

PRESERVATION OF SOFT-BODIED AND OTHER ORGANISMS BY BIOIMMURATION – A REVIEW

by P. D. TAYLOR

ABSTRACT. Bioimmuration is a poorly-known mode of preservation which results from organic overgrowth of sessile organisms. Soft-bodied organisms (and organisms with lightly mineralized skeletons) can be preserved if overgrown by other organisms possessing mineralized skeletons. These bioimmured fossils are visible on the attachment areas of the overgrowing organisms as natural moulds which sometimes become filled by diagenetic mineral growth to give a natural cast. Three types of bioimmuration are distinguished: substratum bioimmuration, epibiont bioimmuration and bioclastration. Common bioimmuring organisms include oysters and oyster-like cemented bivalves, serpulid worms and cyclostome bryozoans. Among organisms found preserved by bioimmuration are algae, marine angiosperms, hydroids and ctenostome bryozoans. Most documented finds of bioimmured fossils are from the post-Palaeozoic, especially the late Cretaceous, reflecting both the stratigraphical distribution of potential bioimmuring organisms and concentration of research effort. Future finds of bioimmured fossils offer considerable scope for adding to our knowledge of the fossil history and ecological contributions of soft-bodied organisms living on firm or hard substrata.

SEDIMENTS containing fossils of soft-bodied marine organisms (i.e. organisms lacking mineralized skeletons) provide invaluable windows into parts of the biosphere which are normally unavailable to the palaeontologist. Several such deposits, described as fossil Lägerstätten, have been intensively studied, notably the Burgess Shale, Hünshuck Shale and Solnhofen Limestone (e.g. see papers in Whittington and Conway Morris 1985). Instrumental in the preservation of these soft-bodied biotas were rather special taphonomic factors generally involving rapid burial in fine-grained sediments and inhibition of organic decay. Because these circumstances have occurred rather infrequently during the Phanerozoic, soft-bodied Lägerstätten are comparatively rare in the marine record.

In contrast, bioimmuration is a process of organic overgrowth which routinely results in the preservation of sessile soft-bodied organisms in unexceptional palaeoenvironments. Very few studies have been undertaken of bioimmuration, and even the existence of this important mode of preservation is poorly known among palaeontologists. Vialov (1961) first recognized immuration as a mode of fossilization. He distinguished two types of immuration: lithoimmuration (e.g. envelopment of snakes by calcareous tufa during hibernation) and bioimmuration (e.g. overgrowth of balanid barnacles by oysters). Only Voigt (1956, 1966, 1968*a, b*, 1972, 1973*a, b*, 1977, 1979, 1980, 1981, 1983; Voigt and Harmelin 1986) has published extensively on bioimmured fossils in a series of mostly German language papers, mainly dealing with bioimmured fossils from the late Cretaceous Chalk-Tuff of Maastricht. The present paper sets out to review the process of bioimmuration and the variety of soft-bodied organisms which have been found as bioimmured fossils.

Specimen repositories: figured specimens are in the collections of the British Museum (Natural History) (abbreviated BMNH) and the Voigt Collection, Universität Hamburg (VH).

TYPES AND PROCESSES OF BIOIMMURATION

To 'immure' means to imprison. Sessile organisms are routinely bioimmured when partially or completely overgrown by other organisms. If the overgrowing organism possesses a mineralized skeleton, then the basal surface of this skeleton may carry a preservable replicate in negative relief

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of the upper surface of the overgrown organism. Such natural moulds are bioimmurations of soft-bodied organisms. For example, many species of present-day animals and plants live as epiphytes on the fronds or stipes of marine plants. The attached undersides of these epiphytes are often adpressed very closely to their plant substrata, thereby creating a natural mould which is revealed when the epiphyte is detached from its substratum. Similarly, epiphytes sharing the same plant substratum are often found to overgrow one another. This too may result in a natural mould of the overgrown (or bioimmured) epiphyte on the base of the overgrowing (or bioimmuring) epiphyte.

It is useful to distinguish three principal types of bioimmuration: (1) *substratum bioimmuration* in which the organism being overgrown is the substratum for the bioimmuring organism (text-fig. 1A); (2) *epibiont bioimmuration* in which the overgrowing and overgrown organism share the same substratum (text-fig. 1B); (3) *bioclaustration* in which the substratum is a living organism and is itself is responsible for overgrowing the bioimmured organism (text-fig. 1C).

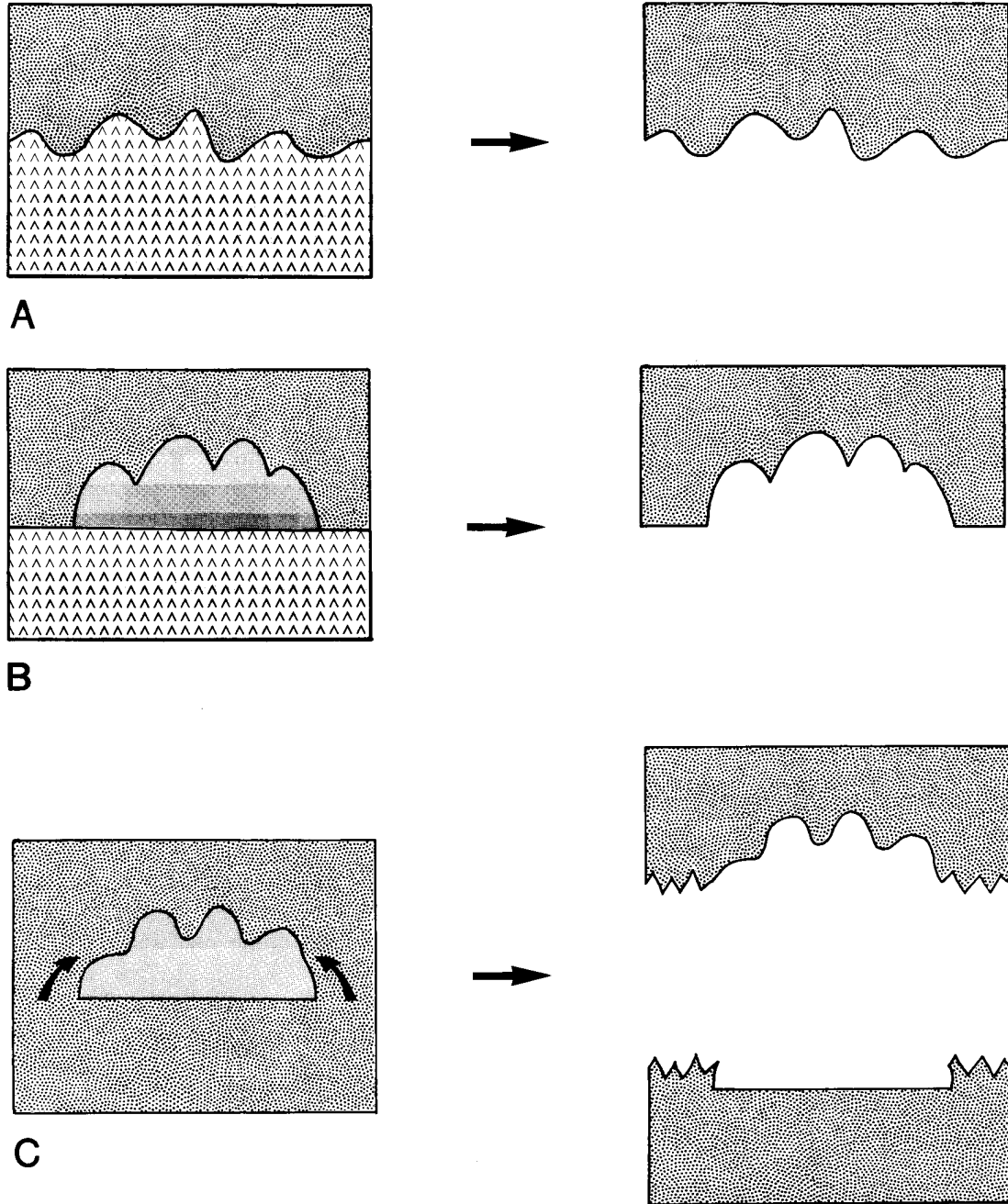
Substratum bioimmurations are two component systems (substratum organism + bioimmuring organism). For example, an impression of an algal frond on the attachment area of an oyster which lived as an algal epiphyte is a substratum bioimmuration. Epibiont bioimmurations are three component systems (substratum + bioimmuring encruster + bioimmured encruster). If two bryozoans encrust the same bivalve shell and one overgrows the other, then the mould of the overgrown bryozoan on the base of the overgrowing bryozoan is an epibiont bioimmuration (note that the term epibiont is here used in accordance with the recommendation of West 1977 for an organism living on rather than within a substratum; there is no implication regarding the nature of the substratum). Bioclaustrations are a special type of bioimmuration with two components (combined substratum/bioimmuring organism + bioimmured organism). An example of bioclaustration is the embedment of a sponge growing on the surface of a coral by continued growth of the coral.

