are made by several cells contributing with a web of filopods that form a basket to lift out the chip. This is an observation, which was already made by Warburton (1958: 560): *'network of thread-like interconnections and pseudopodia, often 50 µ or more long'*. Etching cells undergo cytoplasmolysis during very localised etching and the removal of chips and produce a *'flocculent secretory product'* that was not identified (Rützler and Rieger 1973: 158). However, Rützler and Rieger allowed (1973: 159): *'it is quite possible that the cell types, organelles, and secretory products involved vary among species'*, which appears to be the case when their observations from *P. lampa* are compared to those from *C. celata* (Cobb 1969).

Despite ongoing disagreements over the exact mechanisms, research came full cycle since Nasonov (1881, 1883) and the basic concept was finally sustained by the late 1970s: *'The most tenable mechanism is the combination of a localized chemical dissolution coupled with mechanical dislodging of fragments of the substratum and their subsequent transport out of the sponge galleries* [...] *the mechanism of excavation involves a localized modification of the calcium carbonate solubility*

equilibrium' (Hatch 1980: 135-136). Pomponi (1977, 1979a-c) conducted excellent research on the ultrastructure of the etching cells of 11 different species of bioeroding sponges. The etching cells of these species have a diameter of 10 x 5 µm and processes of 0.25 x 3-20 µm with a high degree of coordination (Pomponi 1977, 1979b). They contain *'an anucleolate nucleolus, Golgi, mitochondria, well-developed rough endoplasmatic reticulum, phagosomes, glycogen granules, and numerous vacuoles'* (Pomponi 1977: 485) and are capable of *'protein synthesis, secretion, absorption and intracellular digestion'* (Pomponi 1979b: 777). Pomponi's (1979a, c) enzyme essays supplemented Hatch's results (1980; see below) that were available to Pomponi in the form of his 1975 PhD thesis. She found carbonic anhydrase activity was associated with etching cell bodies, their processes and spaces between the processes, whereas acid phosphatase activity was most intense on the outer surfaces of the cell processes, but also detectable in cell organelles. She reasoned that phosphatase was involved in the extra- and intracellular digestion of organic components of the substrate, carbonic anhydrase in the dissolution of mineral materials. In her 1980 publication, Pomponi summarised all of the above and put it into a larger context, also pointing out the resemblance between sponge bioerosion and osteoclast bone resorption.

Hatch (1980) first provided biochemical evidence of the enzyme carbonic anhydrase being involved in the shifting of the carbonate equilibrium. Papillate sponges showed slightly higher enzyme activity than encrusting sponges of the *Cliona celata* species complex. Respective free-living specimens exhibited strong enzyme activity in the cortex, but a significantly reduced rate of activity in inner parts. Enzyme inhibition caused a decrease in erosion activity, as evidenced by chip production. He discussed the possibilities that carbonic anhydrase may be responsible for:

1. transporting hydrogen ions across membranes; or
2. exchanging hydrogen ions for bicarbonate ions, lowering the pH and consequently substrate dissolution; or
3. providing a pH optimum for other chemical processes possibly involving chelators or other enzymes.

When studying secondary metabolites, Sullivan and Faulkner (1990) were able to demonstrate the occurrence of calcium chelators in *Aka coralliphaga* (Rützler, 1971). Various siphonodictyals of this sponge were able to bind calcium ions and removed them from the test solution. The authors displayed the reaction as a cycle in which the chelator molecule releases H^+ and receives calcium ions at the site of dissolution and releases calcium into the water column in exchange for a new H^+ ion (Sullivan and Faulkner 1990: fig. 4). Therefore, in this pathway of erosion a lowering of pH would be involved at the sponge-substrate interface. This exciting discovery has since largely been overlooked and has not been shown for any other bioeroding sponge.

Considering the proportion of chemical etching of the crevices around the chips compared to the mechanical removal of the chips, several authors presented different estimates. Warburton (1958) failed to detect an increase in the calcium carbonate

