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# Colony growth strategies, dormancy and repair in some Late Cretaceous encrusting bryozoans: insights into the ecology of the Chalk seabed

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## Abstract

Bryozoans are among the most common macrofossils in the Late Cretaceous Chalk. They include many species that encrusted hard substrates, notably echinoid tests, forming habitat islands on the Chalk seabed. The growth strategies adopted by these bryozoans, as well as the occurrence of reparative structures, provides evidence of the conditions experienced by bryozoans and other benthic animals during the accumulation of this unique pelagic sediment deposited over large areas of the continental shelf. Here, we use historical material in the Natural History Museum, London, to provide qualitative evidence that whereas available substrates, including irregular echinoids, were long-lasting, most individual bryozoan colonies were probably short-lived. Some cheilostome species produced heavily calcified polymorphic zooids at the outer edges of the colony that persisted after loss of the feeding autozooids and became the source of regenerative colony growth. Short-term (possibly annual) periodicity is suggested in the benthic environment experienced by encrusting bryozoans, which may have possibly been a result of cyclical variations in dinoflagellate food supply and/or swamping by unpalatable and potentially poisonous coccolithospheres.

## Introduction

Deposited through a time interval of almost 35 million years, the Late Cretaceous Chalk of northern Europe and western Asia is a pure white limestone formed largely of coccoliths with some other biogenic carbonate grains, especially foraminifera, but very little clastic material (e.g. Hancock 1975). This remarkable deposit has long attracted interest and debate about its depositional setting. Sea-levels varied geographically and through time in the Chalk Sea, ranging in depth from perhaps 100 to 600 m in the main area of deposition over the European continental shelf and with the seabed invariably beneath the photic zone to judge from the lack of benthic algae (Hancock 1975). A key factor in the formation of the Chalk appears to have been the lack of a shelf break front that normally separates stratified, low nutrient oceanic water ('blue water') from coastal waters with higher levels of nutrients (Hay 1995, 2008). Thus, the Chalk is a pelagic sediment that was deposited over the continental shelf during the Late Cretaceous. Seawater chemistry in the Late Cretaceous, with a low Mg/Ca ratio, is thought to have been particularly favourable for coccolithophore population growth (Stanley et al. 2005). Coccolith blooms are often seasonal in modern environments (e.g. Mergulhao et al. 2013). Dominated by coccoliths, sediment cover on the Chalk seabed could potentially have ranged from a soft ooze to firm or even hard in consistency (Hancock 1975). The overall low nutrient levels of the Chalk environment were undoubtedly demanding for sessile, suspension feeding epibenthic animals feeding on plankton. In addition, firm substrates for attachment may have been at a premium and mostly represented by scattered 'habitat islands' created by living skeletons but more particularly by the skeletal remains of various mostly benthic invertebrates. Compared with shallow shelf environments today and at other times in the geological past, the Chalk seabed would have presented a major challenge for many epibenthic animals.

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Bryozoans are among the most abundant macrofossils in the Chalk. Indeed, in some places, bryozoans are dominant components of the sediment, for example, filling channels in the Turonian–Santonian Chalk of Normandy, France (Quine and Bosence 1991) and forming bioherms in the Maastrichtian Chalk of Denmark (Surlyk 1997). In both of these examples, high bryozoan abundance was probably related to the initiation of a benthic carbonate factory due to lowering of sea-level (Mortimore 2011, p. 290). Apart from a few free-living species of *Lunulites* and closely related genera that had larvae capable of settling on tiny substrates, colonies of most Chalk bryozoan species required macroscale hard or firm substrates on which to develop. At least for encrusting species, the commonest of these substrates are irregular echinoids, inoceramid bivalves and belemnite guards. Encrusting bryozoans employed a variety of growth strategies when colonising substrates in the Chalk and show patterns of damage and repair that can potentially provide insights into the palaeoenvironmental conditions on the Chalk seabed. Nevertheless, this is a topic that has been severely neglected: the relatively few studies conducted on bryozoans from the white Chalk have been primarily taxonomic (e.g. the long series of papers by R. M. Brydone, see Taylor et al. 2018a), while research on the palaeoecology of bryozoans and other Chalk sclerobionts colonising hard substrates has tended to focus on patterns of distribution over the surfaces of these substrates (e.g. Müller 1969; Zamora et al. 2008; Borszcz et al. 2013) or biotic interactions between sclerobionts and their hosts (e.g. Neumann and Wisshak 2006; Hammond and Donovan 2017). More is known about the palaeoecology of bryozoans from nearshore facies marginal to the white Chalk as a result of the research of Ehrhard Voigt and his collaborators (e.g. Voigt 1973, 1981, 1987, 1988; Hillmer et al. 1997).

Using historical material in the collections of the Natural History Museum, London (NHMUK), the aims of the current paper are to describe colonial strategies and patterns of repair and episodic growth in Chalk bryozoans from the United Kingdom, and to apply these observations to infer conditions pertaining on the seabed during the deposition of the white Chalk, particularly with respect to possible seasonality in the flux of plankton.

## Material and methods

This study is based on specimens from the fossil bryozoan collection in the NHMUK. Most of the specimens used were collected in the late 19th and early 20th century by three prolific collectors of Chalk fossils: W. Gamble, A. W. Rowe and C. T. A. Gaster. William Gamble was a warder at Chatham prison and subsequently a grocer based in London (Cleevely 1983). He collected Chalk fossils mostly from the pits around Chatham and Maidstone, Kent, selling several lots to the NHMUK (then the British Museum

(Natural History)) and the British Geological Survey between 1893 and 1913. Arthur Rowe (1858–1926) was a physician renowned for his pioneering research on the Chalk stratigraphy of Britain (e.g. Rowe 1900). His Chalk fossil collection was purchased by the NHMUK for £500 in 1926 as part of his will. Finally, Christopher Gaster (1878–1963) was a Sussex-based amateur geologist who published on the Chalk of southern England (e.g. Gaster 1951). His collection of Chalk bryozoans was presented to the NHMUK in 1950 (Cleevely 1983). Material from all three collections is stratigraphically localised to the level of macrofossil zone (e.g. *Micraster coranguinum* Zone) but not to individual bed level. Likewise, geographical localities vary in exactness, from the name of a particular chalk pit to the cliffs between two points on the coast. As a high proportion of the best-preserved specimens come from the Coniacian and Santonian of Sussex and Kent, these are the main focus of the study, although material from the Campanian of Norfolk has also been utilised. The location of these sites and the current stratigraphy is shown in Fig. 1.

The bryozoans studied in these three collections encrust shell substrates. Some of these substrates are more or less intact but the majority are broken and incomplete. For instance, many of the specimens from the Rowe Collection comprise echinoid tests cut into roughly rectangular pieces about a centimetre or less in width. While this procedure has destroyed information on the broader context of the bryozoans, including the exact location of the bryozoans on their substrates, it has furnished specimens of convenient size for scanning electron microscopy (SEM), permitting detailed study of reparative structures etc. In the absence of precise context, from position on the substrate to the exact stratigraphical horizon of collection, information provided by discrete colonies is emphasised here and is used to obtain a general impression of the palaeoenvironment experienced by bryozoans on the Chalk seabed. As neither the exact methods employed during the collection of this museum material, nor the degree of processing and sorting after collection are known, quantitative analyses cannot be justified and the approach taken here is essentially qualitative.

The two extant bryozoan orders with mineralised skeletons—Cheilostomata and Cyclostomata—were almost equally numerous in the Late Cretaceous (Lidgard et al. 1993), contrasting with the dominance of cheilostomes at the present day. Both orders are represented in the material used for the current study. Cheilostomes have box-like zooids with frontal surfaces that may be almost naked or protected by frontal walls with openings (orifice or opesia) for the lophophore to emerge at or close to the distal end of the zooid. Distinctive among Chalk cheilostomes are the so-called cribrimorphs in which the frontal wall is formed by spines called costae overarching the frontal membrane. In contrast, cyclostomes have tubular zooids with terminal openings (apertures) that are subcircular or polygonal and are
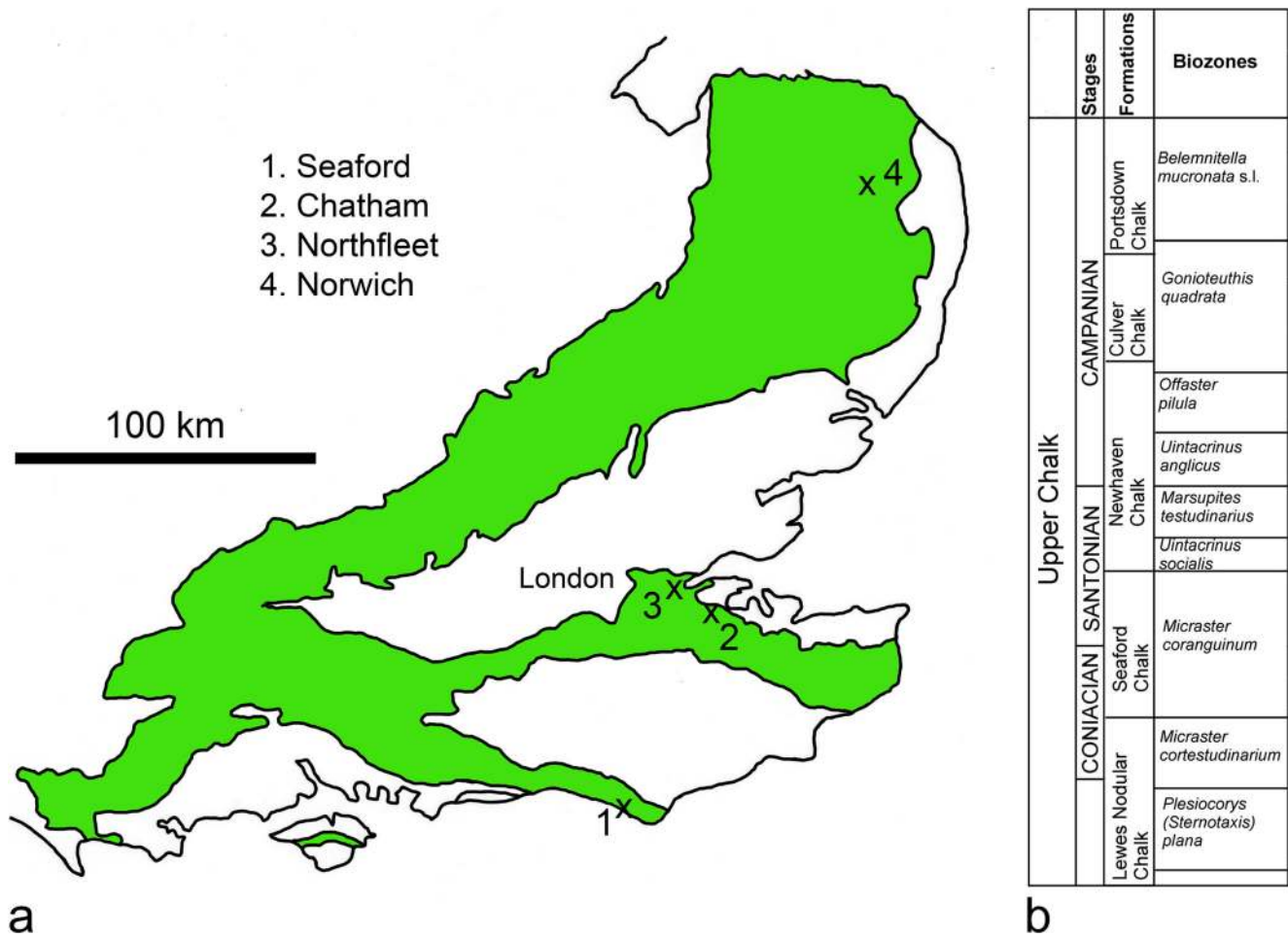
Fig. 1 Locality map (**a**) showing the main sources of the Chalk bryozoans and stratigraphy (**b**) of the Upper Chalk (late Turonian–Campanian) of southeast England. The Chalk outcrop is in green. Map modified after Hopson (2005) and stratigraphy for the Southern Province after Woods (2015)

sometimes grouped into fascicles. Both orders exhibit a wide variety of colony-forms, with many superficially similar colony-forms present in each order. As described below, the different colony-forms exhibited by encrusting bryozoans in the Chalk can be interpreted as alternative colonial strategies for utilising and competing for substrate space.

Scanning electron microscopy was undertaken using a Leo 1455-VP microscope at the NHMUK. The low vacuum chamber of this microscope allowed the study of uncoated and large specimens, which were imaged using back-scattered electrons.

## Results

Colonial strategies

The diversity of colony-forms found among bryozoan species can be explained in terms of different strategies for utilising the living space available to them. Jackson (1979) recognised

six basic colony shapes in bryozoans and other benthic colonial animals: runners, sheets, mounds, plates, vines and trees. The first three of these are encrusting colony-forms relevant to the present study. A fourth encrusting category—spots—was introduced by Bishop (1989), and a fifth—ribbons—represents a commonly occurring intermediate colony-form between runners and sheets (Taylor 1984).