Substratum bioimmurations

These are a consequence of fouling of a biotic substratum, i.e. the settlement of a larva directly onto the surface of the substratum. Such substrata include organisms alive at the time of fouling and also dead, especially skeletal, remains. Although fouling of the shell can be advantageous in some bivalves which are less likely to be victims of predators when fouled (e.g. Pitcher and Butler 1987), fouling is very often disadvantageous to living organisms, e.g. the photosynthetic output of seaweeds may drop as a result of fouling (Cancino *et al.* 1987), and organisms fouling mussels can increase drag and therefore the probability of dislodgement (Witman and Suchanek 1984). Marine organisms frequently possess defences (e.g. antibiotic surface secretions, see Dyrinda 1986) which enable them to resist being fouled. Nevertheless, fouling is of widespread occurrence, especially on the older parts of marine plants, and away from the actively feeding regions of marine animals. Marine plants, colonial coelenterates, crinoids and other organisms with arborescent morphologies may be particularly favoured substrata because they elevate the fouling organism above the sea-bed where mortality caused by sedimentation, predation and competition may be more severe (Jackson 1979).

Epibiont bioimmurations

These result from lateral overgrowth in which one encruster encroaches a second encruster along the surface of their shared substratum and succeeds in overgrowing the edges of the second encruster. Overgrowth may entail a living organism growing onto the surface of a dead organism, or it may involve two living organisms in competition for substratum space. Spatial competition can be intense among encrusters colonizing firm or hard substrata, and a wide variety of physical and chemical methods are utilized by living encrusters both to assist in overgrowing competitors and to defend against being overgrown by them (see Buss 1986). Despite these, interspecific overgrowths can occur with great frequency. The effect on the overgrown organism of substantial overgrowth is usually death or, if the overgrown organism is a colonial animal, partial mortality, i.e. death of some of the zooids within the colony but not the entire colony (see Jackson and Hughes 1985). Some



TEXT-FIG. 1. Diagrammatic vertical sections depicting the three types of bioimmuration and their formation. A, substratum bioimmuration; bioimmuration is revealed on the underside of the overgrowing organism (coarse stipple) following loss of the substratum (chevron ornament). B, epibiont bioimmuration; bioimmuration is revealed on underside of overgrowing organism (coarse stipple) following loss of the epibiont (fine stipple) and its substratum (chevron ornament). C, bioclaustration; bioimmuration becomes visible when the embedding organism (coarse stipple), which formed both the substratum and overgrowing organism, is fractured to reveal the mould of the epibiont (fine stipple) within.

bryozoans are now known to survive in a dormant state pending removal of the covering organism (Todd and Turner 1988).

Bioclaustrations

The term bioclaustration was introduced by Palmer and Wilson (1988) to describe the process of embedment of a soft-bodied infesting organism by the skeletal growth of a host organism. The result of embedment is a pseudoboring, often mistaken for a true boring. Palmer and Wilson (1988, p. 940) regarded bioclaustration as distinct from bioimmuration because bioclaustration is 'a response to an interaction that is of one partner's seeking' whereas bioimmuration 'demonstrates chance competition for space'. However, such distinction depends upon the inference of biological processes (host selection and competition) which in most cases cannot be made with sufficient confidence, and are not always mutually exclusive. When bioclaustration is viewed in terms of the resulting pattern (text-fig. 1c), its close relationship to other types of bioimmuration becomes clear. Furthermore, to exclude from the definition of bioclaustration the embedment of organisms with hard skeletons seems inappropriate if bioclaustration is to be viewed as a category of bioimmuration; Vialov (1961) included organisms with mineralized skeletons in his original concept of bioimmuration. Rugose or tabulate corals embedded within the coenostea of stromatoporoids with which they intergrew during life (see Kershaw 1987) are, for example, here regarded as bioclaustrations.

Opportunities for bioimmuration by fouling, overgrowth and embedment are frequent on hard and firm marine substrata at the present day, and there is no evidence that they have been any less so throughout much of the Phanerozoic. 'Skeletal overgrowths' between organisms with mineralized skeletons have often been recorded among ancient hard substratum assemblages (e.g. Taylor 1979, 1984; Liddell and Brett 1982).

PRESERVATIONAL STATES

Most bioimmured fossils are preserved in negative relief as external moulds (Pl. 1, figs. 1, 5–6; Pl. 2, figs. 1 and 2, 4 and 5; text-fig. 2). These moulds become visible only after detachment of the bioimmuring organism from its substratum. If the substratum is perishable, detachment can occur before burial or shortly afterwards; if it is aragonitic, detachment often follows diagenetic shell dissolution. Oysters and many other bioimmuring organisms may remain firmly cemented to calcitic