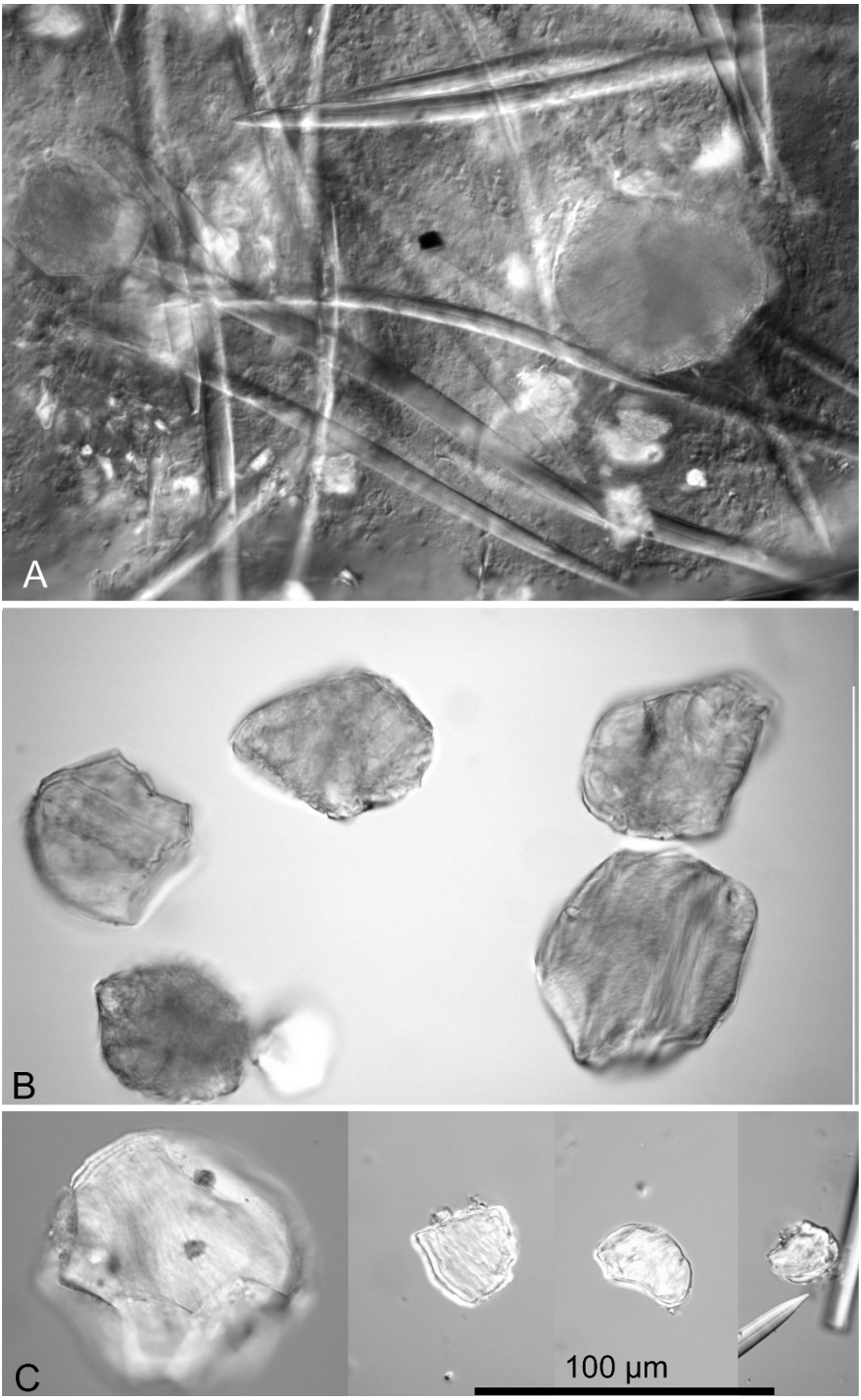
content of his experimental dishes containing *Cliona celata* (Table 1) and deducted that the share of chemical dissolution should be less than 10%. Judging from the width of the etched crevice and the size of the freed sponge chips, Rützler and Rieger (1973) reasoned that 2-3% of the eroded material is chemically dissolved and 97-98% mechanically removed. Very recently, Zundelevich et al. (2007) experimentally evaluated changes in total alkalinity and the amount of expelled chips of *Pione* cf. *vastifica* and concluded that volumes removed by chemical dissolution were three times that of volumes removed as chips. This is an enormous difference compared to earlier estimates and may be related to the fact that Zundelevich et al. (2007) did not consider that a certain amount of chips at least temporarily remains within the tissue of bioeroding sponges (e.g., Warburton 1958; Fig. 10A). However, the erosion traces of *P.* cf. *vastifica* markedly differed from almost all other observations, except for one case of *Aka* sp. (Calcinai et al. 2003: fig. 1E; Calcinai et al. 2004: fig. 4C). Therefore, *P.* cf. *vastifica* and perhaps Calcinai's *Aka* sp. rely much stronger on chemical erosion than most other known bioeroding sponges. Moreover, the role of chemical etching may shift with changing environments (e.g., with ocean acidification).

The above account demonstrates how much effort has been invested into resolving the question of the etching agent, with research on the mechanisms of sponge erosion spanning a period over 180 years (from Grant 1826 and Osler 1826 to Zundelevich et al. 2007). Nevertheless, we still do not know which exact chemical agent sponges use.

Late 1900s to early 2000s: The larger picture – what does sponge bioerosion mean within the system?

Bioeroding sponges attack biogenic calcium carbonate substrates such as corals, mollusc and barnacle shells, and coralline algae (e.g., Hartman 1958; Hoeksema 1983; Mao Che et al. 1996), composite materials containing calcium carbonate and organic materials (e.g., Hoeksema 1983; Schönberg 2002a), natural limestone (e.g., Hoeksema 1983), and even man-made substrates (Scott et al. 1988; Brusco et al. 2005). They cannot penetrate stylolites (Hoeksema 1983), and are slowed down by organic layers such as conchiolin (Nasonov 1924; Old 1942; Warburton 1958; Cobb 1969, 1975; Hoeksema 1983). Encrusting species of bioeroding sponges can overpower live organisms such as neighbouring corals (Schönberg and Wilkinson 2001; Rützler 2002; López-Victoria and Zea 2004; López-Victoria et al. 2006). Avoidance reactions have been described for *Cliona celata* encountering *Polydora* Bosc, 1802 tunnels (Hoeksema 1983) and another individual of *C. celata* (Bromley and Tendal 1973), creating stunted patterns in bioerosion. However, *Cliona mucronata* Sollas, 1878 often appears to mingle much more closely with other species of *Cliona* (Sollas 1878; and *Cliona ecaudis* Topsent, 1932; Schönberg pers. obs. in several preparations made by Topsent, at the Paris Museum).