*Runners*

Runners are encrusters with branches comprising uniserially arranged zooids (Figs. 2e and 3a, b). The branches ramify by terminal division, typically as bifurcations or trifurcations, and/or by lateral branch formation on the flanks of existing branches. Runners disperse their zooids widely over the substrate but leave unoccupied substrate space between their branches. They tend to be poor competitors for substrate space, with no active defence against overgrowth of the sides of their branches by bryozoans and other encrusters. On the other hand, their small, widely spaced lophophores are

advantageous if food supply is low (Okamura et al. 2001), while the widely dispersed zooids indicate a fugitive strategy allowing survival of some zooids in the face of localised mortality of zooids (Buss 1979; Jackson 1979).

◀ **Fig. 2** Photographs of encrusting bryozoans and substrates from the Chalk of southern England. **a** Relatively dense bryozoan encrustation of a crushed echinoid test, NHMUK D4130, Upper Chalk, Chatham, Kent (Gamble Collection). **b** Fragment of an echinoid test encrusted by the ribbon-like cyclostome bryozoan *Proboscinopora toucasiana* (d'Orbigny), NHMUK D11401, Coniacian, Chatham, Kent (Gamble Collection). **c** Fragment of an inoceramid bivalve shell with several spot-like cyclostome bryozoans and part of a sheet-like cheilostome (lower right), NHMUK D46466, *cortestudinarium* Zone, Seaford, Sussex (Rowe Collection). **d** Crescent-shaped bands of kenozooids of the cheilostome bryozoan '*Micropora*' *eleanorae* (Brydone) on a fragment of echinoid test, NHMUK D42247, *mucronata* Zone, Earlham Lime Works, Norwich, Norfolk (Rowe Collection). **e** Runner-like colony of the cheilostome *Herpetopora laxata* (d'Orbigny) ramifying over a belemnite guard, NHMUK D42361, *mucronata* Zone, Edward's Pit, Mousehold, Norwich, Norfolk (Rowe Collection). *Scale bars* **a–c**, **e** 10 mm; **d** 5 mm

In the Chalk, by far the commonest runners belong to the cyclostome genera *Stomatopora* and *Voigtopora* (Fig. 3a), and the anascan cheilostome genus *Herpetopora* (Figs. 2e and 3b, c). The ascophoran cheilostomes *Dacryoporella* and *Andriopora* also have runner colonies but are rarer, which in the case of the former may be due at least in part to the thin and fragile skeleton. While *Stomatopora* and *Voigtopora* commonly encrust echinoid tests, the majority of *Herpetopora* colonies occur on inoceramids and, in the Campanian of Norfolk, belemnite guards (Fig. 2e). In terms of abundance as well as species diversity, runners are subordinate in the Chalk to multiserial encrusters, which is also usually the case elsewhere in the fossil record.

Branch multiplication in *Stomatopora* occurred only through bifurcation at distal growing tips, whereas *Voigtopora* produced lateral branches proximal of the growing tips, endowing colonies of this genus with a greater flexibility in growth, including the option of partly infilling gaps in the substrate between branches (Fig. 3a). Both *Stomatopora* and *Voigtopora* have more robust skeletons than the gracile zooids of the cheilostome runner *Herpetopora*.

*Herpetopora*, distinguished by its cruciform branching pattern and elongate pyriform zooids with narrow proximal caudae (Fig. 3b), is a remarkable bryozoan because of the high capacity of colonies to repair damage (Taylor 1988). Bipolar zooid pairs, consisting of two zooids oriented in opposite directions and joined at their narrow proximal ends, were formed when branches were severed and a new zooid was budded from the proximal end of the broken branch. Damaged zooids may be used as conduits through which new growth links parts of the colony that were evidently still functional. The linkages can be achieved using intramurally budded kenozooids (Fig. 3c) or autozooids, either of which can have the same polarity as the host zooid or may be oppositely oriented. While *Herpetopora* was undoubtedly a 'weed' in performing poorly when competing for space and using the substrate very sparsely, colonies were remarkably persistent due to their ability to survive damage, undertake reparative

budding and re-establish connections between patches of zooids isolated following the severance of branches.
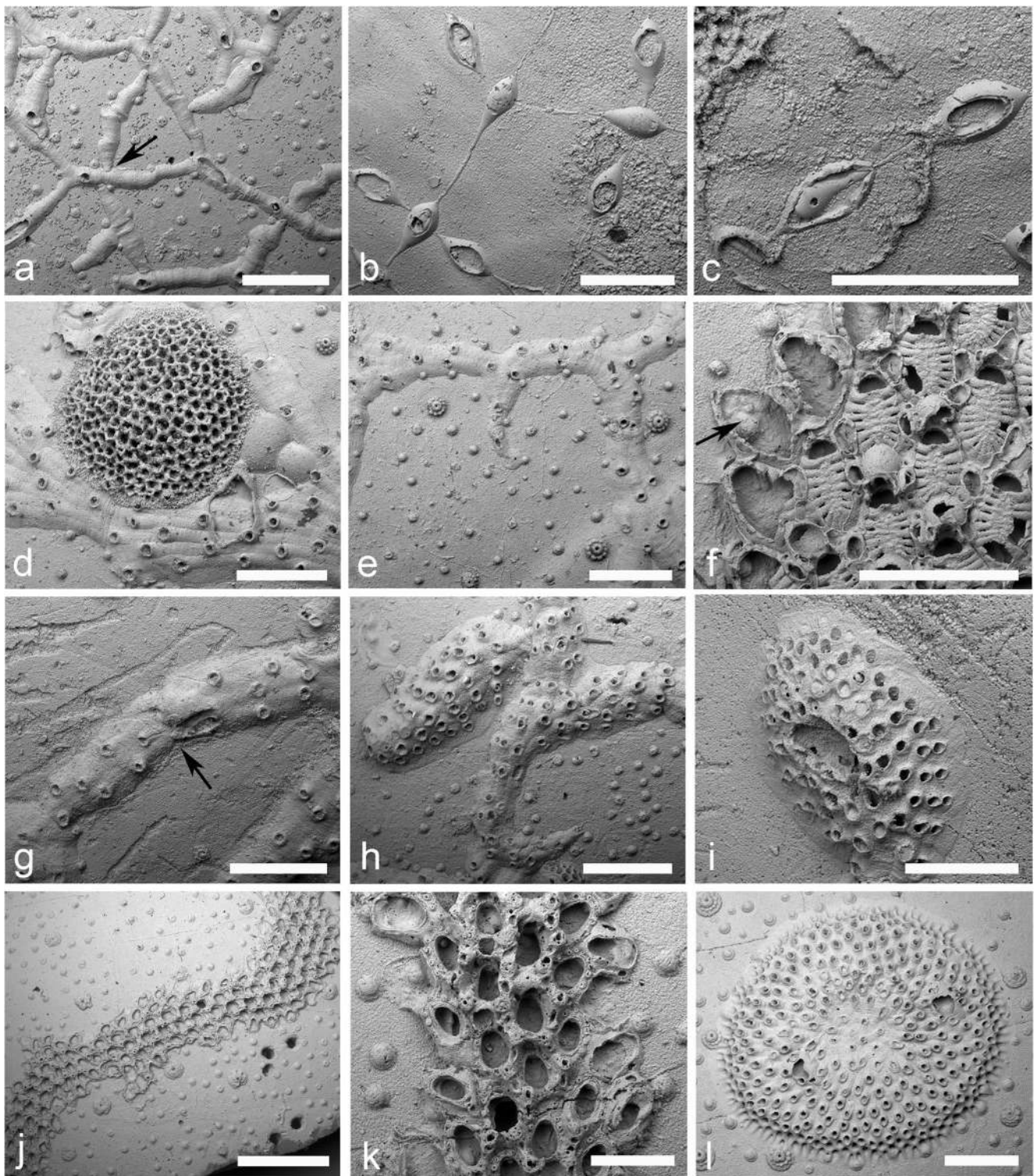
## Ribbons

Ribbons resemble runners in having ramifying colonies but their branches are oligoserial with two to about a dozen zooids across the width of each branch (Figs. 2b and 3e). Terminal branch bifurcation is supplemented in some instances by the formation of lateral branches (Fig. 3h). Like runners, colonies spread widely over substrates but leave gaps between branches where spatial competitors can become established and overgrow the lateral edges of the branches (Fig. 3d). The broader distal growing tips of ribbons improve their abilities in spatial competition compared to runners.

Tubercles on the surfaces of echinoid tests were typically bypassed by the growing branches of ribbon-like cyclostomes (Fig. 3e), an option not available to the broader sheet- and spot-like multiserial bryozoans which either grew around the tubercles or over them, the latter resulting in distortion of the zooids (Fig. 3f).

Nearly all of the ribbon-like colonies in the Chalk are cyclostomes. Their taxonomy is poorly known but most can probably be placed in *Proboscinopora*, *Idmonea* or *Oncousoecia*. Ribbon-like colonies of the stomatoporid genus *Proboscinopora* in the Chalk have large zooids and their colonies sometimes attain moderately large dimensions (Fig. 2b). They had the ability to regrow from the broken ends of damaged branches (Fig. 3g). A ribbon species of *Idmonea* was able to produce lateral branches (Fig. 3h), supplementing the normal mode of branch multiplication by bifurcation at distal growing tips. In contrast, some colonies of *Oncousoecia* are small and appear to have grown to a fixed size, as indicated by the sealing of the zooids at the distal growing edges of the branches (Fig. 3i). A single colony of a ribbon-like cheilostome was found among the material studied here (Fig. 3j, k). This is a very uncommon colony-form for cheilostomes in the Chalk and more generally throughout the stratigraphical record. This colony, provisionally identified as a species of *Pyriporella*, has two sinuous branches growing in opposite directions from the colony origin, each branch 4–6 zooids wide with the flanking zooids oriented obliquely to branch growth direction (Fig. 3k). It is possible that the unusual colony-form is due to growth being constrained between other encrusters that are not preserved.

## Sheets and spots

Sheet and spot colonies are broadly multiserial and generally have a circumferential growing edge. They use substrate space economically, leaving no gaps or open windows of substrate over the area they occupy. Because the colony is totally encompassed by a growing edge, when encountering other

encrusters on the same substrate, they can respond actively through zooidal budding and have a higher probability of success in spatial competition than either runners or ribbons. Whereas sheets are typically large colonies attaining a variable size and shape (indeterminate growth) and continuing to grow after reproducing, spots are small, determinate and early re-producing colonies. Distinguishing between sheets and spots is not straightforward and the two are probably best viewed as end-members of a continuum. Indeed, some Mesozoic encrusting cyclostome species usually formed small and spot-like colonies, while occasional colonies belonging to the same species developed as sheets of larger size, continuing growth after formation of the gonozooids that are indicative of female sexual reproduction (McKinney and Taylor 1997).

◄ **Fig. 3** Scanning electron micrographs of runner (**a–c**), ribbon (**d, e, g–k**) and spot (**l**) colony-forms among Chalk bryozoans from southern England. **a** Branches of the cyclostome runner *Voigtopora* sp. encrusting an echinoid test, showing both bifurcation and lateral branching (arrow), NHMUK D44623, *mucronata* Zone, Edward's Pit, Mousehold, Norwich, Norfolk (Rowe Collection). **b, c** Cheilostome runner *Herpetopora laxata* encrusting belemnite guard, NHMUK D42361, *mucronata* Zone, Thorpe St Andrew, Norwich, Norfolk (Rowe Collection); **b**, zooids with long caudae producing lateral branches initially consisting of zooids with short caudae; **c** damaged zooid containing an intramural kenozooid. **d, e** Ribbon-like cyclostome *Proboscinopora toucasiana*, NHMUK D11401, top *cortestudinarium* Zone or base *coranguinum* Zone, Chatham, Kent (Gamble Collection); **d** bifurcating branch partly overgrown by a sponge and a foraminifer; **e** colony origin (centre) and branches growing between tubercles on the echinoid test substratum. **f** Multiserial colony of the cribrimorph cheilostome *Carydiopora* cf. *transita* (Brydone) growing on an echinoid test, showing tubercle indenting a zooidal chamber (arrow), NHMUK BZ8661, *coranguinum* Zone, Northfleet, Kent (Rowe Collection). **g** Regenerative growth from the broken end of a branch (arrow points to level of fracture) of *Proboscinopora toucasiana*, NHMUK D46434, *cortestudinarium* Zone, Seaford, Sussex (Rowe Collection). **h** Ribbon-like cyclostome '*Idmonea*' with bifurcation and lateral branching (arrow), NHMUK D46436, *cortestudinarium* Zone, Seaford, Sussex (Rowe Collection). **i** Terminal branch of *Oncousoecia* sp., NHMUK D46466, *cortestudinarium* Zone, Seaford, Sussex (Rowe Collection). **j, k** Ribbon-like cheilostome ?*Pyriporella* sp., NHMUK BZ8662, *coranguinum* Zone, Northfleet, Kent (Rowe Collection); **j** colony encrusting an echinoid test; **k** branch showing oligoserial zooids, the outer rows oriented obliquely to the branch axis. **l** Spot-like colony of a cyclostome (?*Hyporosopora* sp.), NHMUK BZ3233(c), *coranguinum* Zone, Northfleet, Kent (Rowe Collection). *Scale bars* **a–i, l** 1 mm; **j** 2 mm; **k** 500 μm

Most of the Chalk cyclostomes forming sheets and spots were formerly classified in the genus *Berenicea*. However, this genus is unrecognisable and is now employed only in open nomenclature as the form-genus '*Berenicea*' for specimens lacking the diagnostic gonozooids allowing them to be assigned to such genera as *Microeciella*, *Reptomultisparsa*, *Hyporosopora*, *Plagioecia* and *Mesonopora* (Taylor and Sequeiros 1982). Other encrusting cyclostomes in the Chalk are species of *Diplosolen* (recognised by its abundant nanozooids), *Actinopora* (having autozooidal apertures arranged in ridge-like radial fascicles) and rectangulates including *Discocavea* and *Unicavea* with open kenozooids between the autozooids. All of these cyclostome genera typically form almost circular colonies a centimetre or less in diameter (Figs. 2c and 3l). Some develop subcolonies, as discussed below.