EXPLANATION OF PLATE 1

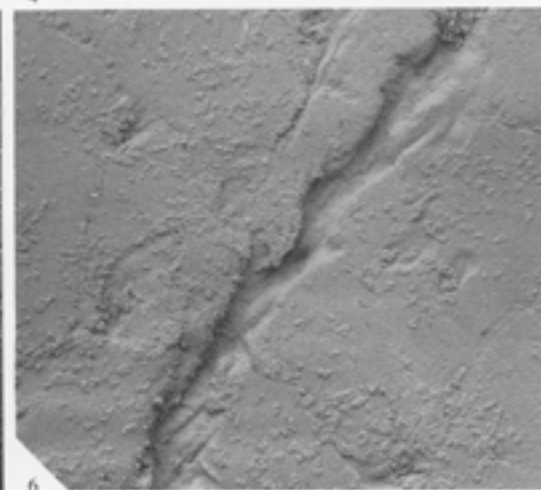
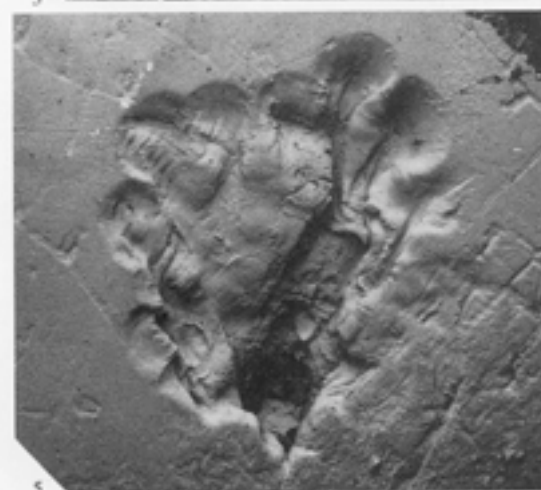
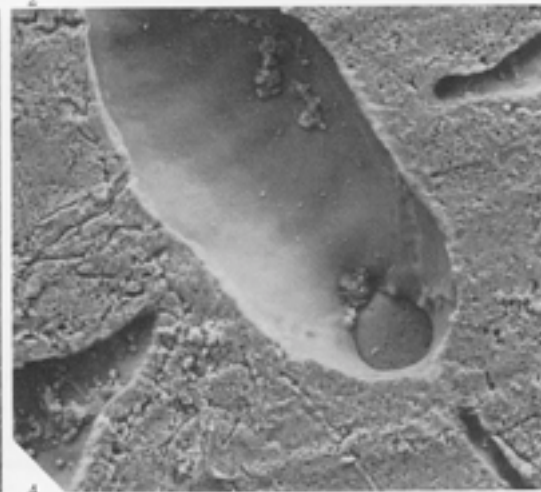
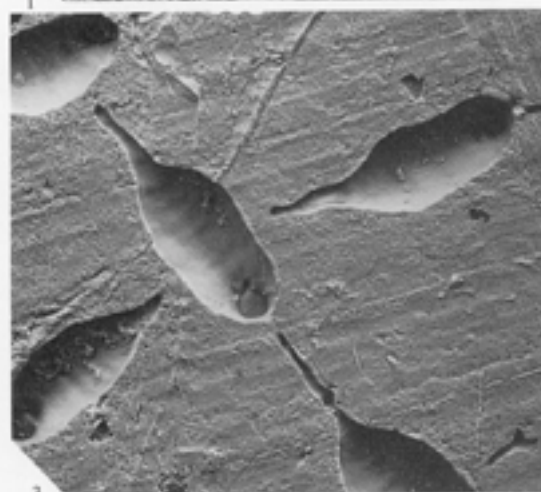
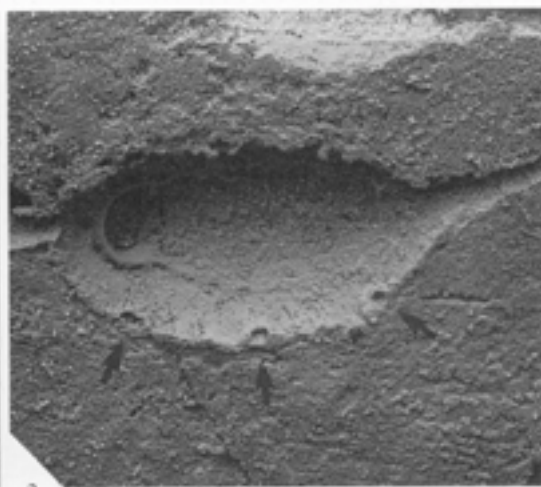
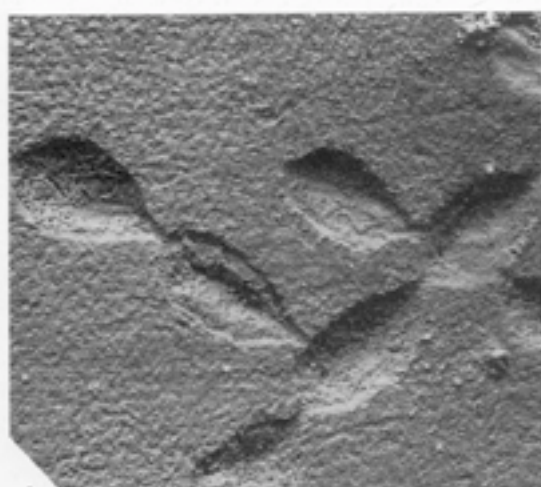
Fig. 1. *Arachnidium smithii* (Phillips), BMNH D 57495, a soft-bodied ctenostome bryozoan preserved as an epibiont mould bioimmuration on the attachment area of *Gryphaea*; note partial collapse of zooid in centre, Villers-sur-mer, Normandy, Oxfordian, $\times 45$.

Fig. 2. *Andriopora major* Larwood, BMNH D 58095, a calcified cribrimorph bryozoan showing 3 pairs of pore chambers (arrowed) which are invisible in conventionally preserved specimens but are seen in this bioimmured zooid on the attachment area of *Pycnodonte vesiculare*, Weybourne, Norfolk, Weybourne Chalk, Campanian, $\times 86$.

Figs. 3 and 4. *Hippothoa flagellum* (Manzoni), BMNH 1988.12.1.1, a calcified ascophoran bryozoan preserved on the attachment area of an overgrowing oyster which encrusted a plastic pipe, Piràn, Adriatic Sea, Recent. 3, zooid (growth direction top left to bottom right) with a distal and two lateral buds, $\times 90$. 4, detail of bud origins showing oyster shell seemingly filling the narrow gap between the slightly raised points of origin of the buds and the substratum, $\times 230$.

Figs. 5 and 6. Bioimmured soft-bodied organisms on the attachment area of the bivalve *Pycnodonte vesiculare*, BMNH H 5501, Thanet, Kent, Santonian, 5, distorted bioimmuration of organism with cusped margins which has collapsed in the direction of overgrowth (top to bottom), $\times 15$. 6, *Eisenackiella thanetensis* Taylor, the erect stem of a probable hydroid pushed flat against the substratum during overgrowth, $\times 25$.

All illustrations are back-scattered electron micrographs of uncoated specimens.



substrata (e.g. other oysters, sedimentary hardgrounds) during fossilization. Therefore, the organisms they overgrew are seldom revealed but may on occasions be visible as hummocks and irregularities on the inner side of the attached valve. Sometimes the mould is filled during diagenesis by calcite or pyrite giving an external cast of the bioimmured organism (see Taylor 1990, text-fig. 1). Cast bioimmurations may become visible through fracturing or exfoliation of the encrusting organism from its substratum. The fidelity of casting can be very high, especially when the casting material is pyrite (Taylor 1990, pl. 2, figs. 1 and 2). Whereas epibiont bioimmurations are found as both moulds and casts, substratum bioimmurations are preserved only as moulds.

Each bioimmuration is formed gradually during the period of progressive overgrowth by the bioimmuring organism. The shorter this period of time, the more likely it is that the process will be completed before significant deterioration of the overgrown organism. Therefore, bioimmurations of the highest fidelity should occur when the bioimmuring organism grows rapidly and/or when the bioimmured organism is small and is consequently overgrown quickly. Organisms which retain their shape during overgrowth should provide the most easily distinguishable bioimmurations. Conversely, flaccid organisms may become flattened and distorted during overgrowth, and can be difficult to identify when bioimmured. The ability of colonial animals such as hydrozoans and bryozoans to sustain partial mortality favours their preservation by bioimmuration because while certain zooids are being overgrown, other zooids remain alive and continue to sustain the colony. Large organisms fouled by small epibionts may be affected insignificantly by overgrowth, suffer little deterioration and therefore yield good quality substratum bioimmurations.