Fig. 10 Sponge chips of *Aka mucosa* (Bergquist, 1965) from Orpheus Island, Palm Island Group, central Great Barrier Reef, Australia. **A** A considerable amount of sponge chips can be found in the endosome of the sponge. **B** Chips of relatively uniform size, but variable shape. **C** Chips of different size. Scale bar applies for A-C


A
B
C
100 µm

A variety of field observations and experimental results became available. They largely ignored the 'how', but focused on estimating rates (erosion: Neumann 1966; Hein and Risk 1975; Rützler 1975; Bak 1976; Hudson 1977; Moore and Shedd 1977; Scoffin et al. 1980; Acker and Risk 1985; Kiene and Hutchings 1992, 1994; Peyrot-Clausade et al. 1999; Pari et al. 2002; Schönberg 2002b; Hutchings et al. 2005; Osnorno et al. 2005; Zundelevich et al. 2007; sediment production: Goreau and Hartman 1963; Neumann 1966; Fütterer 1974; Scoffin et al. 1980; Acker and Risk 1985; Rose and Risk 1985; Young and Nelson 1985; Adjas et al. 1990; Siegrist et al. 1991; Peyrot-Clausade et al. 1999) and pointing out controls and consequences. Sponge bioerosion and the abundance of bioeroding sponges appear to be related to:

1. water flow (de Laubenfels 1950b and Rützler 1975 for *Pione lampa*; Hatch 1980 for *Cliona celata*; Carballo et al. 1996 for *C. celata* and *Cliona viridis* (Schmidt, 1862); López-Victoria and Zea 2005 for *Cliona tenuis* Zea and Weil, 2003 and *Cliona caribbaea* Carter, 1882);
2. nutrient or sewage concentration (Rose and Risk 1985 for *Cliona delitrix* Pang, 1973; Carballo et al. 1996 for *C. celata* and *Cliona viridis*; Muricy 1991 for *C. celata*; Sammarco and Risk 1990; Edinger and Risk 1997; Schönberg et al. 1997; Hutchings et al. 2005 and Osnorno et al. 2005 for bioeroding sponges on the Great Barrier Reef; Holmes 1997, 2000 for Caribbean bioeroding sponges; Holmes et al. 2000 for bioeroding sponges in Indonesia; Rützler 2002 for *Cliona* cf. *caribbaea* and *Pione lampa*; Ward-Paige et al. 2005 for Caribbean *Cliona delitrix* and *Pione lampa*; but also see López-Victoria and Zea 2005 for Caribbean sponges of the *Cliona viridis* species complex);
3. substrate density (Highsmith 1981a and b; Highsmith et al. 1983; Rose and Risk 1985 for bioeroding sponges in the Pacific and Caribbean; Sammarco et al. 1987; Edinger and Risk 1997 for bioeroding sponges on the Great Barrier Reef; Schönberg 2002b for *Cliona orientalis* Thiele, 1900);
4. salinity (Hopkins 1956; Hartman 1958 – showed that lower temperatures increased tolerances against lowered salinities for *C. celata* and *P. vastifica*; Wells 1959, 1961 for *Cliona celata* and various species of *Pione* Gray, 1867; Hopkins 1962);
5. temperature: bioerosion activity of Massachusetts *C. celata* ceased in temperatures below 13°C, but could artificially be maintained by raising the tank temperature above ambient winter conditions (Cobb 1975). Bioerosion rates of *Pione* cf. *vastifica* in the Red Sea varies with season and is lower in cooler waters of the Red Sea (Zundelevich et al. 2007). Bioeroding sponges are more likely to overpower live coral in heat and cold temperature-stress environments (Rützler 2002);
6. light (Rützler 1975), especially if the sponge is symbiotic (Uriz et al. 1992; Hill 1996; Schönberg 2001, 2006; López-Victoria and Zea 2005). But the symbiotic *P.* cf. *vastifica* did not show difference in day and night erosion rates (Zundelevich et al. 2007; see also experimental study described below);

7. water depth (Goreau and Hartman 1963; Acker and Risk 1985; Kobluk and Kozelj 1985; Uriz et al. 1992; Reed and Pomponi 1997; Hill 1999; Schönberg 2001; López-Victoria and Zea 2005);
8. trauma (Rützler 1975; Thomas 1997);
9. general stress situations acting on reef organisms that are more weakened in comparison to bioeroding sponges (Rützler 2002; Márquez et al. 2006; Schönberg and Suwa in press); and
10. age / size of the sponge, i.e., whether a larva or fragment is freshly settling or attaching (fast growth and erosion) or whether it is an established colony (slow growth, less erosion) (Neumann 1966; Rützler 1975).

2000 to today: Sponge bioerosion traces – can they be used in taxonomy and how do they relate to the etching process?

Macroscopic patterns of sponge bioerosion traces (*Entobia* Bronn, 1837) have traditionally been used for taxonomic purposes in detailed descriptions (e.g., Rützler 1974) or for morphometric approaches (e.g., Hoeksema 1983; Rose and Risk 1985; Rosell 1994). However, a considerable range of overlap exists, i.e., one sponge species can produce more than one kind of trace and one trace can be the result of the action of different sponge species (Bromley and D'Alessandro 1984, 1989; see also Calcinai et al. this volume, in press).

More recent approaches focused on the microscopic traces: sponge chips and scars. Originally Rützler and Rieger (1973: table 2) noted considerable variation in the size range of these structures, but thought this may be more strongly related to circumstances than to taxonomy. Their chip diameters ranged from 15 to 71 µm for clionaids, with respective scar diameters of 18-94 µm. Schönberg (2000) agreed that mean sponge chip diameters provide insufficient information for species distinction within the clionaids, but allowed restricted usefulness to distinguish genera, with mean chip diameters from *Aka mucosa* (Bergquist, 1965) being noticeably larger (45 µm) than those from *Zyzzya criceta* Schönberg, 2000 (30 µm) and the 5 studied clionaids (30-35 µm). However, sponge chip and sponge scar sizes are subject to location within the cavity (larger diameters in central, established regions, smaller diameters in pioneer regions; Figs. 6, 8, 10; see also Rützler and Rieger 1973; Ward and Risk 1977; Calcinai et al. 2004). They may also vary with substrate type (Rützler and Rieger 1973; Pomponi 1976). Pomponi (1976) was the first to note differences in the microstructure of sponge scars between genera. Italian and French scientists proposed the use of these patterns for taxonomic purposes (Omnes 1991; Bavestrello et al. 1996; Calcinai et al. 2003, 2004; Borchiellini et al. 2004). Clionaid scars are much smoother, less size-variable and more concentric in outline than scars produced by *Aka* (Pomponi 1976; Calcinai et al. 2003, 2004). *Aka* de Laubenfels, 1936, *Holoxea* Topsent, 1892, *Spiroxya* Topsent, 1896, *Alectona* Carter, 1879, *Delectona* de Laubenfels, 1936 and *Thoosa* Hancock, 1849 produce scars with concentric rings, i.e., microterracing (Pomponi 1976; Calcinai et al. 2003, 2004; Borchiellini et al. 2004). *Alectona* exhibits radial lines overlying the circular grooves (Omnes 1991; Vacelet 1999; Calcinai et al. 2004; Borchiellini et al. 2004). Despite these consistent reports above, comparisons should only be conducted using traces from the same kind