Sheet- and spot-like cheilostomes constitute the majority of encrusting species and colonies present in the English Chalk. The majority are 'membraniporimorph' anascans, formerly assigned incorrectly to the Recent malacostegine genus *Membranipora* (e.g. Brydone 1929), but now recognised as neocheilostomes mostly belonging to the broadly defined family Calloporidae. They include species of *Wilbertopora*, *Flustrellaria*, *Pyriporella*, *Marginaria* and *Dionella* (cf. Taylor and McKinney 2006), all of which have ovicells for brooding embryos before their release as larvae. Other anascan cheilostomes forming sheet-like colonies are onychocellids such as *Aechmellina* which have zooids with extensive cryptocystal frontal walls (see Taylor et al. 2018b). Sheet-like cribrimorph ascophorans are also present, and are characteristically diverse but not abundant. Their zooids have frontal shields formed of costal spines and they may be heavily armoured with avicularia too. Compared to the cyclostomes encrusting Chalk substrates, the multiserial cheilostomes tend to have larger colonies (up to 5 cm in diameter) that are often irregular in shape, seldom having a circular outline except when small.

Multilamellar sheet-like colonies of both cheilostomes and cyclostomes are uncommon in the British Chalk and were lacking among the historical material used for this study.

### Mounds

Mounds according to Jackson (1979, table 1) are regular or irregular massive encrustations with vertical as well as lateral growth, usually attached to the substratum along most of the basal area. Small mound- or dimple-like colonies are present but sparse in the Chalk. An un-named '*Berenicea*'-like cyclostome present in the Coniacian–Santonian Chalk has dimple-like colonies (Fig. 4a) with a thick basal layer or zooids capped by an overgrowing frontal subcolony positioned centrally. The strategy of such colonies is to occupy and defend a small patch of substrate.

Low mound-shaped colonies also occur in the cribrimorph cheilostome *Taractopora obscurata* (Brydone, 1916). The heavily armoured, subcircular colonies reach a diameter of up to about 5 mm before budding vicarious avicularia that seemingly signal termination of further distal colony growth (Fig. 4b, c). However, colonies continued to grow through the formation of a second layer of zooids centred on the colony origin (Fig. 4d).

### Subcolonies

In some bryozoan colonies, clusters of zooids form semi-autonomous subcolonies. These are particularly common in Chalk cyclostomes. Most are marginal subcolonies that developed at the distal growing edge of the colony (Fig. 4e, f) and are typically smaller in size than the parent colony, some partly overgrowing the parental colony. Not uncommonly, gonozooids are lacking in the main part of the colony but are present in the marginal subcolonies (Fig. 4e). However, in one species of '*Berenicea*', the colony consists of a succession of almost equal-sized subcolonies, each having the shape of a broad fan that originates from the growing edge of a preceding subcolony (Fig. 4g, h).

Another type of subcolony—frontal subcolonies—originating by eruptive budding from older, more central parts of the parent colony (Fig. 4i) were mentioned above with respect to mound-shaped colonies. Growth of frontal subcolonies provides
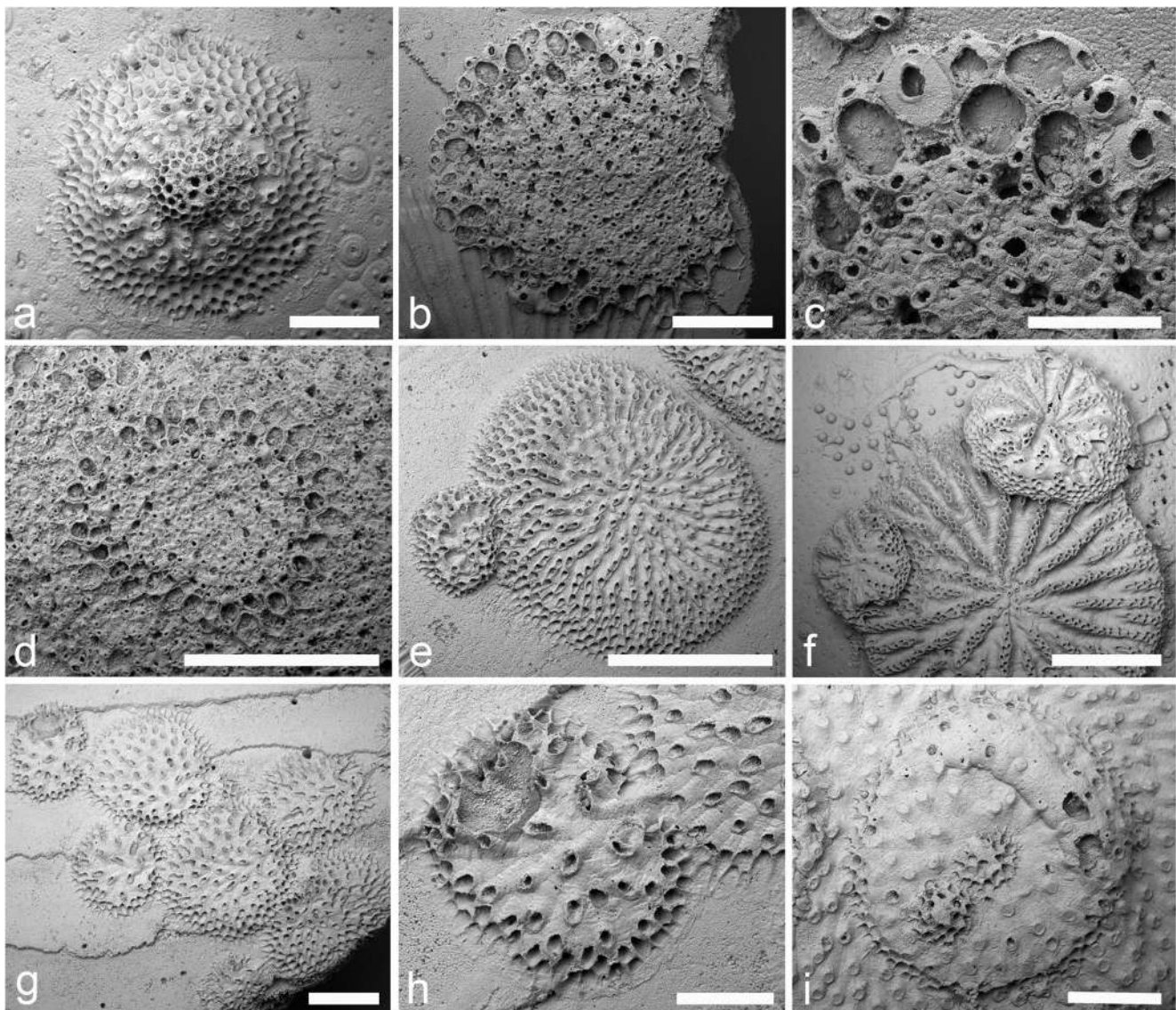
**Fig. 4** Scanning electron micrographs of colony-forms among Chalk bryozoans from southern England. **a** Dimple-like cyclostome colony, with a thick peripheral growing edge and central overgrowth, NHMUK BZ8663, *coranguinum* Zone, Northfleet, Kent (Rowe Collection). **b–d** Spot-like colonies of the cribrimorph cheilostome *Taractopora obscurata* (Brydone), NHMUK D46463, *cortestudinarium* Zone, Seaford, Sussex (Rowe Collection); **b** small colony encrusting an inoceramid shell; **c** detail of colony edge with large vicarious and smaller interzooidal avicularia; **d** another colony with an overgrowth originating from the centre. **e** Cyclostome *Plagioecia* encrusting an inoceramid shell and budding a marginal subcolony (left) that contains a broken gonozooid, NHMUK D46466, *cortestudinarium* Zone, Seaford, Sussex (Rowe Collection). **f** A pair of marginal subcolonies in the cyclostome *Actinopora* sp. encrusting an echinoid test, BZ8664, *coranguinum* Zone, Northfleet, Kent (Rowe Collection). **g, h** Colony of the cyclostome 'Berenicea' comprising a chain of discoidal subcolonies encrusting an inoceramid shell, NHMUK D8830, *coranguinum* Zone, Strood, Chatham, Kent (Gamble Collection); **g** subcolonies of successively younger age from bottom right to top left; **h** origin of a subcolony (with a broken gonozooid) from an earlier subcolony top right. **i** Frontal subcolony with crescent-shaped gonozooid and two incipient subcolonies in the cyclostome *Plagioecia* sp., NHMUK BZ8665, *cortestudinarium* Zone, Luton, Chatham, Kent (Rowe Collection). *Scale bars* **a, b, g, i** 1 mm; **c, h** 500 μm; **d–f** 2 mm

a means by which the colony can continue to bud new zoids without expanding its area on the substrate and facing competition from other organisms sharing that substrate. Instead, the colony overgrows its own old and moribund zooids, as well as any organisms that have fouled the living surface of the colony. Both frontal and particularly marginal subcolonies may potentially indicate discontinuous or episodic colony growth, new subcolonies being formed by rejuvenation of growth.

### Dormancy and episodic colony growth

One of the most intriguing features of several encrusting species of cheilostomes in the Chalk is evidence for dormancy followed by renewed colony growth. The three best examples are provided by '*Micropora*' *eleanorae* (Brydone, 1936), *Stichomicropora sussexiensis* (Brydone, 1936) and *Wilbertopora inhospita* (Brydone, 1929).