The time required for the formation of a bioimmuration obviously depends on the growth rate of the bioimmuring organism. Rather than being instantaneous 'snap-shots', bioimmurations are summations over time of the morphology of the substratum and its epibionts as they were progressively covered by the advancing growing edge of the bioimmuring organism. This has two implications. First, the morphology of a bioimmured organism need not necessarily correspond to its appearance at any one time during its life. This may be especially true for large and/or colonial organisms which do not suffer mortality immediately on commencement of overgrowth. For example, the single specimen of bioimmured hydroid *Eisenackiella thanetensis* described by Taylor (1988) may have been a large colony or a narrow strip-like colony which inhabited the substratum just in front of the bioimmuring bivalve *Pycnodonte vesiculare* and advanced with growth of the bivalve. Secondly, bioimmurations can document temporal successional changes in the organisms living on firm or hard substrata; the early growth stages of the bioimmuring organism overgrow epibionts recruited during early stages of ecological succession, the later formed parts overgrow epibionts recruited during later successional stages. This offers a potentially useful way of studying short-term ecological succession in fossil material.

Erect components of soft-bodied organisms are generally pushed over during overgrowth and are flattened against the substratum, resting in an orientation parallel to the growth direction of the bioimmuring organism. A good example of this is found in the weakly-calcified cheilostome bryozoan *Aetea* which has been described as a bioimmuration from the Pliocene and Recent by Voigt (1983). The zooids of *Aetea* each have an adnate proximal part and a tall erect distal 'peristome'. Adnate parts of the zooid remain in position during bioimmuration, but erect peristomes are pushed over so that they lie flat and parallel to the growth direction of the bioimmuring oysters and to one another. Similarly (Pl. 1, fig. 6), erect stems of the late Cretaceous hydroid *Eisenackiella thanetensis* were flattened against the substratum by the overgrowing bivalve *Pycnodonte vesiculare*. Interpretation of bioimmured fossils must take into account such distortions. Structures formed by pushing over can be distinguished by their orientation which is parallel to the local growth direction of the bioimmuring organism.

BIOIMMURING ORGANISMS

Potential bioimmuring organisms comprise a taxonomically diverse variety of encrusting animals with mineralized skeletons. These include attached foraminifers, sponges, corals, serpulid

polychaetes, cemented brachiopods, bryozoans, oysters and oyster-like bivalves (see Nicol 1978). However, only serpulids, cyclostome bryozoans and oysters have been described frequently as bioimmuring organisms, although bioimmuration has also been recorded involving foraminifers, sponges and trepostome bryozoans.

An obvious property required of a bioimmuring organism is that it should be capable of overgrowing fellow epibionts or of fouling organic substrata. Barnacles seem rarely to yield epibiont bioimmurations, possibly because they tend to prise competitors off the substratum rather than overgrowing them. Encrusters with sheet-like morphologies (as opposed to runner-like, ramifying organisms) are generally adept at overgrowing competitors for substratum space. These are highly likely to result in bioimmuration.

The probability of an encruster encountering an epibiont, and the likelihood of successful overgrowth occurring should each increase with the size of the overgrowing organism. Furthermore, large organisms provide larger sampling areas. Therefore, large encrusters with large attachment areas are more likely to be found with bioimmurations of epibionts than are smaller encrusters.

As noted on page 6, rapid overgrowth should produce bioimmurations of the highest quality. The fastest shell growth rate known in a present day oyster occurs in *Crassostrea cuttackensis* (Smith and Newton) living in Madras Harbour. Shells may grow 0.27–0.62 mm per day (see Stenzel 1971, p. N1014). An oyster shell growing at this rate could, for example, completely overgrow an average bryozoan zooid in a matter of one or a few days, presumably before any marked deterioration in the condition of the zooid. No data appear to be available on growth rates in cyclostome bryozoans, but some Recent sheet-like cheilostomes with a similar colony morphology grow at rates of 30–110 mm per year (Jackson and Coates 1986, p. 9), i.e. 0.08–0.30 mm per day. Although these rates would not be expected to yield such good quality bioimmurations as those of the fastest growing oysters, small organisms might still be overgrown in a matter of days.

The basal calcified skeletons of encrusting animals are not usually in direct contact with the substratum but are separated from it by an organic layer which contains the cement causing adhesion of the encruster, and onto which the calcified layers are seeded. However, because these organic layers tend to be exceedingly thin, their presence seems to have little effect on the fidelity of the bioimmuration impressed on the calcified skeleton. For example, the periostacum of oysters, secreted by glands in folds of the mantle lobes, is described as 'very thin' by Stenzel (1971, p. N977; see also Carricker, Palmer and Prezant 1980), while the initial thickness of the cuticle in some cheilostome bryozoans is only a few microns (see Ryland 1976, p. 295).

Because the organic basal layer in some encrusters is very thin, the calcified layer is able to enter and mould extremely confined recesses on the substratum and any overgrown epibionts. A Recent specimen from the Adriatic Sea provides a good illustration (Pl. 1, figs. 3 and 4). Here an oyster, once attached to a plastic pipe, has bioimmured a runner-like colony of the cheilostome bryozoan *Hippothoa flagellum* (Manzoni). In *H. flagellum*, new zooids originate as buds from the pore windows of parent zooids. The pore windows are apparently situated a little above substratum level, giving a very low 'arch' before the bud regains the substratum during distal growth. The fact that this arch has apparently been filled by calcite of the oyster shell in the illustrated specimen (leaving parent and daughter zooids apparently separated) demonstrates that extremely small-scale aspects of morphology are capable of being moulded by oysters.

BIOIMMURED SOFT-BODIED ORGANISMS

The overwhelming majority of bioimmured soft-bodied organisms have been described from the Jurassic and Cretaceous. This reflects both the focus of Professor E. Voigt's research, especially on the type Maastrichtian, as well as the undoubted abundance of good bioimmuring organisms, such as cemented bivalves, serpulids and cyclostome bryozoans, in the Jurassic and Cretaceous of north-west Europe. Furthermore, the abundance of aragonitic substrata, subsequently dissolved to reveal the attachment surfaces of their encrusters, also increases in the post-Palaeozoic. Very few bioimmurations of soft-bodied organisms have been described from the Palaeozoic and there is clearly much potential for further discoveries.

Soft-bodied or poorly-mineralized organisms belonging to the following taxonomic groups have been found as bioimmurations:

1. *Algae*. Voigt (1956, 1966, 1973a) has described many examples of bryozoans from the Maastrichtian Chalk-Tuff of Maastricht which were apparently attached to the stems and leaves of macroalgae. In a sample of 1800 bryozoans with intact colony bases, 79% of colonies were inferred to have been algal epiphytes (Voigt 1973a). The substratum bioimmurations of these algae often have smooth and glossy surfaces, and in some cases it seems possible that the epiphytic bryozoan did not make close contact with its algal substratum (Voigt 1973a described some Recent epiphytic bryozoans having strut-like outgrowths at the bases of their colonies). Putative algal stem bioimmurations are recognizable as cylindrical hollows around which the bryozoan colony was wrapped (Voigt 1956, pl. 1, figs. 1-4, text-figs. 2 and 3). Some of these colonies have tubular erect branches, a colony growth-form described as cavariiform (however, not all cavariiform bryozoans were algal epiphytes: examples in which the hollow is partitioned by skeletal walls cannot have grown around algae). Specimens of the worm *Spirorbis* with concave basal parts (Voigt 1956, text-fig. 4) were also apparently epiphytes of algal stems. Bryozoans such as the cyclostome *Actinopora disticha* (v. Hagenow) sometimes bioimmured algal fronds which are preserved as narrow tubular voids around which the colony is wrapped (Voigt 1956, pl. 2, figs. 9 and 10).