of substrate. Even though clionaids are said to erode smooth scar-walls, concentric groves have been observed in clionaid scars in bivalve shells, presumably caused by the alternating layers of calcium carbonate and conchiolin (Cobb 1975), but also in the very homogeneous substrate of Iceland spar (Cobb 1969 for *Cliona celata*; Rützler and Rieger 1973 for *Pione lampa*). Similar variations to the basic patterns may be observed in a wider range of substrate types and environmental situations (Pomponi 1976). Recently Zundelevich et al. (2007) found sponge scars in which a central knob of material remained standing. This microtrace is presently only known for the Red Sea *Pione* they used and which appears to be closely related to *Pione vastifica*, and for *Aka* sp. from Indonesia (Calcinai et al. 2003, 2004).

Very recently, Calcinai et al. (this volume, in press) studied erosion traces of a single species (*Cliona albimarginata* Calcinai, Bavestrello and Cerrano, 2005) in different types of substrata. They came to the conclusion that while microsculpturing of scars remained the same in different substrates, other microscopic traces (diameter of sponge scars) and macroscopic traces (*Entobia*) can vary between substrates. This is in part caused by the substrate microtexture (orientation of the calcium carbonate crystals) and in part by its mineralogy (Calcinai et al. this volume).

One alleged consequence of sponge erosion is the phenomenon of the putative growth 'phases' of bioeroding sponges: initial alpha-papillate, later beta-encrusting and last gamma-massive, free-living morphology (Topsent 1888; Topsent 1900; Vosmaer 1933; Hartman 1958). This principle has been studied in most detail in *Cliona celata* in the Atlantic, where the sponge can be found in all three forms. It has also been postulated for species of the *Cliona viridis* group (e.g., *C. viridis* being the papillate growth stage of *Cliona nigricans* (Schmidt, 1862) in massive growth, e.g., Rosell and Uriz 1991). It is important to note, however, that

1. no sponge has ever been monitored from larval settlement to free-living sponge, and the principle was never experimentally confirmed (see Hartman 1958),
2. not all growth forms can be found in all habitats (no gamma form bioeroding sponges observed on the Great Barrier Reef, C. Schönberg pers. obs.; no beta and gamma form of *C. viridis* group sponges found in Japan, Y. Ise pers. comm.; Mediterranean gamma form *C. celata* only in deep water, T. Perez pers. comm.),
3. some growth 'phases' are lacking or do not very commonly occur in distinctive morphology (e.g., the fully encrusting beta form for *Cliona viridis / nigricans* in the Mediterranean), and
4. most known species of bioeroding sponges retain the alpha growth form, even when occurring in small, restrictive substrates (e.g., Hartman 1958).

There are also physiological observations that may indicate that different growth forms may represent different species. Gamma form sponges of *C. celata* have been shown to be capable of bioerosion, but with lesser efficiency than the respective alpha form (Hartman 1958). Moreover, its gamma form contains unusually high concentrations of carbonic anhydrase in the cortex when compared to alpha and

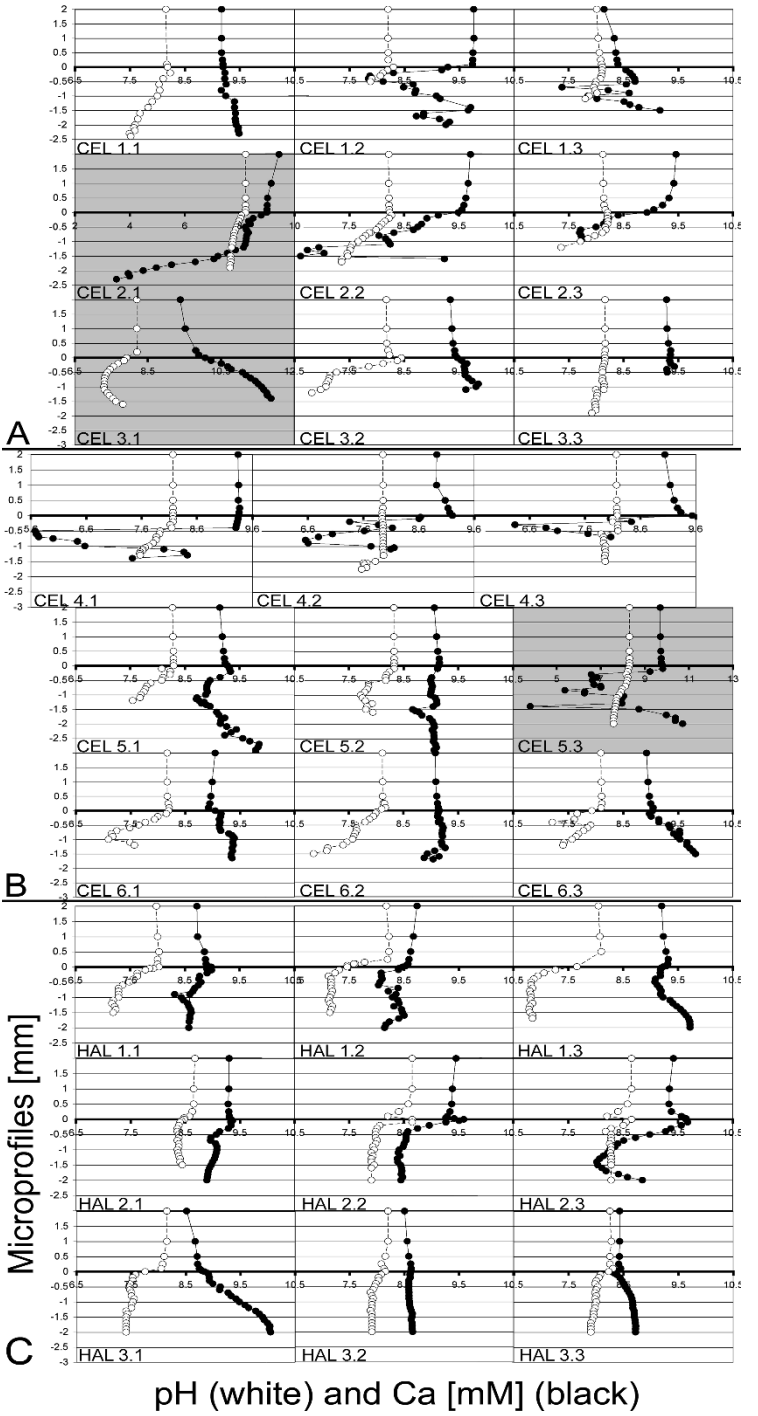
beta form, with carbonic anhydrase being involved in the process of bioerosion (Hatch 1980). Alpha and gamma form sponges of the Mediterranean *C. viridis / nigricans* group showed different adaptation to hetero- and autotrophy via their dinoflagellate symbionts under the same conditions (Schönberg et al. 2005). If (alpha, beta, gamma) growth form is species-specific, rather than related to age or growth stage, then this morphological consequence of sponge bioerosion can be used for taxonomic purposes as well.

