The bivalve shell as a preservation trap, as illustrated by the Late Jurassic gryphaeid, *Deltoideum delta* (Smith).

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Three processes by which a bivalve shell can preserve soft-bodied organisms during its secretion are described. These are: a) bioimmuration by the attachment area of a cementing bivalve, b) bioimmuration by a growth lamella and, c) deformation of the periostracal sheet. Examples of all three are provided by the Late Jurassic gryphaeid *Deltoideum delta* (Smith, 1817); Recent examples are also given. Extrapallial cement - here termed the Harper layer - is shown to have been produced throughout growth in this species, which allowed accurate lamellar bioimmuration as well as facultative re-cementation of the left valve. The importance of bivalve shell secretion for the preservation of unmineralized, hard-substrate-dwelling epibionts in the fossil record is outlined.

Contents

Introduction

The bivalve shell can in many ways act as a trap, preserving organisms otherwise lost to the fossil record. Of these, examples include the spectacular shoals of teleost fish found preserved within the shell cavity of the gigantic inoceramid *Platyceramus platinus* (Logan) from the Late Cretaceous of Kansas, U.S.A.. The fish apparently hid in the mantle cavity of the living bivalve to shelter from predators (Stewart, 1990). Far less spectacularly, ichnofossils, such as the burrow *Arachnostega*, may be confined to the sediment infilling articulated bivalves (Bertling, 1992) or from between the growth lamellae of strongly lamellose bivalves, for example, the gryphaeid *Bilobissa* (pers. obs.), presumably having been destroyed by intense bioturbation elsewhere.

However, in this paper I shall confine my attention to three processes by which traces of (chiefly) soft-bodied organisms are produced on the external surface of a

valve during its 'normal' growth. Internal features involving pearl-formation or shell-repair will not be discussed here. For recent compilations of the fossil record of the former see Boucot (1990) and Kauffman (1990). Two of the three processes discussed below involve bioimmuration; for a recent review see Taylor (1990a). Bioimmuration may be defined as the process and result of the overgrowth of a sessile organism by the skeleton of another, so producing an external mould (at least) of the smothered organism within the overgrowing surface.

Living-space on hard substrates is at a premium in almost all shallow seas. Inevitably encrusters engage in spatial competition for substrate, this being one of the major structuring elements in epifaunal communities (see Jackson, 1983). As soft-bodied or weakly-mineralized encrusters have probably been as important a component of hard substrate biomass throughout the Phanerozoic as they are today, so fossil oysters, many being large and having presumably grown rapidly, have routinely bioimmured many smaller sessile organisms.

Despite Voigt's large number of papers (from 1956 to the present) dealing with bioimmured organisms (referenced in Taylor, 1990a), the ubiquity of the process, and the often abundant fossils so preserved, it has until recently escaped widespread attention. Taylor (1990a), notes that 'even the existence of this important mode of preservation is poorly known among palaeontologists'.

Surprisingly, considering the world-wide importance of ostreiculture, the mechanism of bivalve cementation had, until Harper's recent work (1991, 1992), remained entirely unstudied. So it now seems opportune to bring these two neglected topics together, by discussing briefly the manner by which secretion of the bivalve shell can trap and preserve organisms, both by bioimmuration and by other means.

The processes described are:

a) bioimmuration by a cemented attachment area,

b) bioimmuration by a growth lamella, and,

c) epibiont deformation of an uncalcified periostracal sheet.

Each of the above will be discussed for cementing bivalves in general first, and then specific examples will be given. To allow best comparison of the processes, one bivalve species will be used to demonstrate all - the Late Jurassic gryphaeid oyster *Delto'deum delta* (Smith, 1817). This will be supplemented by other examples where appropriate.