The Recent chlorophytacean *Codium bursa* (L.) from the Mediterranean is a cushion-shaped alga which often supports a fauna of epiphytic bryozoans (33 species) growing on cryptic surfaces beneath the overhanging edge of the plant (Voigt and Harmelin 1986). The mammilate surface of the alga, consisting of the ends of the utriculi, is replicated on the undersides of epiphytes such as the cyclostome *Tubulipora plumosa* Harmer (text-fig. 2D). Very similar patterns have been found by Voigt and Harmelin on the encrusting bases of the fossil cyclostomes *Osculipora tetragona* (Michelin) from the Middle Cenomanian of Le Mans (France), and *O. houzeaui* Pergens, *O. truncata* (Goldfuss) and *Reteporidea lichenoides* (Goldfuss) from the Chalk-Tuff of the Maastricht region (Voigt and Harmelin 1986, pl. 2, figs. 4 and 5, pl. 3, figs. 9, 12 and 13). These are interpreted as bioimmurations of a *Codium*-like alga.

An Upper Jurassic dasycladacean alga, *Goniolina geometrica* (Roemer), from West Germany, is preserved on the cementation areas of small oysters as bioimmured impressions of the regular hexagonal surface pattern (Voigt and Harmelin 1986, pl. 4, figs. 15 and 16).

A rare example of bioimmuration in the Palaeozoic is provided by a specimen from an Ordovician erratic boulder from Gotland. Hillmer and Schallreuter (1987, fig. 3I-J) figure the bioimmuration of a putative alga with a *Goniolina*-like surface overgrown by a cryptostome bryozoan.

2. *Marine angiosperms*. The Chalk-Tuff of Maastricht contains bioimmured seagrass leaves which were described by Voigt (1956, 1966). Bioimmuring organisms include the oyster *Exogyra*, the cyclostomes *Actinopora disticha* and *Lichenopora* sp., and the foraminifer *Planorbulinella cretae* (Marsson). On their basal surfaces are moulded the patterns of epidermal cells and veins of seagrass leaves (see Voigt 1956, pl. 4, figs. 1 and 2). It seems possible that some of these leaves are from the seagrass *Thalassocharis bosqueti* (Debey ex Miquel) which occurs commonly as silicified axes and

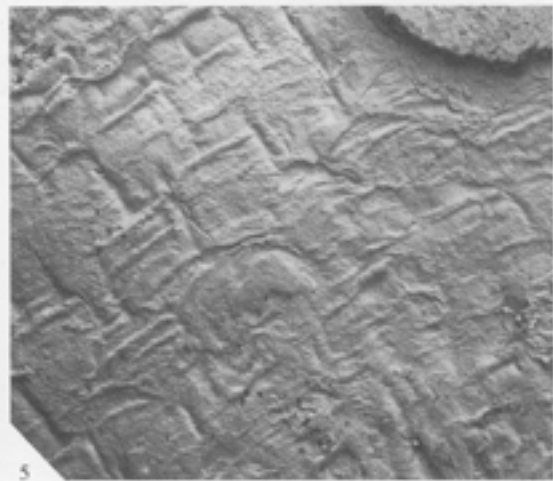
EXPLANATION OF PLATE 2

Figs. 1 and 2. Ventriculitid sponge preserved as a substratum mould bioimmuration on the underside of the cemented bivalve *Pycnodonte vesiculare*, BMNH S 10250, England, Chalk. 1, general view, $\times 1.4$. 2, detail of sponge surface, $\times 23$.

Fig. 3. Xenomorph of trigoniid bivalve on the unattached, right valve of a *Gryphaea*, BMNH 24065, Weymouth, Jurassic, Oxford Clay, $\times 0.8$.

Figs. 4 and 5. Substratum bioimmurations of unknown identity visible on the attachment areas of cemented bivalves. 4, BMNH Z 1062, Le Mans, Sarthe, Cenomanian, Sables du Perche, $\times 8$. 5, BMNH D 32168, Bognor, Sussex, Eocene, London Clay, $\times 28$.

Figs. 2, 4 and 5 are back-scattered electron micrographs of uncoated specimens.



rootlets, sometimes bryozoan encrusted, at Kunrade 30 km ESE of Maastricht (Voigt and Domke 1955; Voigt 1973a).

3. *Protists*. Ernst (1985) reported the occurrence of cylindrical tubes, up to 1.5 mm long and 0.10–0.15 mm in diameter, within zoecia of the cheilostome bryozoans *Onychocella piriformis* and *O. cyclostoma* from the Maastricht Chalk-Tuff. The tubes were apparently secreted by the bryozoans in response to the presence of an infesting organism and are thus bioimmurations of the bioclastration type. Ernst regarded the infesting organism as probably a folliculinid ciliate.

4. *Poriferans*. The spiculate surface of a putative monactinellid sponge bioimmured by a cyclostome is described by Voigt (1966, pl. 34, figs. 1 and 2).

5. *Hydrozoans*. Although very abundant members of present-day hard and firm substratum communities, hydrozoan cnidarians (excepting a few well-calcified groups such as milleporids and stylasterines) have a meagre fossil record, and many putative body fossils of hydrozoans from the Palaeozoic require confirmation (Hill and Wells 1956). Scrutton (1975) described the hydroid *Protulophila gestroi* Rovereto preserved by bioclastration. This Middle Jurassic to Pliocene species occurs in association with serpulid worms, having become embedded in the tubes as they grew.