1802 to 2007: A summary of knowledge on sponge bioerosion

After two centuries of research, we know that the organisms in question are endolithic sponges that produce the cavities they inhabit. Sponge erosion proceeds chemically (etching of cup-shaped fissures) and mechanically (removal of sponge chips). Proportions of the two components of sponge erosion were estimated between 2% chemical to 98% mechanical and 75% chemical and 25% mechanical activity. The sponges are able to attack calcium carbonates and organic materials, which involves specialised etching cells with filipodia providing a very localised application of an etching agent and the enzymes carbonic anhydrase and phosphatase. Sponge bioerosion does not apparently follow diurnal rhythms. It produces characteristic traces: the chambers and tunnels in the substrate that often end in minute pioneering ducts (*Entobia*), the pitting of the chamber walls (sponge scars) and the loosened silt-size particles with a smooth convex lower side and a concavely-facetted upper side (sponge chips). These traces may be of limited help in taxonomy. A large variety of environmental parameters can influence bioerosion rates and bioeroding sponge abundances, of which flow, nutrient concentration and substrate density appear to be the main magnifiers in common species. Despite over 200 years of research some questions still remain unsolved: Which is the exact chemical agent used in sponge erosion? Can sponge erosion proceed from larval settlement over papillate and encrusting growth forms to the entire removal of substrate and free-living sponges?

Present results

Microprofiles of pH and calcium concentrations in the bioeroding sponge *Cliona celata* and the free-living sponge *Halichondria panicea* did not reveal immediately clear patterns (Fig. 11). Overall, data taken from *H. panicea* were more stable than those from *C. celata* and were more uniform along the microprofiles into the sponges (Fig. 11C). However, some data series of *C. celata* were comparable to those of *H. panicea* (e.g., Fig. 11A-B; CEL 1.1 and CEL 3.3), and some of the *H. panicea* profiles were as erratic as were some of those for *C. celata* (Fig. 11C; HAL 1.2 and HAL 2.3). Calcium concentrations in *C. celata* did not uniformly increase with distance into the sponge, even though eight of the 18 profiles showed an increase of 0.5 to 1 mM Ca^{2+} ions when considering the entire profile (Fig. 11B; CEL 1.1 and 1.3, CEL 3.1 and 3.2, CEL 5.1 and 5.3, CEL 6.1 and 6.3). Of these eight profiles, two were so erratic that they should be discounted (Fig. 11A-B; CEL 1.2 and CEL 5.3). There were also eight profiles of the 18 for *C. celata* for which the calcium concentration decreased


A
CEL 1.1
CEL 1.2
CEL 1.3
CEL 2.1
CEL 2.2
CEL 2.3
CEL 3.1
CEL 3.2
CEL 3.3
CEL 4.1
CEL 4.2
CEL 4.3
B
CEL 5.1
CEL 5.2
CEL 5.3
CEL 6.1
CEL 6.2
CEL 6.3
C
HAL 1.1
HAL 1.2
HAL 1.3
HAL 2.1
HAL 2.2
HAL 2.3
HAL 3.1
HAL 3.2
HAL 3.3
Microprofiles [mm]
pH (white) and Ca [mM] (black)

with distance into the sponge (Fig. 11A-B; CEL 1.2, CEL 2.1-2.3, CEL 4.1-4.3, CEL 6.2), but of these, four profiles were so erratic, that they should be discounted (Fig. 11A-B; CEL 1.2, CEL 4.1-4.3). Three of the eight decreasing calcium profiles were fairly regular, but still displayed strong negative trends that cannot be explained (Fig. 11A; CEL 2.1-2.3). In two profiles calcium concentrations appeared to remain more or less constant with tissue depth (Fig. 11A-B; CEL 3.3 and CEL 5.2). Nevertheless and overall, calcium concentrations in *C. celata* increased with tissue depth (0.5 mM in the first series and 0.3 mM in the second series on average; see Table 2). But there were a few *H. panicea* profiles that also displayed calcium increases with distance into the sponge (Fig. 11C; HAL 1.3, HAL 3.2 and 3.3). The overall mean for *H. panicea* was an increase by 0.03 mM Ca^{2+} (Table 2), that was mainly influenced by the strong increase in the first measurement of the third specimen (Fig. 11; HAL 3.1).