The host

Deltoideum delta is a medium to large-sized oyster (up to 20 cm high), which is abundant in certain clayey facies of Late Oxfordian and Early Kimmeridgian age in England, NW France and Poland (Arkell, 1930). Typically both valves are very flat, sickle-shaped to triangular (Fig. 1), and contain a very small shell cavity (see Stenzel, 1971). Usually it lived as a flat recliner on soft mud substrates (Fürsich, 1977; Machalski, 1989) and can often be found in this life position. Machalski also demonstrated it living as a mud-sticker (Seilacher, 1984) in low energy environments with a high sedimentation rate. Small clumps of *Deltoideum*, representing a number of generations cementing to each other by much of their left valves, are not uncommon in the Late Oxfordian of England.
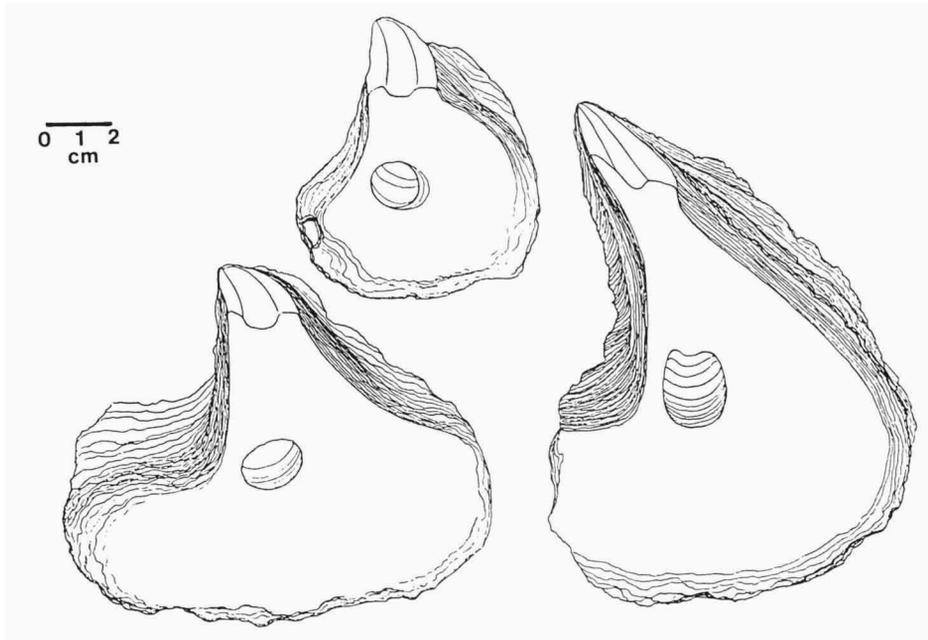
Fig. 1. Interior of left valves of *Deltoideum delta* (Smith, 1817) from the Late Oxfordian - Early Kimmeridgian of southern England; from Arkell (1930).

Bioimmuration by the attachment area of cemented bivalves
An introduction

Ten extant bivalve families have 'shell-cemented' members (cf. cementation via a calcified byssal plug) (Vermeij, 1987: 306). All but one have been shown to attach via a carbonate cement (Harper, 1991, 1992). Detailed experimental work has demonstrated the mode of cementation for three Recent ostreids and has shown that the model proposed is applicable to all Recent shell-cementing taxa, and, by extension, to extinct members of extant cementing clades (Harper, 1992).

The discovery of the bivalve cementation mechanism has extremely important implications for understanding the mode and style of preservation of bivalve-immured organisms. As such it is necessary to briefly summarize this below, adding details of its role in bioimmuration.