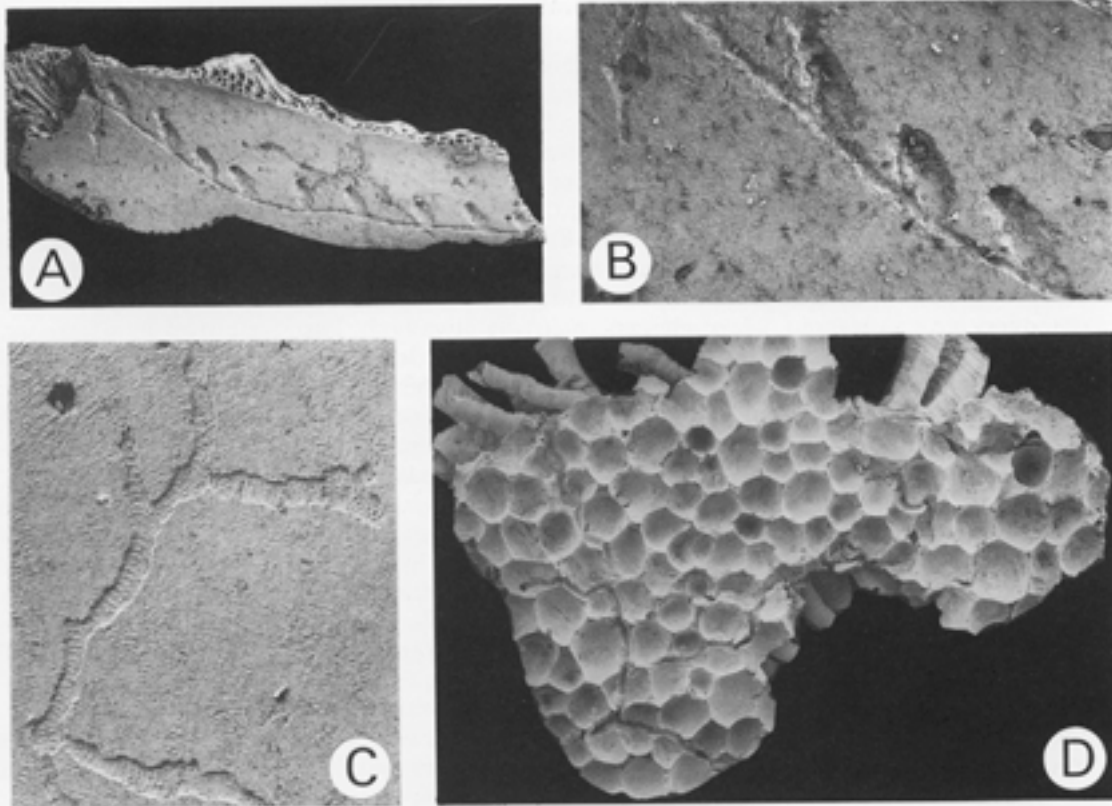
Epibiont bioimmurations of thecate hydroids have been described by Voigt (1973b) and Taylor (1988). *Hydrallmania graptolithiformis* Voigt, 1973b, preserved as a mould on the underside of the cyclostome *Actinopora disticha* from the Maastricht Chalk-Tuff, is the only known fossil of the Sertulariidae, a family of hydroids which is common at the present day. The Maastrichtian species closely resembles some Recent species of *Hydrallmania* in having an imbricate arrangement of hydrothecae along one side of the branch. Of more problematical affinity is *Eisenackiella thanetensis* Taylor, 1988, based on a single specimen bioimmured by the bivalve *Pycnodonte vesiculare* (Lamarck) from the Santonian of Kent. The colony appears to have an adnate system of hydrothecae-bearing stolons which gives rise to a series of erect stems also bearing hydrothecae (Pl. 1, fig. 6). Both the upright distal parts of the stolonial hydrothecae, and the erect stems have been flattened in the direction of growth of the bioimmuring bivalve. Stolonial morphology recalls that of certain Recent Lafoeidae, whereas stem morphology is reminiscent of the Family Sertulariidae. *E. thanetensis* is possibly a compound organism resulting from chance juxtaposition of stolon forming and an erect hydroid species. Voigt (1966, fig. 1) illustrates an unidentified bioimmured Maastrichtian hydroid which he compares with the living species *Syncoryne sarsi* Lovén.

6. *Octocoral anthozoans*. One of the few bioimmurations recognized from the Palaeozoic is of an inferred gorgonian octocoral. *Plumalina conservata* was described by Glinski (1956) from the Middle Devonian of the Eifel. It is represented by a single pinnate specimen bioimmured by a trepostome bryozoan determined as *Heterotrypa* sp.

7. *Ctenostome bryozoans*. The Ctenostomata are an exclusively soft-bodied, primitive, paraphyletic order of bryozoans. A minority of species bore into calcareous substrata and are found as trace fossils, and encrusting species preserved by bioimmuration are not uncommon in the Mesozoic (see Taylor 1990). Although ctenostome classification is somewhat contentious, it has been traditional to distinguish two groups of ctenostomes: the Stolonifera in which the autozooids are linked by a stolonial system comprising kenozooids, and the Carnosa in which stolons are wanting.

Voigt (1966, 1972, 1979) has described bioimmured stoloniferan species assigned to one extinct and two extant genera. *Stolonicella* Voigt, 1966 is a probable ctenostome known only as bioimmurations. The colony consists of a stolonial system bearing erect autozooids at intervals (text-fig. 2A and B), and resembles the living ctenostome *Avenella fusca* Dalyell. Zooids often possess a fine transverse ornament. Three species of *Stolonicella* occur in the Chalk-Tuff of Maastricht (*S. schindewolfi* Voigt, 1966; *S. filosa* Voigt, 1966; *S. hillmeri* Voigt, 1979) bioimmured by bryozoans and oysters, and one in the Turonian Greensand of Mülheim-Broich, West Germany (*S. westfalica* Voigt, 1966) bioimmured by *Ostrea (Lopha) semiplana* Sowerby and small *Exogyra*. Voigt (1979, pl. 3, figs. 1 and 2) illustrates an unusual colony of *S. filosa* which apparently encircled a colony of the cyclostome *Stellocavea francquana* d'Orbigny before being overgrown by the cyclostome.

The extant ctenostome genus *Amathia* is characterized by erect stolons which bear biserial clusters of autozooids (see Chimonides 1987). *A. immurata* Voigt, 1972 from the Maastricht Chalk-Tuff is



TEXT-FIG. 2. Bioimmured organisms preserved as moulds on the undersides of overgrowing organisms. A and B, VH 8611, the probable ctenostome bryozoan *Stoloniceella* sp., Blom Quarry, near Maastricht, Upper Maastrichtian. A, zooids arising from a stolon, $\times 12$. B, detail of zooids and stolon $\times 33$. C, ribbon-like thallus of the alga *Fosliella inexpectata* Voigt, VH 9494, Blom Quarry, Maastricht, Upper Maastrichtian, $\times 60$. D, VH 10522, bioimmuration of the chlorophytacean alga *Codium bursa* (L.) on the underside of the cyclostome bryozoan *Tubulipora plumosa* Harmer, Mediterranean, Recent, $\times 20$. Electron micrographs kindly provided by Professor E. Voigt.

the only known fossil species, owing its preservation to bioimmuration by the cyclostome *Idmidronea macilenta* (v. Hagenow). Colonies of the Recent *A. cornuta* Lamouroux bioimmured by the foraminifer *Acervulina adhaerens* (Schultze) were shown by Voigt (1972) to have an appearance very like the Maastrichtian fossil. Another extent stoloniferan genus, *Buskia*, is represented by two fossil species preserved as bioimmurations (Voigt 1979): *B. inexpectata* Voigt from the Upper Maastrichtian of Curfs preserved on the base of the cyclostome *?Ditaxia* with which it shared an algal substratum, and *B. hachti* Voigt from the Pliocene of Puget sur l'Argens (France) bioimmured by a serpulid tube.