The pH measurements yielded additional evidence for sponge erosion, as 15 of 18 cases of *C. celata* revealed a decrease of pH with distance into the sponge tissue (Fig. 11A-B). In the remaining profiles, pH values rose slightly with depth but remained lower than in the superficial layers (Fig. 11A-B; CEL 3.1, CEL 5.2, CEL 6.1). In *H. panicea* the tissue pH was lower than that of the ambient water, but once the sensor penetrated the sponge's superficial layers, the values remained fairly constant (Fig. 11C).

Table 2 Means of pH and calcium concentrations in the culture water (at 2 mm above the sponges) and each individual of *Cliona celata* (CEL) and *Halichondria panicea* (HAL). Erratic and atypical microprofiles for calcium were omitted when calculating the values below (CEL 1.2-1.3, CEL 2.1-2.3, CEL 4.1-4.3, CEL 5.3). Data are given for the following steps in the microprofiles: in the water above the sponge (2 mm), on the surface of the sponge (0 mm), in superficial layers of the sponge, but below the level of the papillae (-0.3 mm) and at the endpoint of the measurements (varying depths). An overall difference (Δ) of the measured parameters was calculated between the values on the surface and the endpoints

	Sponge #	**pH**					**Calcium [mM]**				
		(2 mm)	(0 mm)	(-0.3 mm)	endpoint	Δ pH	(2 mm)	(0 mm)	(-0.3 mm)	endpoint	Δ Ca^{2+}
Series 1	CEL 1	8.1	8.2	8.1	7.7	-0.5	9.2	9.2	9.2	9.5	+0.3
									(CEL 1.1)		
	CEL 2	8.2	8.2	8.1	7.4	-0.8	-	-	-	-	-
	CEL 3	8.2	8.2	7.8	7.5	-0.7	9.3	9.6	9.9	10.3	+0.7
Series 2	CEL 4	8.1	8.1	8.1	7.7	-0.4	-	-	-	-	-
	CEL 5	8.3	8.3	8.2	7.7	-0.6	9.1	9.2	9.1	9.4	+0.2
									(CEL 5.1-5.2)		
	CEL 6	8.1	8.0	7.8	7.3	-0.7	9.0	9.1	9.1	9.4	+0.3
	HAL 1	8.1	7.7	7.2	7.1	-0.6	8.9	8.9	8.7	8.8	+0.1
	HAL 2	8.7	8.6	8.2	8.2	-0.4	9.4	9.5	9.1	8.7	-0.4
	HAL 3	8.2	8.0	7.9	7.7	-0.3	8.5	8.6	8.7	9.1	+0.4

Fig. 11 Microsensor microprofiles for pH (white) and calcium concentration (black) for the sponges *Cliona celata* (**A** and **B**) and *Halichondria panicea* (**C**). Each series was conducted on three sponge specimens (CEL 1-3, CEL 4-6 and HAL 1-3; graphs vertically distributed), measured in three places (graphs horizontally distributed). All graphs with white backgrounds were made to scale; grey background indicates differing scale. Standard deviations not displayed, as they were smaller than the data points

Patterns became clearer after taking means of the replicate measurements per sponge and then means of the sponges per series (Fig. 12). Whereas pH and calcium concentration in *H. panicea* remained fairly uniform from -500 µm downwards (Fig. 12C), in *C. celata* pH continually decreased and calcium concentration slightly increased (Fig. 12A-B). However, as these means were obtained by omitting erratic data sets, results are not entirely objective and should be treated with care.