'*Micropora*' *eleanorae* is a peculiar cheilostome originally described from the *mucronata* Zone (Campanian) of Norfolk and represented in the NHMUK Rowe Collection by colonies encrusting fragments of echinoid tests. Most of these colonies are preserved only as crescent-shaped remnants comprising closed zooids that are here designated as kenozooids (Fig. 2d). Brydone (1936, p. 61) described colonies as "growing in a great variety of odd shaped patches which show a strong tendency to have the growing edge a true segment of a circle and to be disposed with that edge outwards here and there round a very large imaginary circle, very much as toadstools are disposed in 'fairy rings'". The kenozooids diminish in size distally and taper in thickness towards the convex outer edge of the colony. Closure plates are granular and covered by irregular pores (Fig. 5a). They lack the scar of an operculum that would be expected if these zooids had originated as autozooids and
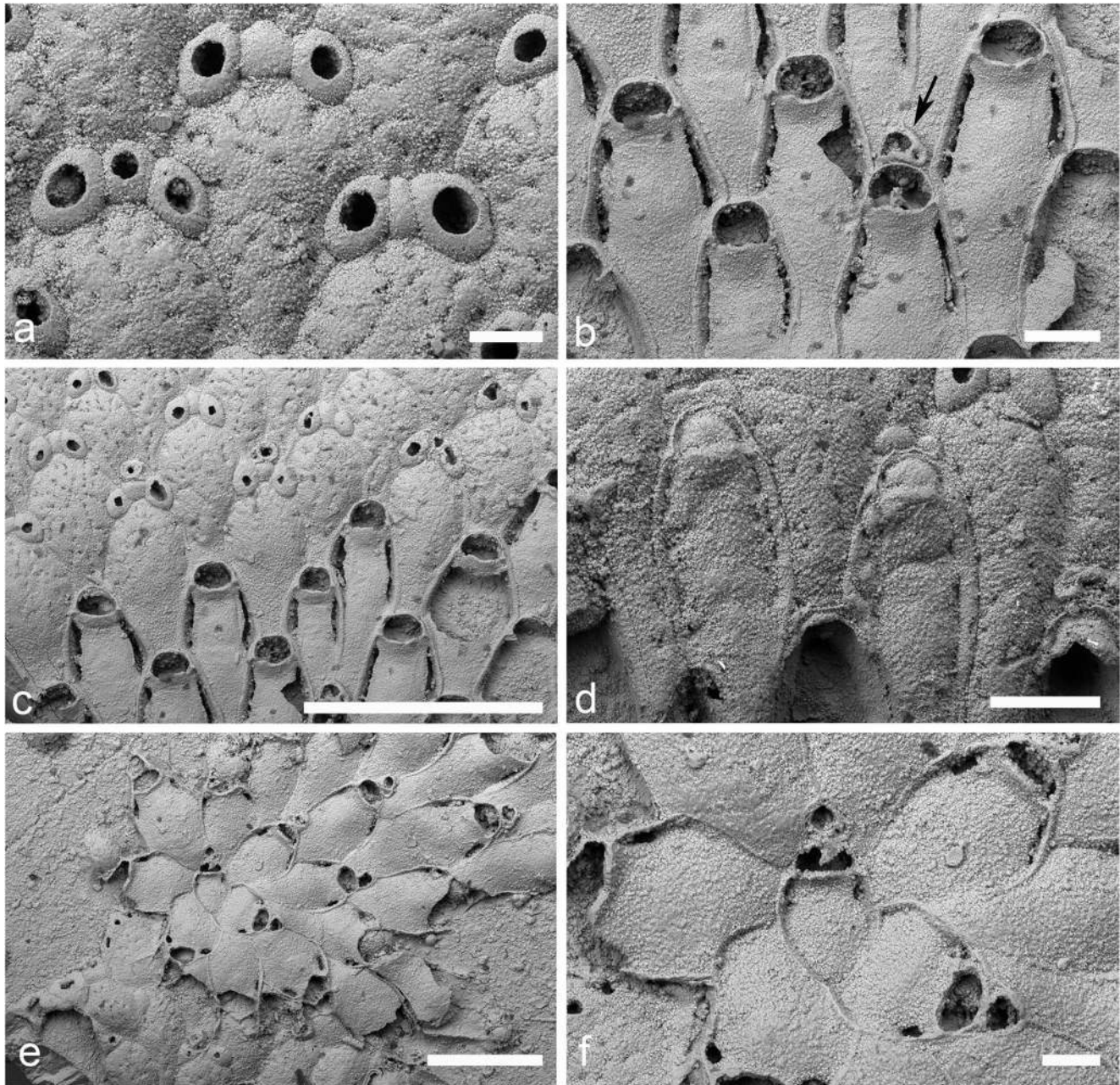


**Fig. 5** Scanning electron micrographs of '*Micropora*' *eleanorae* (Brydone), a Chalk cheilostome bryozoan showing evidence of dormancy and regrowth; *mucronata* Zone, Earlham Limeworks, Norwich, Norfolk (Rowe Collection). **a, d** NHMUK D42246; **a** kenozooids with three small distal polymorphs, most open; **d** transitional zooids with rugose cryptocysts and closed opesia. **b, c, e, f** NHMUK D42162; **b** autozooids showing elongate opesiules and a single small avicularium (arrow); **c** transition between autozooids (bottom) and distal band of kenozooids (top); **e** subcolony originating from band of kenozooids (bottom); **f** detail of subcolony showing small 'pseudoancestrula' at the centre. *Scale bars* **a, f** 100 μm; **b, d** 200 μm; **c, e** 500 μm

then degenerated. Each closed zooid is succeeded by up to four tiny oval structures, interpreted as small polymorphs, which can be closed or have an ovoidal opening (opesia). The small polymorphs are typically in pairs distolaterally of the closed zooid, the pair sometimes being separated by a third, slightly smaller median kenozooid which is occasionally followed distally by a fourth kenozooid. One of the colonies from the Rowe Collection (NHMUK D42162) contains autozooids with a more conventional microporoidean morphology (Fig. 5b). These have smooth, sunken cryptocystal walls pierced distolaterally by a pair of elongate opesiules and distally by semicircular opesia. A small avicularium is present distally of some of the autozooids. However, ovicells are absent in this and all other known specimens of 'Micropora' eleanorae. The autozooids are located proximally of the kenozooids and there is a gradual transition between the autozooids and the distal zone of kenozooids. Some intermediate zooids initially have the appearance of an autozooid, with a smooth, slightly depressed cryptocyst grading distally into a porous closure plate (Fig. 5c). Alternatively, transitional zooids may have a granular cryptocyst and small semicircular closure plate filling the opesiae (Fig. 5d).

Voigt (1975) noted the synonymy of 'Micropora' eleanorae with Micropora bedensis Brydone, 1936, which was described from Hampshire later in the same publication. He regarded the contrast between the closed zooids and the normal autozooids as an extreme example of heteromorphy in a bryozoan. Noting that the autozooids had sometimes disappeared before the substrate was finally buried as their former sites could be occupied by other bryozoans, Voigt considered the autozooids to perhaps have been of aragonitic composition and lost by leaching as he found no evidence that they were eroded or nibbled by predators. He was unable to explain why 'Micropora' eleanorae should have two distinct kinds of zooids, i.e. 'normal' autozooids and closed kenozooids.

The location of the bands of kenozooids at the very outer edges of colonies shows that they were formed after budding of autozooids ceased. While this may appear to indicate the final phase of colony development, one exceptional specimen (NHMUK D42162) demonstrates otherwise. New subcolonies in this specimen can be seen originating from the distal edges of the kenozooidal bands (Fig. 5e). The subcolonies are fan-shaped, consist only of autozooids, and may overgrow the kenozooids from which they originate. Each subcolony can be traced back to a tiny pseudoancestrula surrounded by 6 or 7 autozooids (Fig. 5f). Autozooid size increases distally away from the pseudoancestrula, defining a secondary zone of astogenetic change. More than one subcolony may be formed from a single band of kenozooids but all are located on the outer distal side and never the inner, proximal side of the band. The formation of a pseudoancestrula is possible because of the existence in the most distal kenozooids of open communication pores that could apparently function as potential budding

sites. Although very few subcolonies have been observed, this is not surprising in view of the pervasive loss of autozooids in 'Micropora' eleanorae and it is probable that they played a key role in the growth of colonies. Indeed, the layering of kenozooids evident in some colonies suggests a pattern of colony growth involving repeated cycles of budding of autozooids transitioning into kenozooids from which new subcolonies of autozooids later originated. Under this model, the kenozooids are interpreted as having been budded when growth slowed down as a prelude to the colony becoming dormant. During dormancy, the autozooids ceased to function and most were lost, perhaps because they were not maintained and therefore vulnerable to biotic and abiotic destruction, or alternatively through skeletal resorption. In contrast, the heavily calcified kenozooids survived on the substrate surface, becoming the loci for the formation of subcolonies consisting of autozooids when colony growth was resumed.

A similar pattern of inferred dormancy followed by renewed colony growth is evident in a species of the cheilostome Stichomicropora occurring in the Coniacian of Kent. This species, provisionally identified as S. sussexiensis (Brydone, 1936) and corresponding to the Stichomicropora sp. 3 of Ostrovsky and Taylor (2005), also developed bands of closed kenozooids around the colony margins (Fig. 6a–d). The kenozooids have a sealed rudimentary orifice which may have a pair of vestigial oral spine bases (Fig. 6b) like those of the autozooids. The paired opesiules penetrating the cryptocysts of the autozooids are lacking in the kenozooids. Only two generations of kenozooids are generally present in each band, with those constituting the outer, more distal generation being slightly smaller (Fig. 6a, c). Some examples of S. sussexiensis comprise a 'fairy ring' of kenozooids (Fig. 6d) in which only traces of the vertical walls of the autozooids remain intact. As with 'Micropora' eleanorae, subcolonies consisting of autozooids originated from the distal edges of the kenozooidal bands (Fig. 6e, f). The first zooid—pseudoancestrula—of each subcolony is relatively small but progressively larger autozooids were budded through a secondary zone of astogenetic change. Some of these autozooids may overgrow the kenozooids of the parent colony. Thus, the pattern of colony development in S. sussexiensis resembles that evident in 'M.' eleanorae, with the budding of peripheral bands of kenozooids immediately prior to periods of presumed dormancy, followed by resumption of growth through the formation of subcolonies of autozooids from the outer edges of the kenozooidal bands.