Several Jurassic and Cretaceous bioimmured carnosan ctenostome species have been described, all referred to the extant family Arachnidiidae (see Taylor 1990). Their encrusting colonies are composed of uniserial chains of zooids which ramify across the substratum (Pl. 1, fig. 1). The zooids have a pyriform outline shape and sometimes possess a long and narrow proximal portion (cauda). *Arachnidium brandesi* Voigt, 1968a is founded on a single specimen from the Lower Cretaceous (Barremian) of Hoheneggelsen (West Germany). The colony is preserved as a cast bioimmuration which was revealed when the bioimmuring serpulid, *Proliserpula* (*Proliserpula*) *bucculenta* Regenhardt, was stripped away from the substratum, a guard of the belemnite *Oxyteuthis*

brunsvicensis v. Stromb. A similar species, *Arachnidium jurassicum* Voigt, but with smaller zooids, was subsequently described by Voigt (1977) from the Middle Jurassic (Aalenian) of Goslar (West Germany). As in *A. brandesi*, the ctenostome is preserved as a cast bioimmuration on the guard of a belemnite (*Megateuthis*). In this case, however, the bioimmuring organism is an oyster. Taylor (1978) recognized that the type specimens of two nineteenth-century species of Jurassic bryozoans previously regarded as belonging to the cyclostome genus *Stomatopora* Bronn were in fact cast bioimmurations of *Arachnidium*. The first of these had been described by Phillips (1829) as *Cellaria smithii* and originated from the Middle Jurassic ('Cornbrash'; probably Callovian) of Scarborough (Yorkshire). The holotype of *Arachnidium smithii* (Phillips) is a cast bioimmuration attached to the bivalve *Cardium citrinoideum* Phillips, and was possibly bioimmured by an oyster though little remains of the bioimmuring organism. The second species, *Stomatopora phillipsii* Vine, 1892, placed in synonymy with *A. smithii*, is represented by a cast bioimmuration, overgrown by an oyster, attached to the brachiopod *Obovothyris* from the Middle Jurassic (Bathonian, Cornbrash) of Thrapston (Northamptonshire). Three new species of arachnidiids from the Jurassic are described by Taylor (1990) who emphasizes the relative abundance of these bioimmured ctenostomes in late Jurassic deposits. Finally, Voigt (1980) described *Arachnidium longicauda* from the Chalk-Tuff of Maastricht. This species is represented by a mould bioimmuration of a colony originally attached to an algal leaf and overgrown by the cyclostome *Truncatulipora*. Many of the zooids have extremely long caudae which serve to distinguish *A. longicauda* from previously described species of *Arachnidium*.

8. *Incertae sedis*. Very many bioimmurations are taxonomically indeterminate. This may be a consequence of distortion of the bioimmured organism during overgrowth, insufficient morphological characters for identification, lack of knowledge of the appearance when bioimmured of comparative living organisms, or a combination of these factors. Two particular morphotypes of *incertae sedis* occur commonly among epibiont bioimmurations: threads and mounds.

Bioimmurations of narrow thread-like structures are often encountered on the attachment areas of Mesozoic to Recent oysters and bryozoans. The threads may ramify and cover substantial areas of substratum. Several different groups of organisms are potentially responsible, including stoloniferan ctenostome bryozoans (zooids of Recent stoloniferans are sometimes deciduous, their loss leaving an undiagnostic stolonial system), hydroids, filamentous fungi and algae.

Mound-shaped bioimmurations are commonly distorted as a result of overgrowth of a semiflaccid organism. Only the basal outline shape of the organism may be preserved as a potential distinguishing character. For example, an Upper Cretaceous mound bioimmuration (Pl. 1, fig. 5) occurring with the holotype specimen of *Eisenackiella thanetensis*, was evidently a soft-bodied organism with a scalloped edge which was pushed over and severely distorted during overgrowth by *Pycnodonte vesiculare*. This and similar mound bioimmurations may possibly be zoanthid or actiniid cnidarians, ascidiaceans or sponges.

Two substratum bioimmurations of unknown identity are shown in Pl. 2, figs. 4 and 5. Both occur on the attachment areas of cemented bivalves. The Cretaceous example (Pl. 2, fig. 4) overgrew a substratum of matted fibres, and the Eocene example (Pl. 2, fig. 5) a substratum with a pattern of conjugate ridges.

Rohr and Boucot (1989) have recently described a substratum bioimmuration preserved by individuals of the oyster *Lopha ramicola* Beurlen from the Upper Cretaceous of Brazil. These oysters bioimmured stem-like structures, about 1 cm in diameter, which were covered with closely-spaced circular nodules arranged in a spiral pattern. The bioimmuration is replicated in positive relief on the unattached valves by xenomorphism. Rohr and Boucot regard the bioimmured organism as of unknown affinity, but make comparisons with gorgonacean octocorals and axes of plants (e.g. gymnosperm stems bearing the traces of leaf scars).

The bioclaustated ichnotaxon *Catellocaula vallata* Palmer and Wilson, 1988, embedded in trepostome bryozoan colonies from the Upper Ordovician of the Cincinnati area of the USA, is another organism of unknown affinity. The fossil consists of a series of 2 mm wide radiating tunnels connecting pits in the surface of the host bryozoan colony. Palmer and Wilson interpret the

organism as a stoloniferous colony, possibly a hydroid but more probably a colonial ascidiacian tunicate.

Circular-parabolic pits are commonly found in fossil echinoderms, particularly Palaeozoic crinoids (see Brett 1985 and references therein). They were apparently produced by a combination of boring and embedment (i.e. bioclastration). Brett introduced the ichnogenus *Tremichnus* for such structures and regarded them as the work of a sessile, host-selective, probably filter-feeding epibiont.

BIOIMMURED SKELETAL ORGANISMS

Although the most interesting bioimmured fossils are undoubtedly those of soft-bodied organisms, bioimmurations of organisms with mineralized skeletons may also be valuable in certain circumstances. This is true if the skeletons are normally disarticulated, suffer from diagenetic dissolution, or cover only part of the external surface of the organism.

Aragonitic shells

Many fossil assemblages lack molluscs with diagenetically unstable shells of aragonite. For example, aragonitic molluscs are generally absent from the Aptian Faringdon Sponge Gravel of Oxfordshire. However, some aragonitic gastropods at Faringdon are preserved as substratum bioimmurations formed on the undersurfaces of cyclostome bryozoans and neuroporid sponges which fouled the gastropod shells. These natural moulds accurately replicate details of shell ornamentation and permit taxonomic identification of the gastropods (R. J. Cleavelly, in prep.). Similar moulds of mollusc shells occur in the Bathonian of Normandy (T. J. Palmer, pers. comm. 1988).

Celleporid bryozoans from the Neogene occasionally bioclastrate small solitary corals (Pouyet 1978). Whereas the bryozoans are calcitic, the corals are aragonitic and their skeletons tend to be lost during diagenesis. However, their past presence can be indicated by horn-shaped cavities remaining in the surface of the host bryozoan colony (e.g. in material from the Pliocene Coralline Crag of Suffolk).

Numerous examples have been described of oysters bioimmuring lost substrata such as ammonites and other aragonitic molluscs (see Stenzel 1971 and references therein). Most accounts focus on the positive relief replica of the aragonitic mollusc carried by the free valve of the oyster (Pl. 2, fig. 3) as a result of the two valves maintaining a constant separation during growth across the mollusc shell, a process termed xenomorphism by Stenzel. However, it is the cemented valve which plays the primary role in the preservation of these substratum bioimmurations. To use a photographic analogy, the cemented valve captures the image as a negative, while the free valve makes a positive print from the negative. Xenomorphic impressions on the free right valves of oysters are rarely as sharp as bioimmurations on the attached left valves. Therefore, they are of less value in identifying the overgrown organism.