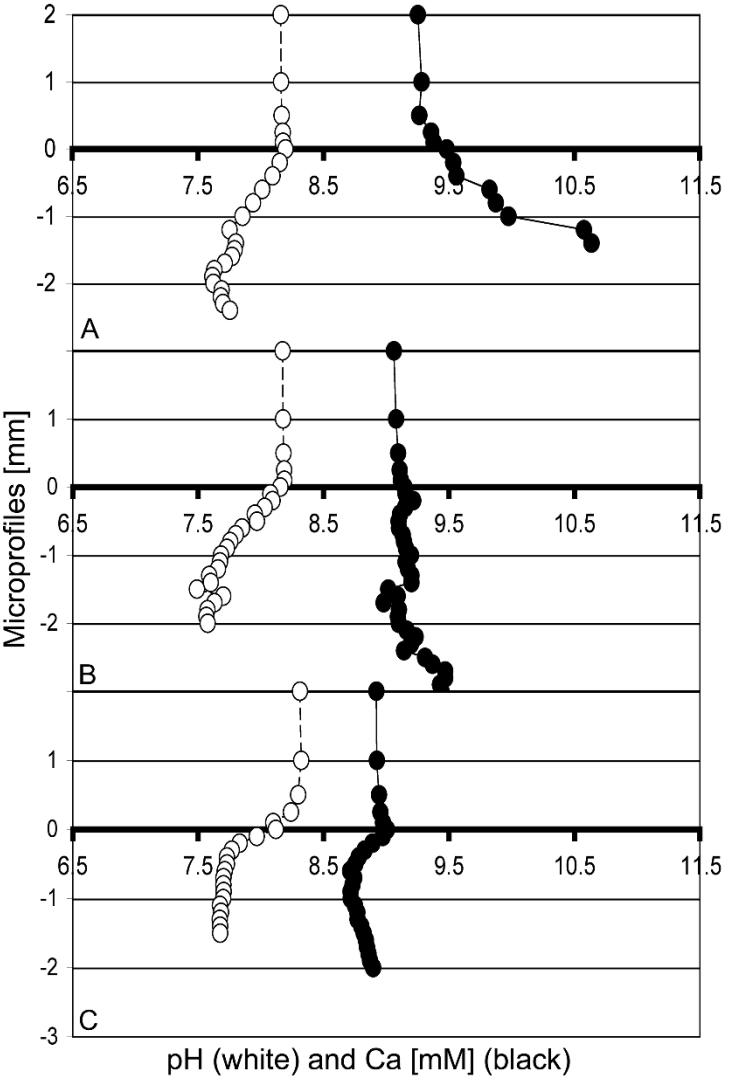


Fig. 12 Gradients of mean pH (white) and calcium concentrations (black) in *Cliona celata* (**A** and **B**) and *Halichondria panicea* (**C**). Very erratic calcium profiles of *C. celata* and the extreme negative trend of calcium in CEL 2 were omitted before calculations: CEL 1.2-1.3, 2.1-2.3, 4.1-4.3 and 5.3. Of all replicate measurements per sponge means were taken, and then the means of the sponges per series. Standard deviations not displayed, as they were smaller than the data points in the graphic

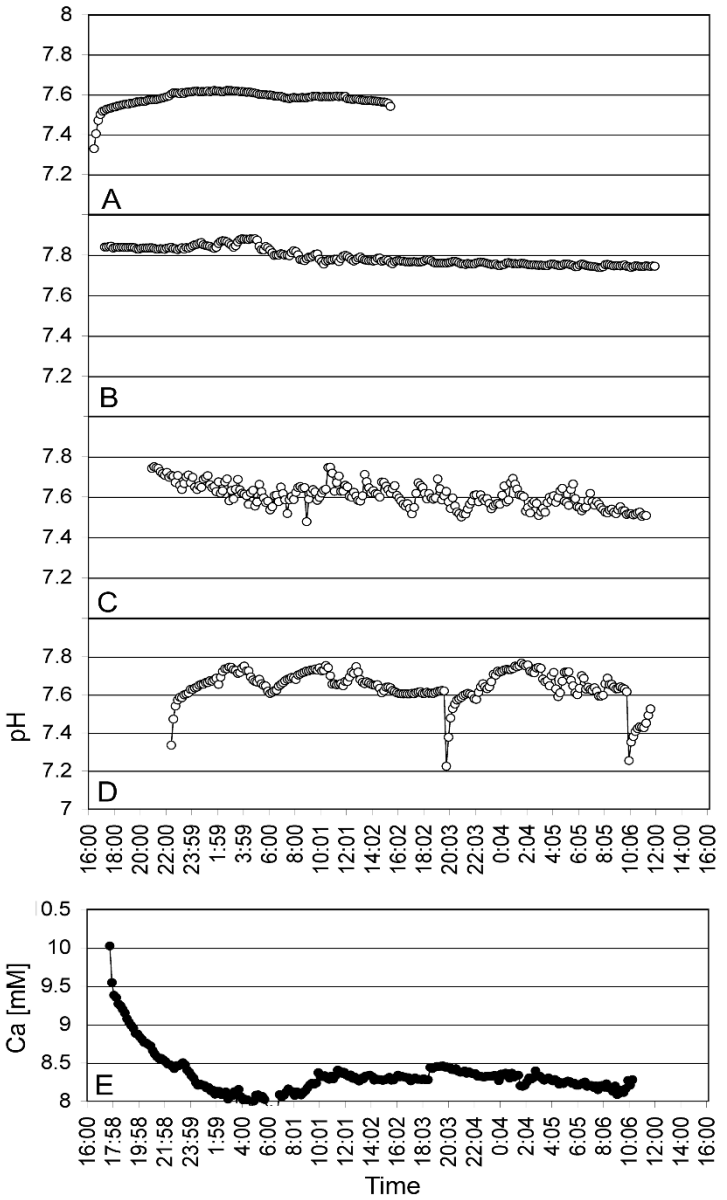


Fig. 13 Time series of microsensor measurements for pH (**A**-**D**) and calcium concentration (**E**) at the tissue-substrate interface of *Cliona celata*. The sensors were positioned in the sponge tissue against the substrate and not disturbed over the period of the measurements. Extreme negative peaks in A and D are unlikely to represent real decreases in pH, but were caused by the initial disturbance of applying the sensor (A) and at least in one case by a slamming door (D). The steadily decreasing values in the first third of E may not represent the true calcium concentration, but may have been caused by a sensor drift. Please note that curves for B and C display some areas with small, periodic oscillations of the pH, which may also be the case for the last third of D

Moreover, absolute values of pH and calcium concentration were weaker evidence of the acid-etching theory than expected. Mean pH and calcium concentrations at the tissue-substrate interface in *C. celata* were 7.55 and 9.65 mM, respectively, compared to ambient conditions of pH 8.2 and 9.2 mM Ca^{2+}. Especially the pH values at the endpoints of the profiles were thus much more subtle than expected, and only went below neutral in two cases: CEL 3.2 and CEL 6.2, both with a pH of 6.8 at the endpoint of measurements (Fig. 11A-B).

Time series of pH and calcium concentration at the tissue-substrate interface of *C. celata* showed no diurnal rhythm (Fig. 13). Initial high values for calcium were probably due to a sensor drift (Fig. 13E). It is interesting to note, however, that a shorter-term, slightly irregular periodicity may exist in some individuals, with small pH peaks occurring in intervals of about 1 to 3 hours (Fig. 13B-C). Extremely negative peaks were very likely due to physical disturbance of the work place (e.g., door slamming; Fig. 13A, D).