Another Coniacian species, resembling Wilbertopora inhospita (Brydone, 1929), also buds sealed kenozooids at colony margins but differs from both S. sussexiensis and 'M.' eleanorae in having 'membraniporimorph' autozooids without a cryptocyst (Fig. 7a, lower right). In addition, autozooids with closure plates are also developed in W. cf. inhospita. These are slightly larger than the closed kenozooids and, importantly, bear a crescent-shaped impression of the operculum at the distal
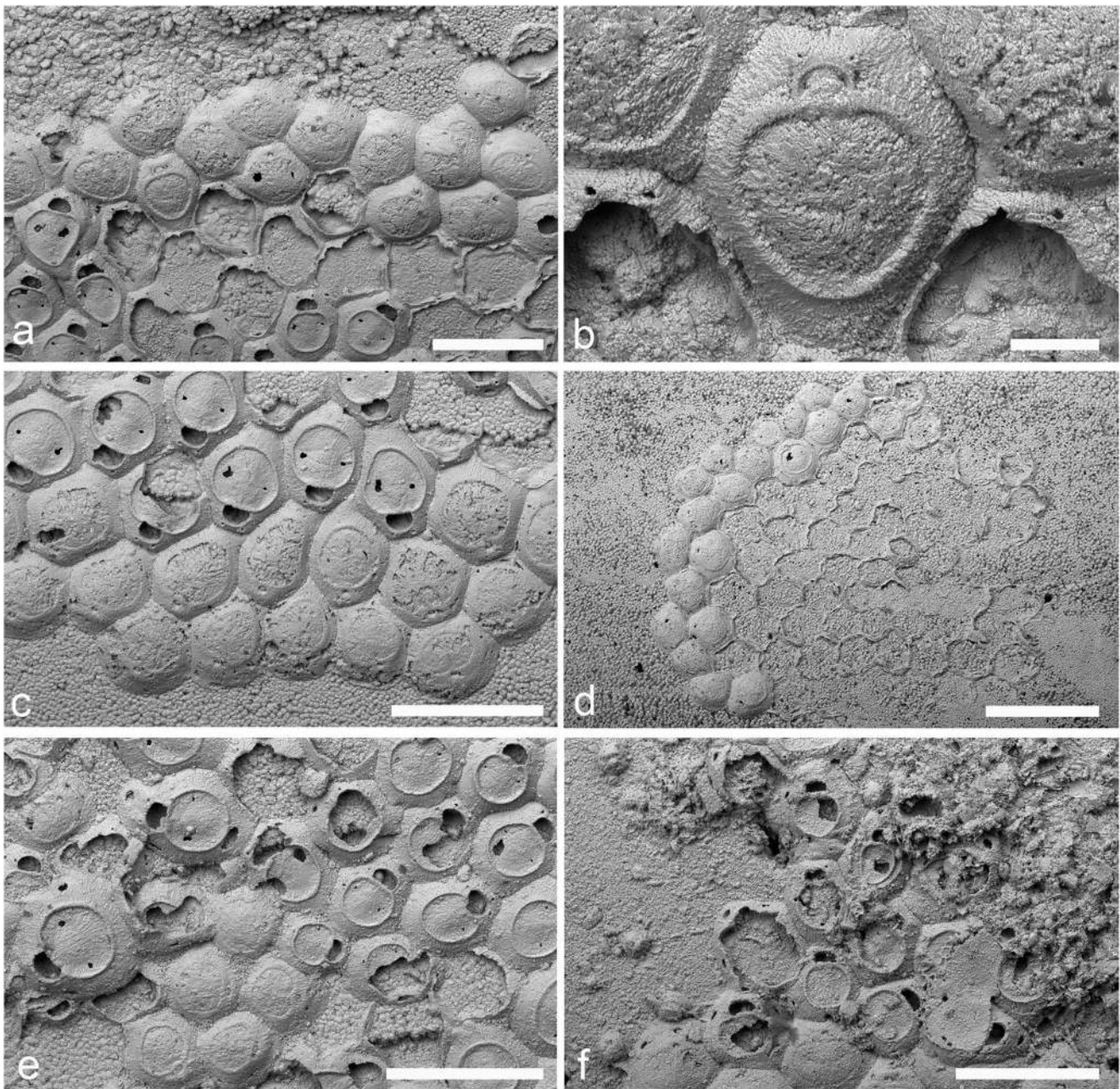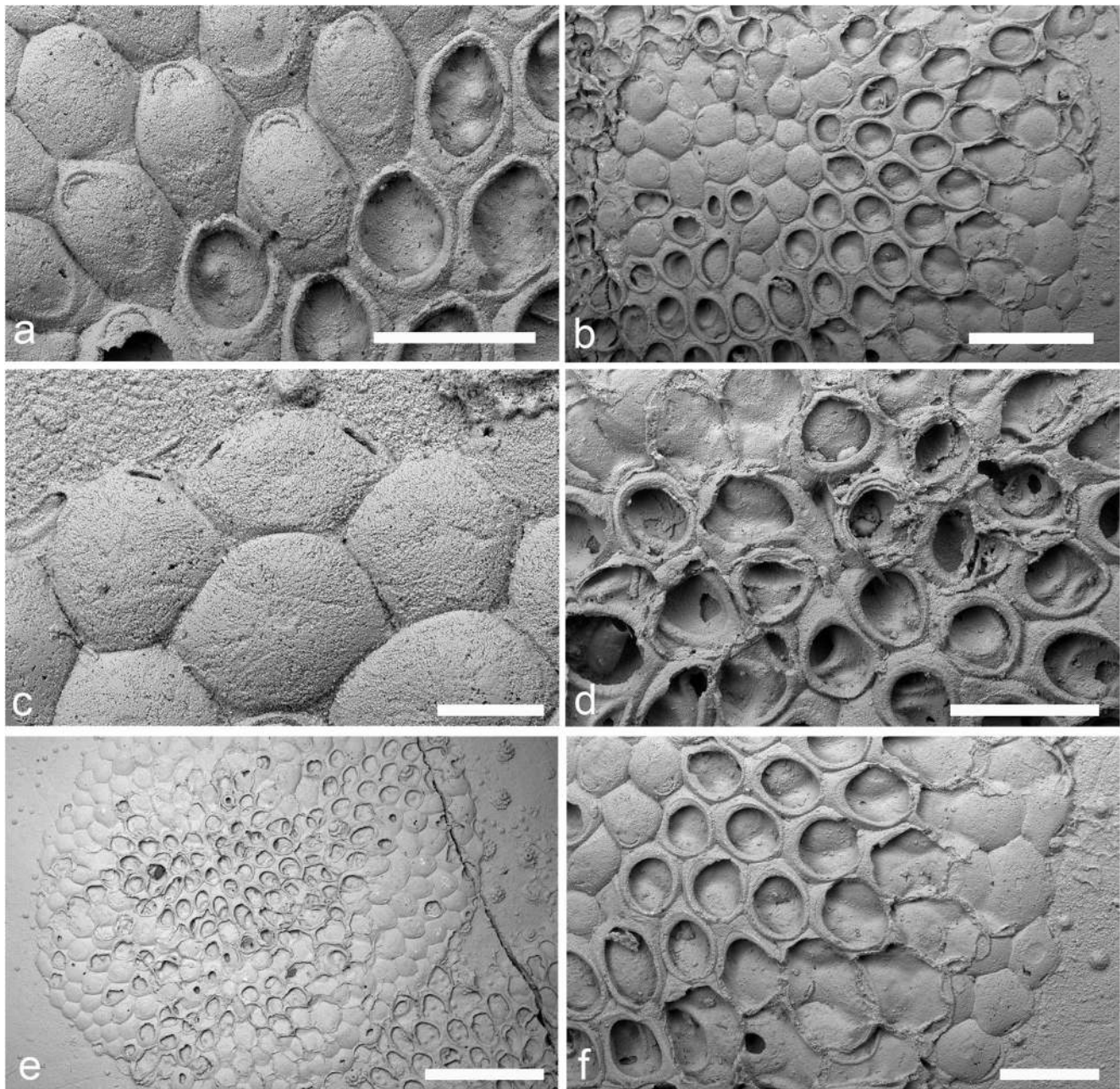
**Fig. 6** Scanning electron micrographs showing evidence for dormancy and regrowth in the Chalk cheilostome bryozoan *Stichomicropora sussexiensis* (Brydone). **a–e** NHMUK D3878, Upper Chalk, Chatham, Kent (Gamble Collection); **a** closed kenozooids at the distal edge of a colony; **b** detail of a closed kenozooid showing rudimentary orifice and a pair of oral spine bases; **c** transition from autozooids (top) to kenozooids (bottom); **d** 'fairy ring' of closed kenozooids remaining after destruction of the less calcified autozooids; **e** autozooids in a subcolony originating from a band of closed kenozooids. **f** Autozooids developing from a band of closed kenozooids (bottom), NHMUK D12124, *cortestudinarium* Zone, Luton, Chatham, Kent (Gamble Collection). *Scale bars* **a**, **c**, **e**, **f** 500 μm; **b** 100 μm; **d** 1 mm

end (Fig. 7a, upper left), showing that they formerly had a feeding capability. The closed autozooids occur immediately proximal of the band of closed kenozooids and can also be developed in the oldest parts of the colonies (Fig. 7b). Unlike *S. sussexiensis* and '*M.*' *eleanorae*, subcolonies have not been observed developing from the distal bands of closed kenozooids, even though these may have open communication pores (Fig. 7c) that could potentially function as budding loci

for such subcolonies. Instead, colonies possess overgrowths (frontal subcolonies) that originate from close to the centre of the colony (Fig. 7d), spreading outwards over earlier formed closed and open zooids (Fig. 7e, f). The pattern of colony growth inferred for *W.* cf. *inhospita* entailed budding of autozooids to form a subcircular colony up to 10 mm in diameter. As the colony developed, the oldest autozooids at the centre became sealed by closure plates, a common feature of

**Fig. 7** Scanning electron micrographs of the Chalk cheilostome bryozoan *Wilbertopora* cf. *inhospita* (Brydone), NHMUK D11377, top *cortestudinarium* Zone or base *coranguinum* Zone, Chatham, Kent (Gamble Collection). **a** Transition from open autozooids (bottom right) to autozooids with closure plates to kenozooids (top left). **b** Overgrowth, the distal zooids of which are open autozooids. **c** Closed kenozooids at the edge of a colony with slit-like pore windows. **d** Origin of a frontal sub-colony. **e** Low magnification view of colony with overgrowth showing mix of open and closed zooids. **f** Detail of overgrowth shown in **b**. *Scale bars* **a**, **d**, **f** 500 μm; **b** 1 mm; **c** 200 μm; **e** 2 mm

*Wilbertopora* and its close relatives (e.g. Cheetham et al. 2006). Colony dormancy was apparently initiated by the secretion of similar closure plates in distal zooids and the formation of a band of small, closed kenozooids immediately prior to cessation of budding at the growing edge of the colony. Further colony growth occurred through eruptive budding near the colony centre to give a new layer of zooids that grew radially outwards over the older zooids.

Comparable features have also been observed in *Biaviculigera lafrenzi* Voigt, 1989 from the late Cenomanian of Saxony, Germany. Colonies re-imaged by Martha et al. (2017) show marginal rows of kenozooids that are sealed by closure plates lacking scars of an operculum. Although very similar to inferred dormancy patterns in the English Chalk cheilostomes, renewed colony growth has not been observed in any of the colonies of *Biaviculigera lafrenzi*.
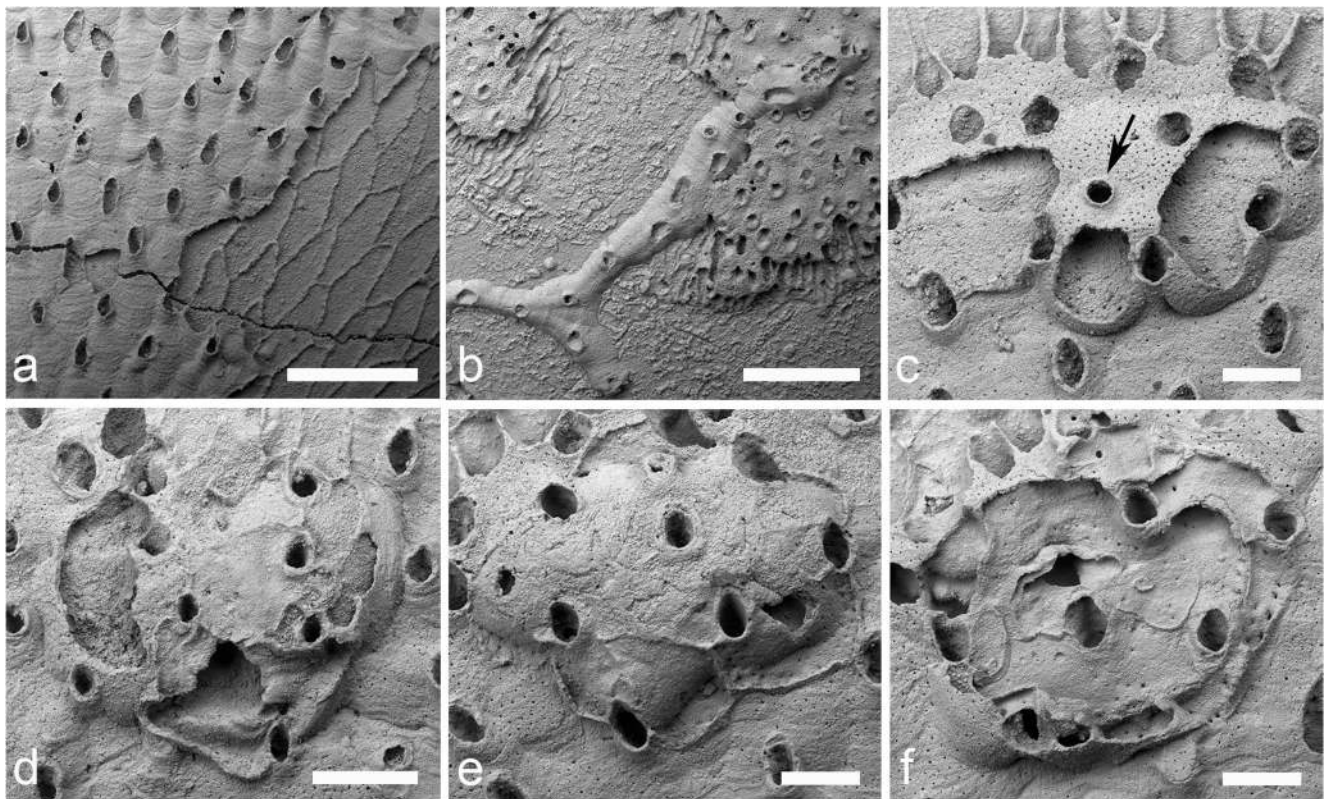
## Damage and repair

Colonial animals such as bryozoans are able to sustain substantial amounts of damage and yet survive. This is possible because of their modular construction: individual zooids, which are functionally semi-autonomous, can die without causing death of the colony as a whole, a phenomenon known as partial mortality (e.g. Sebens 1987). Subsequently, the damaged parts of colonies may be repaired using the resources of the surviving zooids. Skeletal damage is common in Chalk bryozoans but has been seldom documented, probably because resolving the small-scale diagnostic structures requires well-preserved material (i.e. clean colony surfaces not obscured by sediment or cement) and the availability of a scanning electron microscope.

Skeletal damage without repair (Fig. 8a) can occur not only during the lifetime of the colony (i.e. *syn-vivo*) but also post-mortem but pre-burial, as well as post-burial (e.g. by contemporary surface weathering). The ambiguous timing of such damage makes it less useful as evidence for the palaeoenvironment on the Chalk seabed.

However, instances of damaged parts of colonies overgrown by other encrusters (Fig. 8b) show unequivocally that some damage occurred before burial of the substrate and also furnish evidence that hard substrates on the Chalk seabed were available to sclerobionts for considerable lengths of time.

### Gonozooid repair

Colonies of an un-named cyclostome bryozoan referred to as *Mesonopora laguncula* (Voigt) by McKinney and Taylor (1997) but distinct from this species and belonging to a new genus are common in *coranguinum* Zone Chalk of Kent. The gonozooid in this species varies in shape, tending to be roughly subtriangular or transversely elliptical, and has the ooeciopore located at the centre of the brood chamber (Fig. 8c), directly above the opening to the proximal part of the fertile zooid which is visible when the roof of the brood chamber is missing. This species is remarkable among cyclostomes in general as it commonly shows evidence for repair of the brood chamber. Several



**Fig. 8** Scanning electron micrographs of Chalk cyclostome bryozoans from southern England showing damage and repair structures. **a, c–f** 'Mesonopora' laguncula sensu Taylor and McKinney *non* Voigt, NHMUK BZ1053, *coranguinum* Zone, Northfleet, Kent (Rowe Collection); **a** colony with large area (lower right) of zooids lacking frontal walls; **c** gonozooid in another colony showing partly broken roof and ooeciopore (arrow); **d, e** two gonozooids from the same colony showing evidence of repair in the form of a second roof seemingly secreted within the damaged primary roof; **f** roofless gonozooid from a different colony with an unusual pattern of calcification suggestive of damage repair. **b** Ribbon-like cyclostome overgrowing worn part of a colony of 'Berenicea' indicating damage before final burial, NHMUK BZ8666, *cortestudinarium* Zone, Luton, Chatham, Kent (Rowe Collection). *Scale bars* **a, b** 1 mm; **c–f** 200 μm

brood chambers of 'Mesonopora' laguncula sensu Taylor and McKinney have brood chambers with broken roofs within which is visible a second roof presumably formed after damage of the primary roof (Fig. 8d–f). Buttress-like radial walls may extend between the two roofs. It is unclear exactly how or why such reparative calcification of these gonozooids was undertaken but the brooding embryos would undoubtedly have been an attractive food source to small predators, which may explain their breakage. Breakage of gonozooids in other species of Chalk cyclostomes is common but without evidence of repair it is impossible to know whether this occurred *syn-vivo* or was post-mortem.