Exposed soft tissues

Not all organisms with mineralized skeletons have their entire external surface covered by hard material. Sponges have a spicular skeleton enveloped during life by soft parts. Hexactinellid sponges of the Family Ventriculitidae (see Reid 1962) are sometimes bioimmured by cemented bivalves (notably *Pycnodonte vesiculare*) in the late Cretaceous Chalk of England. These bioimmurations reveal the original surface morphology of the sponge including the ostia (Pl. 2, figs. 1 and 2). As early as 1847, Toulmin Smith (p. 89) observed bioimmurations made by oysters which had grown on the surface of ventriculitids. He used their structure to testify to 'the firmness of the texture of the body and to its noncontractility, as well as to its durability'. This enabled him to assert that structures visible in conventionally preserved ventriculitids were not artefacts resulting from post-mortem distortion.

Frontal membrane morphology in bioimmured cheilostomes has been described by Voigt (1968,

1979a) and Voigt and Ernst (1985). In *Taenioporina arachnoidea* (Goldfuss), the cuticle is ornamented by numerous small projections and pores (Voigt 1968b, pl. 4, figs. 3 and 4). The Maastrichtian onychocellid cheilostome *Nudonychocella nuda* Voigt and Ernst, 1985, has greatly reduced cryptocystal frontal wall calcification in post-ancestrular zooids giving it a resemblance to a membraniporimorph. A serpulid bioimmured colony (Voigt and Ernst 1985, pl. 2, fig. 5) confirms the onychocellid affinities of the species, and shows clearly the position of operculum and orifice.

Lightly mineralized skeletons

The coralline alga *Fosliella* Howe has weakly calcified thalli which are unknown as body fossils. However, Voigt (1981) has described a new species of this genus from the Maastrichtian of Maastricht and Kunrade which is preserved only by bioimmuration. *F. inexpectata* Voigt has narrow, ribbon-like thalli with files of cells arranged in transverse bands (text-fig. 2C). Cover cells, germination discs and conceptacles are preserved. The alga was an epiphyte of macroalgae and was overgrown by the cyclostome *Truncatulipora*. Previous notions of *Fosliella* being a primitive member of the Corallinaceae are substantiated by this early occurrence of the genus.

Although all cheilostome bryozoans have mineralized skeletons, mineralization can be very slight and certain living groups are unknown as body fossils. Hence bioimmuration provides a valuable opportunity for fossilization of lightly calcified cheilostomes.

A new cheilostome from the Maastricht Chalk-Tuff was described by Voigt (1966) as *Taeniocellaria setifera*. The delicate erect colony, with long setose vibraculae, was flattened during overgrowth by an individual of *Exogyra* and is preserved as a mould bioimmuration on the attachment area of the oyster along with *Stolonicella schindewolfi*, and small cyclostomes, bivalves and *Vermetus*. Such excellent preservation of this fragile colony suggested to Voigt (1979a) that overgrowth occurred rapidly, possibly during the life-time of the colony. The affinities of *T. setifera* within the Cheilostomata are obscure, but the orifice with sinus (see reconstruction in Voigt 1966, fig. 3) suggests that the species is an ascophoran.

Laterotecatia pseudamathia Voigt, 1979a is a hippothoid ascophoran from the Maastrichtian which is known only from bioimmurations. Zooids of *L. pseudamathia*, named because of its resemblance to bioimmured *Amathia immurata*, are arranged in characteristic transverse rows. Colonies were algal epiphytes bioimmured by organisms such as the cyclostome *Stellocavea francuana*.

Despite frequent citation as a fossil, the extant cheilostome genus *Aetea* Lamouroux had no certain fossil record until Voigt (1983) described bioimmured specimens from the Pliocene. This weakly calcified anascan possesses zooids with an adnate proximal part from which there arises an erect tubular part containing the frontal membrane and orifice. Fossil examples (identified as *Aetea* sp., *A. truncata* (Landsborough) and *A. truncata pygmaea* Hincks) from Crete and southern France are preserved as a result of bioimmuration by oysters. Their appearance is very similar to that of Recent Mediterranean specimens of *Aetea* bioimmured by oysters, the foraminifer *Miniacina miniacea* Pallas, and the cheilostome *Watersipora cucculata* Busk.

Chitinous exoskeletons of crustaceans commonly disintegrate before burial and fail to fossilize. A bioimmured example of the lobster *Linuparus* preserved has been described by Bishop (1981) from the late Cretaceous Ripley Formation of Mississippi. The carapace of *Linuparus* was overgrown by the oyster *Exogyra costata* Say probably after the death of the lobster because living lobsters groom themselves to remove epizoans. Using growth lines on the oyster shell, Bishop estimated that complete overgrowth of the carapace took almost a year, and therefore that the carapace remained intact for at least this length of time. This period far exceeds the four weeks quoted by Schäfer (1972) for decapod cuticle to lose its strength in the North Sea at the present day.

Exposure of hidden undersides

Bioimmuration in conjunction with substratum loss, especially dissolution of aragonitic substrata, can also be useful in revealing the undersides of encrusters with mineralized skeletons which are normally juxtaposed with the substratum and hidden from view. For example, adnate cheilostome

bryozoans are usually very firmly cemented to their substrata when found as fossils, and the colony underside is not accessible for study. However, the undersides of colonies overgrown by bivalves and other bioimmuring organisms may become visible after detachment from their substratum. These include species with colonies which are too fragile to survive intact unless held together by the bioimmuring organism. Bioimmurations of zooids of *Andriopora major* reveal the existence of pore chambers (Pl. 1, fig. 2), not recorded from conventionally preserved material (Larwood 1962).

DISCUSSION

Bioimmuration is a preservational process which can preserve soft-bodied organisms, as well as lightly mineralized or unmineralized components of organisms possessing hard skeletons. Clearly, therefore, it offers considerable potential for adding to our knowledge of biotas of the past. This potential has been little explored. In particular, very few bioimmured fossils have been reported from the Palaeozoic. Potential bioimmuring organisms in the Palaeozoic include cemented articulate and inarticulate brachiopods, sheet-like trepostome and cystoporate bryozoans, cornulitids, corals and stromatoporoids.

Future research directions should include:

1. A concerted and systematic search for bioimmurations. Many examples of bioimmured fossils doubtless remain unrecognized in existing collections. Oysters with large attachment areas are a particularly fruitful source of bioimmurations in the Mesozoic and Cenozoic. The development of techniques to separate oysters and other encrusters from their substrata, thereby exposing bioimmured organisms, would surely increase the probability of making such finds.

2. Study of the details of overgrowth processes in present-day hard substratum communities, and the taphonomy of the organisms being overgrown. Nothing is currently known regarding the relative preservation potentials during bioimmuration of different organisms. Fossil finds suggest that runner-like encrusters provide the most easily preservable (and readily recognizable) subjects for bioimmuration, but this supposition requires testing by reference to modern bioimmurations.

Organisms preserved by bioimmuration are usually sessile inhabitants of firm or hard substrata. Fossil assemblages of firm or hard substrata are especially good subjects for palaeoecological studies because their constituent fossils are demonstrably *in situ*, thereby retaining their original spatial relationships to one another and to the substratum. Fouling and overgrowth interactions between organisms, and interactions between organisms and their substratum (e.g. patterns of spatial recruitment, see Bishop 1988) can be recorded with minimal interpretive assumptions. This additional information on biotic interactions, taken in conjunction with evidence of soft-bodied organisms preserved by bioimmuration, should permit inferences to be made for hard substrate which are beyond those normally possible in palaeoecological studies.

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