Discussion of present results: the mystery continues

Microsensor measurements revealed that pH and calcium properties in the tissue of the bioeroding sponge *Cliona celata* slightly differed from those of the free-living *Halichondria panicea.* Regrettably, differences were not as clear as could be wished, but in contrast to *H. panicea*, *C. celata* showed a continually decreasing pH with tissue depth, and in the first measurement series for *C. celata* calcium strongly increased with tissue depth (Fig. 12). These values were opposite in trend and very similar in dimension to previously found gradients for calcification processes in corals and the calcifying alga *Halimeda* measured with LIX microsensors (de Beer et al. 2000; de Beer and Larkum 2001; Al-Horani et al. 2003). However, as the present means were obtained by subjectively omitting erratic data sets, results have to be regarded with care.

Much variation between and within individuals existed, masking the observations. Within a given individual of *C. celata* variation was probably influenced by the heterogeneity of the sponge tissue and the distribution of the remaining substrate (Fig. 1). *C. celata* consists of branching erosion chambers (see Schönberg and Shields this volume) in which its tissue is located, which in turn surrounds the canal system. The tip of the microsensor may occasionally pass through lumina of the canal system and measure conditions similar to the ambient water (Fig. 11; e.g., pH for CEL 3.1), or come close to a protruding shelf of substrate and measure conditions similar to the endpoints of the profiles (Fig. 11; e.g., pH for CEL 6.3). Measured values in the first 250 µm of the profiles could occasionally be slightly different compared to the rest of the profiles and represented conditions in the sponge's papillae and superficial layers that contain less cellular and much more skeletal material than the rest of the sponge. Additionally confounding were situations in which equipment problems may have played a role (Fig. 11; e.g., calcium values for CEL 4.1 to CEL 4.3 and CEL 5.3). Unexpected results from *H. panicea* cannot easily be explained (occasional increases in calcium, initial decrease in calcium

upon insertion of microsensor; Fig. 11). Calcium plays an important role in marine sponges for cell motility and tissue contractions (e.g., Prosser 1967; Pavans de Ceccatty 1971; Lorenz et al. 1996). Sponges have no nervous system, and cell-to-cell communication is used to affect coordination. Intracellular calcium concentrations may be elevated by stress or by tissue contractions (Leys and Meech 2006). As *H. panicea* presented more resistance when trying to insert the sensors into the tissue than *C. celata* (higher spongin content), changed calcium concentrations may be a consequence of squeezed cells before the sensors pierced the tissue and possibly of a resulting if unobserved contraction.

If we assume that the gradual decrease in pH in *C. celata* is related to its etching activities, the present study is the first example of experimentally showing that acid production may play a role in sponge bioerosion. Previous attempts to detect acid in bioeroding sponges failed, because employed tools were not sensitive enough and not applied locally enough (Table 1). It may be reasoned, however, that the overall mean pH of 7.55 at the tissue-sponge interface of *C. celata* may not be low enough to signify active bioerosion, especially when considering that human stomach contents have a pH between 1 and 2 and the oral pH commonly reaches a value of 5.5 during sugar intake (Cleffmann 1979). But one has to keep in mind that this value is maintained against an external pH of about 8.2 and that the positioning of the microsensors was conducted 'blindly' (Fig. 1), i.e., due to the opacity of the tissue and substrate a sensor would only by chance come to rest directly on a erosion crevice between sponge chip and scar to detect the very local application of the etching agent. This may have been more or less achieved for CEL 3.2 and 6.2 (Fig. 11A-B). If it were possible to visually guide a microsensor to fit directly over or into the etched crevice of a future chip and the remaining substrate, we could probably expect more striking results. Moreover, if *C. celata* employs chelators as has been found for *Aka coralliphaga* (see Sullivan and Faulkner 1990), then the pH values may not have to be as low as for purely acid-achieved etching. Nevertheless, very similar values of pH in the deeper tissue of *H. panicea* make the above reasoning perilous and present data should be understood as the product of a pilot study that provides preliminary evidence only. A repetition of the approach would probably help to confirm the observations. Calcium gradients may be the safer indicators in this case and definitively point towards calcium dissolution in *C. celata*, at least for the first series of measurements (Fig. 12A-B).

One intriguing outcome is the possible short-term periodicity in sponge etching as evidenced in oscillating pH values at the tissue-substrate interface of some individuals of *C. celata* (Fig. 13B-C). Sponge scar microstructures contain concentric grooves that may be caused by substrate properties (e.g., Cobb 1969; Rützler and Rieger 1973), but were previously also explained by a putative periodic etching activity of the sponges (Cobb 1969). If the latter theory is true and the present changes in pH are directly related to the bioerosion activity, then one etching cycle takes 1 to 3 hours and the production of one chip that leaves a scar with about 5 distinct concentric grooves may take 5-15 hours (deepest grooves counted in figures from, e.g., Calcinai et al. 2003). In this context it is also important to consider that

there may be individual differences in the etching process, as one of the present individuals of *C. celata* did not show any periodic changes in pH measured at the tissue-substrate interface (Fig. 13A), when another individual displayed pronounced oscillations of pH (Fig. 13C). Therefore, the clear occurrence, the depth and the number of concentric grooves in sponge scars may be not as good a taxonomic aid as previously thought (Omnes 1991; Bavestrello et al. 1996; Calcinai et al. 2003, 2004; Borchiellini et al. 2004). Earlier findings that sponge bioerosion does not display a diurnal rhythm (Zundelevich et al. 2007) are here supported.

Overall, it still remains somewhat unclear whether observed gradients of pH and calcium in the tissue of *C. celata* were related to sponge bioerosion, as most of them were gradual and subtle, and the means were not distinctly different compared to the free-living sponge (Table 2). However, as changes in pH were uniformly represented in different individuals of *C. celata* and because changes in calcium concentrations were so pronounced in the first series, it is quite likely that the findings demonstrate chemical etching involving acid production. Hopefully this study can be repeated with more replicates and time, making it possible to obtain better means. In this case it would be interesting to include different growth forms of bioeroding sponges or a symbiotic and an asymbiotic species in comparison.

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