### Intramural buds

Termed '*régéneration totale des bryozoaires*' by Levinsen (1907), and not to be confused with polypide regeneration (e.g. Gordon 1977), intramural buds formed by the budding of a new zooid within the skeletal chamber of an existing zooid have been described from a wide range of cheilostome bryozoans (Buchner 1918; Taylor 1988; Berning 2008). However, almost nothing is known about their mode of formation, although Berning (2008) argued that the most plausible explanation for intramural buds was through reparative budding following predation of the original zooid.

Taylor (1988) described the occurrence of intramural buds in the runner-like Chalk bryozoan *Herpetopora*. These most often have the same proximal–distal orientation as the host zooid but sometimes are reversed in polarity. The latter are interpreted to indicate that the intramural bud arose from a distal rather than a proximal zooid. One or a series of concentrically younger intramural buds may be present within the same host zooid, indicating a succession of reparative zooids occupying a zooidal chamber of ever-decreasing size. Intramural buds within the autozooids of *Herpetopora* can comprise other autozooids (Fig. 9a) or kenozooids (Fig. 3c).

Calloporid cheilostomes in the Chalk very frequently contain intramural buds, visible as 'Russian Doll'-like concentric mural rims (Fig. 9b, c). The ribbon-like species of *Pyriporella* mentioned and figured above (Fig. 3j, k) includes some zooids containing up to three intramural autozooids (Fig. 9d).

The onychocellid cheilostome *Hoplitaechmella vespertilio* (von Hagenow, 1839) is represented in the NHMUK collections by a large colony from the Chalk (?early Maastrichtian) of Trimingham, Norfolk containing several autozooids that have been repaired (Fig. 9e, f). Within each damaged zooid is an apparent intramural bud with a new opesia, slightly smaller than usual, bordered distally by a row of oral spine bases parallel and proximal to those of the host zooid. The cryptocyst of the intramural bud overlaps that of the host zooid but does not extend all the way to its proximal end. In some instances, the two distolateral avicularia associated with the

autozooid are 'double-walled', indicating that they too represent intramural buds.

A zooid of the cribrimorph cheilostome *Pelmatopora repleta* (Brydone, 1917) (Fig. 10a) contains an extraordinary intramural bud (Fig. 10b). Emerging from the broken ends of the costae of the host autozooid are a new series of costae that form the frontal shield of the intramural autozooid (Fig. 10c). This reparative autozooid has an orifice with a distal rim having 4 oral spine bases, located just inwards of the distal rim of the orifice of the host autozooid. Destruction of the frontal shield of the host zooid is difficult to explain except as a result of the single zooid being attacked by a micropredator, following which the adjacent zooids were the source of an intramural bud that grew its costae through the lumens of the broken costae of the host zooid.

### Colony repair

Extreme resilience among the Chalk encrusting bryozoans is illustrated by a colony of the cyclostome genus *Actinopora* from the *coranguinum* Zone of Kent (Fig. 11a). The remnants of what was evidently a colony comprising two subcolonies of more or less equal size occurs on the test of an echinoid. Only the distal edges of these subcolonies are preserved as an outer rim of very worn zooids (Fig. 11b). Originating close to the junction of the two subcolonies is a patch of new growth. This comprises pristine zooids and a fresh distal growing edge that extends out across the area of substrate formerly occupied by the two original subcolonies towards the rim of worn zooids. While it is possible that the new growth represents a different colony that fouled the abraded colony, the position of origin and parallel growth favour its interpretation as due to reparative growth following almost total destruction of the original colony.

### Chalk hard substrate colonisation

The distribution of encrusting sclerobionts on the Chalk seabed was controlled by the availability of hard or firm substrates. The most important hard substrates were the tests of irregular echinoids, particularly *Echinocorys* and to a lesser extent *Micraster*, which dominate the historical collections used here. Therefore, the following discussion focuses mainly on echinoid substrates.

A high proportion of *Echinocorys* tests found in the Chalk of southern England are encrusted or bored (Donovan and Lewis 2011). These shallow infaunal deposit feeding holasteroids (e.g. Engelke et al. 2016) formed 'benthic islands' on the seabed that were colonised post-mortem by both encrusters and borers. Nebelsick et al. (1997) noted that encrustation of dead echinoid tests, although they are less robust than mollusc shells, is rather common in the fossil record. As suggested for sclerobiont-bearing tests of *Micraster* from the Late Cretaceous of northern Spain (Zamora et al. 2008), exhumation of the *Echinocorys* tests
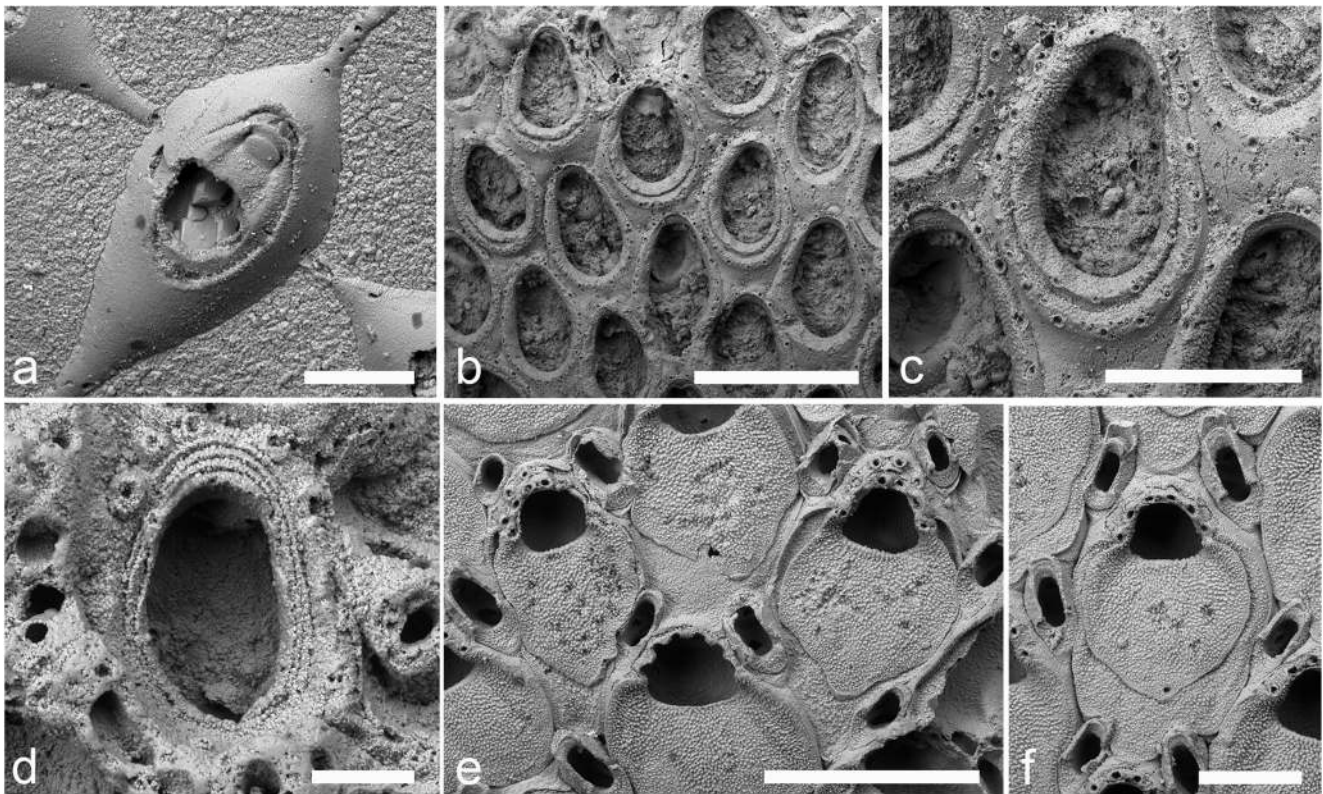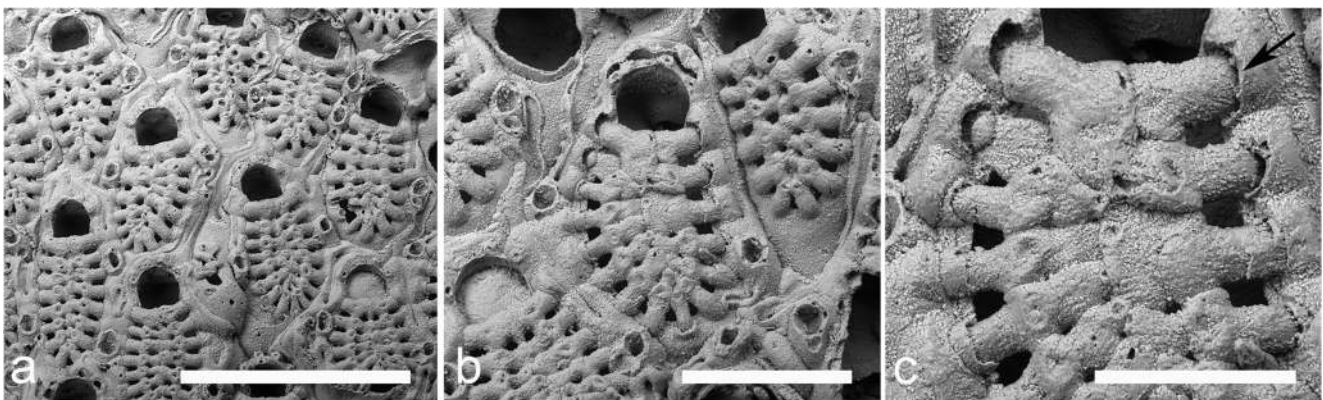
**Fig. 9** Scanning electron micrographs of intramural buds in some Chalk cheilostome bryozoans from southern England. **a** Autozooid of *Herpetopora laxata* (d'Orbigny) containing an intramural autozooid with a broken closure plate bearing an impression of the operculum, NHMUK D42361, *mucronata* Zone, Thorpe St Andrew, Norwich, Norfolk (Rowe Collection). **b**, **c** *Flustrellaria ?hopensis* (Brydone) showing several autozooids containing intramural buds (**b**) with a close-up of a single autozooid hosting an intramural bud (**c**), *cortestudinarium* Zone, Seaford, Sussex (Rowe Collection). **d** Three intramural buds within a single autozooid of ?*Pyriporella* sp. (Fig. 3j, k), NHMUK BZ8662, *coranguinum* Zone, Northfleet, Kent (Rowe Collection). **e**, **f** *Hoplitaechmella vespertilio* (von Hagenow), NHMUK D15590, Upper Chalk [?Lower Maastrichtian], Trimingham, Norfolk; **e** group of zooids, the left and right autozooids containing intramural autozooids indicated by the additional row of oral spine bases; **f** autozooid with an extra layer of cryptocystal wall and two distolateral avicularia that both host reparative intramurally budded avicularia. *Scale bars* **a**, **f** 200 μm; **b** 1 mm; **c**, **e** 500 μm; **d** 100 μm

may have occurred by three processes: storm-induced currents, the action of 'bulldozing' bioturbators, or as a result of the echinoids themselves coming to the surface. The overall distribution of the sclerobionts covering all parts of the tests suggests that they were rolled on the seabed during the period of their colonisation (e.g. Hancock 1975). Almost all of the bryozoans in the collection studied encrust the external surface of the tests. Broken tests often reveal extensive growth of



**Fig. 10** Scanning electron micrographs of damage and repair in the Chalk cheilostome bryozoan *Pelmatopora repleta* (Brydone) encrusting an echinoid test, NHMUK BZ8667, *coranguinum* Zone, Northfleet, Kent (Rowe Collection). **a** Group of zooids, the autozooid in the lower right occluded by a closure plate. **b**, **c** Autozooid in which the original costate frontal shield was mostly destroyed and the new costate frontal shield of an intramural bud grew from inside the broken ends of the original costae (arrow in **c**). *Scale bars* **a** 1 mm; **b** 500 μm; **c** 300 μm
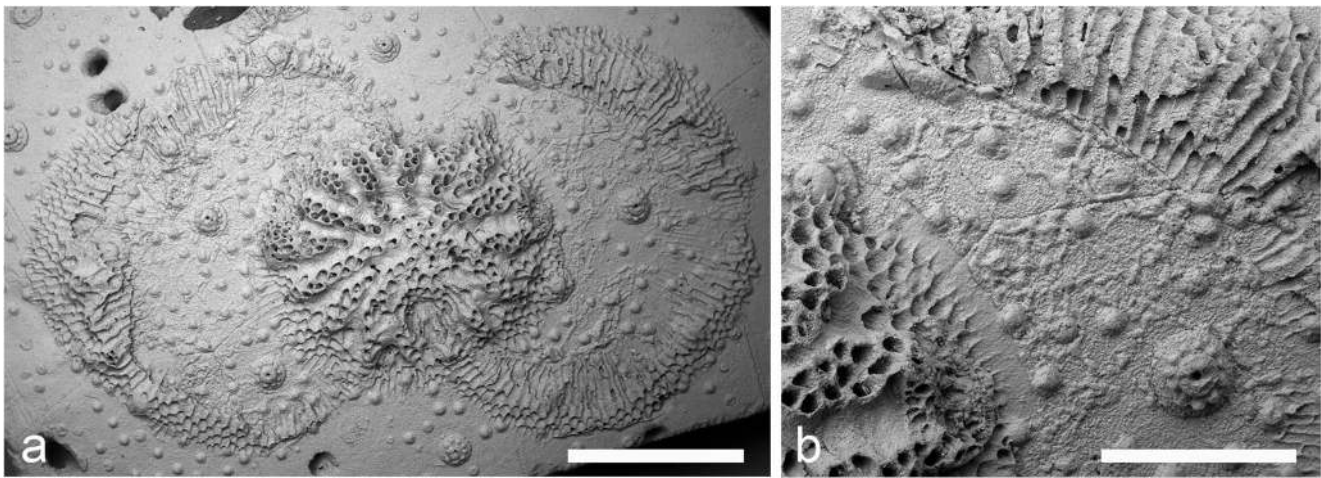
**Fig. 11** Scanning electron micrographs of damage repair in the Chalk cyclostome bryozoan *Actinopora*, NHMUK BZ8668, *coranguinum* Zone, Northfleet, Kent (Rowe Collection); **a** original bilobate colony (possibly consisting originally of two almost equal-sized subcolonies) almost totally destroyed, revealing the tubercles of the echinoid substrate, and partly overgrown by a new subcolony (centre); **b** new subcolony (lower left) budding zooids over the exposed substrate towards the worn remnants of the original colony (upper right). *Scale bars* **a** 2 mm; **b** 1 mm

coarse syntaxial cement on the inner surfaces of the plates, and this would likely mask or obliterate any encrusters on the test interiors.

Erosion of test surfaces is evident from the common truncation of the spine bases, as well as the damage to some of the bryozoans (e.g. Fig. 8a, b). This is assumed to be biologically mediated (i.e. bioerosional), even though clear examples of ichnofossils such as *Gnathichnus* produced by the gouging teeth of regular echinoids are seldom apparent. Erosion of the tests suggests that they spent a significant residency time on the seabed and were available as substrates for colonisation by and growth of encrusting sclerobiont communities over a considerable period of time. Yet the density of encrusters is invariably low. Figure 2a depicts one of the most heavily encrusted echinoid tests in the collection but even in this example less than one third of the surface is encrusted. Large areas of test typically remain between distantly spaced bryozoan colonies on all of the material studied. Hammond (1988) in an unpublished doctoral thesis collected echinoids from four different stratigraphical levels in the English Chalk and quantified the surface areas of the echinoids and their encrusting sclerobionts. At all four levels, he found that less than 20% of the test surfaces were encrusted, with less than 10% at two levels.

Bryozoans occupy a greater area than any of the other encrusters in the material studied. While selection by collectors in favour of bryozoans may partly account for this observation, experience of collecting echinoids from the Chalk of southern England suggests that bryozoans are indeed the predominant group of encrusters present. The bryozoan-encrusted echinoid tests used in the current study may be cohabited by encrusters belonging to other taxonomic groups, such as foraminifera (Fig. 12a) *Neuropora*-like sponges (Fig. 12b), thecidean brachiopods (Fig. 12c), small cemented

bivalves (Fig. 12e) and serpulid worms. In addition, the raised edges of some bryozoans (Fig. 13a) point to overgrowth of encrusters that are not preserved. These may have been soft-bodied or have had spicular or aragonitic skeletons, lost respectively by dissociation and dissolution. Less common are examples of bioclaustration in which a bryozoan has evidently overgrown a tubular organism on the same substrate, leaving a hollow (Fig. 13b).

Despite the apparent availability of ample free substrate space, bryozoans still competed for living space. Competition can be inferred from the presence of skeletal overgrowths (Figs. 3d and 12b, d), with the usual caveats that *syn-vivo* and post-mortem overgrowths cannot always be unequivocally distinguished (see Taylor 2016). The chance settlement of two larvae in close proximity will inevitably result in contact between the growing adults as they expanded across the substrate, resulting in marginal overgrowths. Notable is an example (Fig. 12f) in which an 'exclusion zone' of apparently bare substrate surrounds much of the perimeter of a cyclostome bryozoan ('Berenicea'). The orientation of zooids of a neighbouring cheilostome towards this zone may indicate the former presence of another encruster ringing the cyclostome.

Compared to these marginal overgrowth encounters, instances of fouling overgrowth, in which one encruster settled on the surface of another, are relatively uncommon in the Chalk (Fig. 13c). Fouling is strongly resisted by many living organisms, although those with unprotected exoskeletons may be vulnerable to fouling and the example illustrated here involves a foraminifer fouling dead or dormant bryozoan zooids with closure plates (Fig. 13d). In contrast, skeletons of dead organisms are readily fouled, acting as secondary substrates on the echinoid tests. The few examples of fouling of the encrusters in the Chalk suggests that the sclerobiont assemblages on each echinoid approximate to census communities
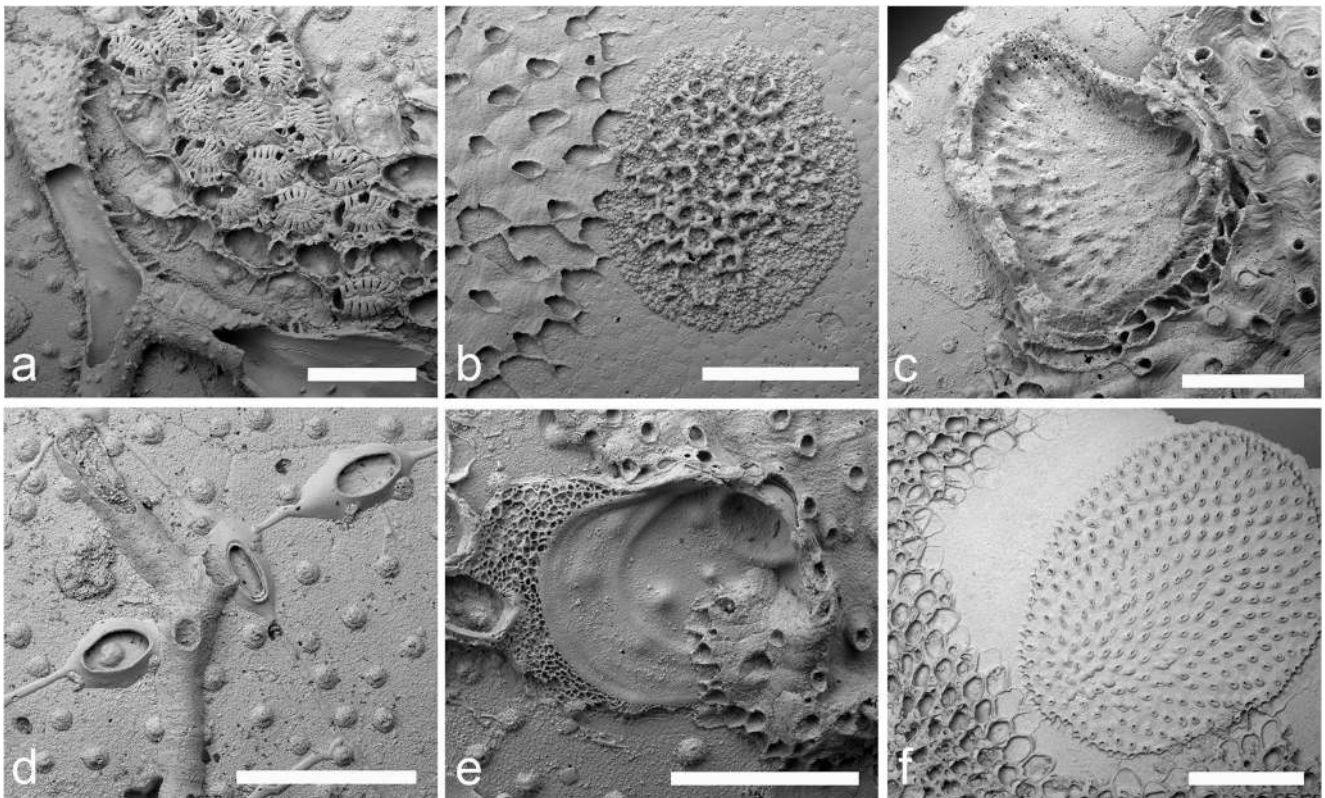
Fig. 12 Scanning electron micrographs of interactions between Chalk bryozoans and other encrusters from southern England. **a** Cribrimorph cheilostome *Carydiopora* cf. *transita* (Brydone) growing on an echinoid test towards a fistulose foraminifer (left), NHMUK BZ8661, *coranguinum* Zone, Northfleet, Kent (Rowe Collection). **b** '*Mesonopora' laguncula* sensu Taylor and McKinney *non* Voigt, edge of colony (left) beginning to overgrow a small sponge, NHMUK BZ1053, *coranguinum* Zone, Northfleet, Kent (Rowe Collection). **c** Cemented valve of a small thecidean brachiopod forming a barrier to the growth of the cyclostome bryozoan *Hyporosopora* sp. (bottom right), NHMUK BZ8669, *coranguinum* Zone, Northfleet, Kent (Rowe Collection). **d** Runner cyclostome *Stomatopora media* (von Hagenow) overgrowing runner cheilostome *Herpetopora laxata* (d'Orbigny) (elsewhere on the same echinoid substrate the overgrowth polarity is reversed), NHMUK D44681, *mucronata* Zone, Edward's Pit, Mousehold, near Norwich, Norfolk (Rowe Collection). **e** Cyclostome bryozoan *Diplosolen* sp. (upper right) with post-mortem overgrowth onto the inner surface of the left valve of a small cemented bivalve, NHMUK D44731, *mucronata* Zone, Edward's Pit, Mousehold, near Norwich, Norfolk (Rowe Collection). **f** Colony of the cheilostome *Pyriporella seafordensis* (Brydone) encroaching the cyclostome '*Berenicea*' sp. partly surrounded by a non-encrusted zone on the inoceramid shell substrate, NHMUK BZ8672, *cortestudinarium* Zone, Hope Gap to Cuckmere Haven [a few kms south-east of Seaford], Sussex (Gaster Collection). *Scale bars* **a–e** 1 mm; **f** 2 mm

of living encrusters showing little time-averaging. On the other hand, the evidence of destructive erosion of encrusters points to the likelihood that each test may have hosted a succession of discrete encrusting sclerobiont communities through ecological time, older communities being almost obliterated by (bio)erosion before the establishment of new ones.

## Discussion

Studies based on museum material that has been accumulated haphazardly without a specific sampling strategy, and which may lack precise details of stratigraphy (e.g. bed number, height above a datum) or geographical provenance, can be criticised as being anecdotal. Such material is certainly not well-suited to quantitative analysis. Nevertheless, museum material can furnish useful data for palaeoecological and palaeoenvironmental inference. This is especially true for hard substrates that formed discrete habitat islands on the seabed each colonised by its own independent sclerobiont 'microcommunity', as is the case here.

The Chalk was once considered to be a homogeneous and monotonous deposit, reflecting uniform and stable environmental conditions throughout its long period of formation (cf. Mortimore 2011). However, this concept has been challenged in recent years with the recognition of important lateral and vertical variations. Among the latter are sedimentary cycles attributed by some to orbital forcing, i.e. Milankovitch cycles (but cf. Algeo and Wilkinson 1988). These include apparent 21 ka precession cycles reflected in chalk–marl rhythms in the Cenomanian (Paul 1992), as well as alternations of laminated and bioturbated layers in the Maastrichtian (Damholt and Surlyk 2004). Variations at smaller temporal scales may be difficult to detect in the Chalk which lacks varves and is mixed
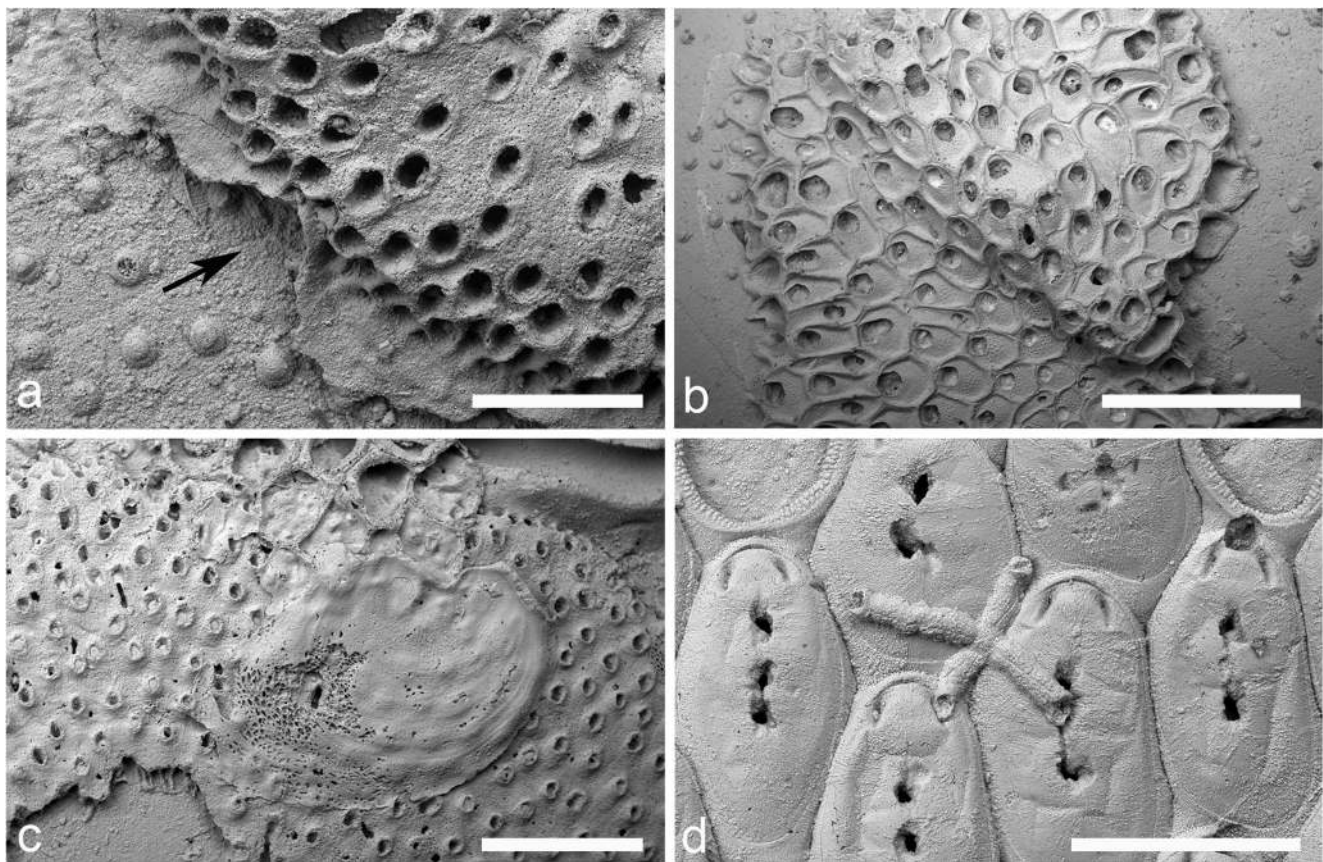
**Fig. 13** Scanning electron micrographs of Chalk bryozoans showing evidence of overgrowth of non-preserved sclerobionts (**a**, **b**) and fouling (**c**, **d**). **a** Locally raised growing edge (arrow) of the cyclostome '*Berenicea*' sp. suggesting overgrowth of a non-preserved (e.g. soft-bodied) encruster, NHMUK BZ8670, *cortestudinarium* Zone, Luton, Chatham, Kent (Rowe Collection). **b** Encrusting colony of the cheilostome *Rhagasostoma* sp. with a pronounced ruck extending from top left to bottom right inferred to be due to the overgrowth of an unpreserved elongate encruster, NHMUK BZ8671, *coranguinum* Zone, Northfleet, Kent (Rowe Collection) **c** small cemented bivalve fouling the surface of a colony of '*Berenicea*' sp., NHMUK BZ8666, *cortestudinarium* Zone, Luton, Chatham, Kent (Rowe Collection). **d** Autozooids of *Wilbertopora* sp. with closure plates fouled by the tiny cruciate foraminifer *Discoramulina* sp. (the same colony is visible in the lower right of Fig. 2c), NHMUK D46466, *cortestudinarium* Zone, Seaford, Sussex (Rowe Collection). *Scale bars* **a**, **d** 500 µm; **b** 2 mm; **c** 1 mm

by bioturbators (e.g. Ekdale and Bromley 1984). Fossil skeletons have the potential to provide evidence for environmental variations at annual or even shorter time scales.

The typically small size of most bryozoan colonies encrusting Chalk substrates compared to the sizes of the substrates themselves, which are relatively sparsely covered by encrusters, suggests that individual bryozoan colonies grew slowly and/or for limited periods of time. Slow growth is favoured by the abundant presence of reparative structures described in the current paper; these might not be expected if the colonies were extremely short-lived. Successive generations of encrusters are often present, showing that the total residency time of individual substrates on the seabed was appreciably greater than the lifespans of the bryozoan colonies that encrusted them. What then was limiting the growth and longevity of the bryozoans? Reparative structures at zooidal and colonial level are common in Chalk bryozoans. These likely reflect the activities of small predators of the kind that are almost ubiquitous among modern bryozoans (Lidgard

2008). These, however, seem unlikely to have restricted colony size to the extent observed in the Late Cretaceous Chalk. Interactions with other encrusters competing for substrate space also cannot account for the small colonies and low encrustation densities despite occasional evidence of non-fossilised sclerobionts in the form of raised edges in some bryozoan colonies and tubular bioclaustrations. The occurrence of colonies showing clear signs of dormancy and episodic growth points to periodicity in the environmental conditions experienced by the bryozoans. The clearest examples are *Stichomicropora sussexiensis* from the Coniacian of Kent (Fig. 6) and '*Micropora*' *eleanorae* from the Campanian of Norfolk (Fig. 5). In both species, bands of kenozooids were formed at the edges of colonies, signalling cessation of colony growth before rejuvenation of growth from subcolonies budded from the kenozooids. Although the temporal duration of this growth periodicity is unknown, the closest analogues among modern bryozoans, which are discussed below, favour annual dormancy.

The runner-like ctenostome bryozoan *Victorella* produces dormant zooids called hibernacula when ambient temperature decreases. Hibernacula are encased by a thickened cuticle that survive the winter and germinate when the temperature rises in the spring (Carter et al. 2010). Germination of hibernacula occurs through splitting of the cuticle and emergence of a fresh white zooid, from which zooidal budding then commences. Although hibernacula in *Victorella*, which are believed to survive through only one winter, differ from the kenozooids described from Chalk cheilostomes in lacking a hard skeleton, they may be functionally equivalent. Hibernacula are not confined to ctenostomes inhabiting environments experiencing large seasonal temperature ranges. Wood and Okamura (2017) recently described hibernacula in a species of *Hislopia* from the Amazon River basin, and hibernacula have also been recorded in a congeneric species from Thailand (Wood et al. 2006). Polymorphic zooids called sacculi in the runner-like cheilostome *Aetea* have been interpreted as functioning in asexual reproduction (Balduzzi et al. 1991), quite possibly allowing persistence and regrowth following destruction of the feeding zooids.

Bock and Cook (2001) described in the Australian cribrimorph cheilostome *Corbulipora* zooids with occluded orifices and interiors filled by orange-coloured tissue, likening them to hibernacula and suggesting a storage function. Closed zooids in the malacostegine cheilostome *Conopeum tenuissimum* (Canu, 1928) from Ghana were described by Cook (1985, p. 87) as often remaining on shell substrates when the rest of the colony had died, prompting her to suggest that they functioned as hibernacula, possibly in response to desiccation, raised temperatures or salinities. She did not state whether budding was resumed from the closed zooids of *C. tenuissimum*.

Comparisons can also be made with the aberrant Recent bryozoan *Harmeria scutulata* (Busk, 1855) from the Arctic. Colonies in this ascophoran cheilostome initially bud large feeding zooids but then switch to small polymorphic zooids that form a ring up to 6 generations deep around the perimeter of the near-circular colony. The small polymorphs are gonozooids in which embryos are brooded (Kuklinski and Taylor 2006). Some of the gonozooids survive the winter when strong current action or ice scour destroy the weakly calcified autozooids. It is inferred that the embryos are released from the gonozooids in the spring to initiate new colonies elsewhere. While most colonies of *Harmeria* seem to be annuals, some that colonised settlement panels survived over the winter and subsequently began budding new subcolonies consisting initially of autozooids. This growth pattern is reminiscent of *Stichomicropora sussexiensis* and '*Micropora*' *eleanorae* from the Chalk. However, the kenozooids in these two Cretaceous species lack large enough openings through which larvae could emerge (cf. *Harmeria* gonozooids) and therefore cannot also have functioned as brooding zooids.

What factor/s could explain the apparent seasonality in growth of bryozoans from the Chalk? It seems unlikely that seasonal variations in water temperature at the depths inhabited by the bryozoans would have been the immediate cause as such variations may have been minor given the relative warm and equable Late Cretaceous climate at the palaeolatitude (*c*. 30–40°N) of Chalk deposition (Steuber et al. 2005). A more appealing possibility is that seasonal bryozoan growth was driven by variations in qualitative and quantitative plankton availability on the seabed.

Supply of coccoliths onto the seabed from the rain of dead coccolithophores is often seasonal in modern environments (e.g. Mergulhao et al. 2013). For example, the living coccolithophore *Emiliania huxleyi* forms blooms seasonally when waters are temporarily depleted in nutrients. While living bryozoans feed on phytoplankton, coccolithophores do not appear to feature in their diets. Indeed, naked phytoplankton are the food source of all bryozoans except for a small number of species that have gizzards capable of crushing diatom frustules (McKinney 1990). Furthermore, there is evidence that at least some coccolithophore species are toxic to bryozoans (Jebram 1980; Houdan et al. 2004). Blooms of coccolithophores might therefore have created temporarily inimical conditions on the Chalk seabed for bryozoans and other epifaunal suspension feeders. On the other hand, blooms of naked phytoplankton—particularly the dinoflagellates which feature prominently in the diets of living bryozoans—would have been favourable for bryozoans; the occurrence of dinoflagellate cysts in the Chalk (e.g. Pearce et al. 2003) proves that dinoflagellates were present in the Chalk Sea. A parallel can be drawn with the present-day Antarctic where the feeding activity of bryozoans is at least in part correlated with phytoplankton blooms (Barnes and Clarke 1995). Coccolithophore blooms in the Chalk Sea may even have been closely correlated with reductions in other types of phytoplankton. Tyrrell and Holligan (1999) modelled the impact of coccolithophore blooms on the irradiance of the ocean showing that while the top few metres become brighter, deeper waters become darker, suggesting a negative impact on phytoplankton beneath the very surface layers of the ocean.

In summary, seasonal cycles in the plankton inhabiting the photic zone above the deeper waters of the Chalk seabed are hypothesised to have impacted the feeding and the growth of epifaunal suspension feeders such as bryozoans. During favourable times, the flux of phytoplankton would have contained a high proportion of dinoflagellates, providing food for the bryozoans which were able to flourish and grow, even if only for short periods perhaps of a few weeks or months. At other times, coccolithophores may have dominated the phytoplankton flux. These would not only have been unsuitable as bryozoan food but also potentially toxic and could have shaded all but the very surface of the ocean reducing photosynthesis and consequently edible phytoplankton supply to bryozoans

on the seabed. Limited periods or discontinuous abundance of naked phytoplankton as food could account for the characteristically small size of the bryozoan colonies compared to the large substrates such as echinoids that were available for their growth. While many bryozoan colonies would have perished during blooms of inedible and possibly toxic coccolithophores, a few were apparently able to survive these adverse conditions by developing hibernacula-like kenozooids.

Based on functional ecological inferences from encrusting bryozoans only, a tentative hypothesis proposes seasonal alternations between coccolithophore- and dinoflagellate-rich plankton fluxes to the Chalk seabed. Supporting morphological evidence is required from other groups of benthic suspension feeders which might also show seasonality in skeletal growth patterns, as well as geochemical and isotopic profiling (cf. Walliser et al. 2018) to test this hypothesis.

## Compliance with ethical standards

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