An ultra-thin sheet (<0.5 μm in ostreids) of highly flexible periostracum unfurls from between the middle and outer folds of the protruded extensible mantle. As this pushes forward over the substratum so erect organisms or erect portions of encrusters are pushed-over in the local direction of growth (see Voigt, 1983; Taylor, 1988; Todd & Taylor, 1992). Carbonate-charged extrapallial fluid leaks through the porous periostracum of the cementing valve to eventually crystallize between it and the substratum, nucleating on either (see Fig. 2). Not being under direct biotic control, a sparry mosaic of calcite crystallites (cf. spherulites; Harper, 1992) grows in the larger
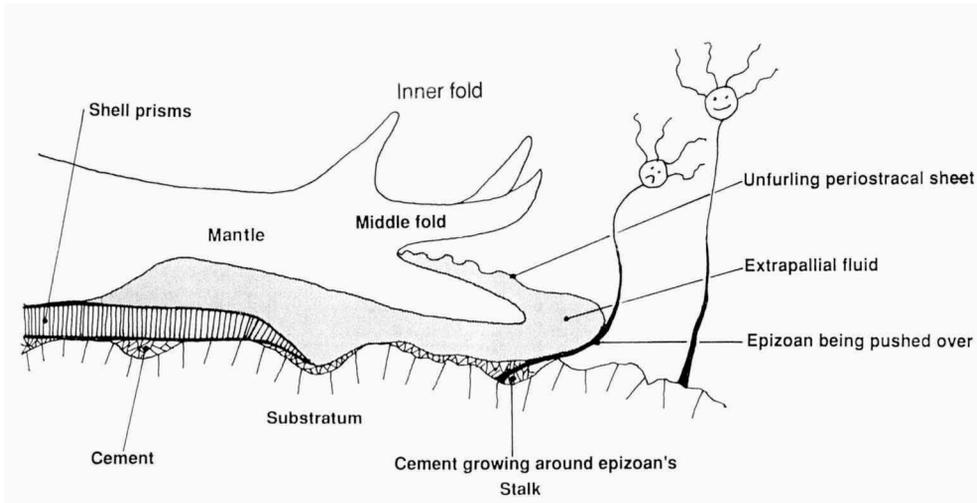
Fig. 2. Schematic cross-section of epibiont push-over and bioimmuration by the attached valve of a cementing bivalve; modified from Harper (1992).

voids. As Harper (1992) notes, this fabric can resemble that produced by the precipitation of pore water carbonate during diagenesis.

The role of cement in bioimmuration

As the cement may nucleate directly onto a bioimmured organism, so the latter is often exceptionally preserved within it as a mould bioimmuration (Taylor, 1990a, b). Unpublished work shows that features as small as 200 nm can be replicated in negative in this way. Furthermore Harper's suggestion (1992: 45) that the cement may be able to bioimmure organisms internally can be confirmed. Extrapallial fluid may enter an organism through an orifice or damaged body-wall to precipitate as a sparry mosaic within. This may fill, partially or entirely, internal voids such as the coelom of ctenostome bryozoans, moulding features of their internal anatomy (Todd, in press).

Both Recent ostreoideans and fossil ones unaltered by the addition of diagenetic cement tend to separate from their substrates in an identical manner. Lying between the extrapallial cement layer and the immuring valve is a plane of weakness corresponding to the position of the now-decayed periostracum (Todd & Taylor, 1992). As a result, upon separation, the immured substrate, together with its epibionts, tends to be obscured by a thin but tenacious layer of cement. To acknowledge her fundamental work on bivalve cementation I herein term this cement layer the *Harper layer*. As this layer has only been described from transverse sections (Harper, 1991, 1992), I shall take the opportunity to describe and figure it in more detail.

Characterizing the Harper layer

In ostreoideans (here including the Gryphaeidae, contra Carter, 1990: 357) the Har-

per layer is believed to be calcitic, being derived from the same extrapallial fluid from which the shell is composed (Harper, 1991, 1992). It should be noted that in muddy conditions it can be very 'dirty', with abundant clay-grade inclusions. In mud-filled pockets between shell and substratum the visual discrimination of muddy cement from surrounding mud can be difficult. On natural surfaces the Harper layer generally forms a continuous sheet, from several μm to over a mm in thickness. In planar view - from the periostracum-bounded side - it has a characteristic ultramicrocrystalline fabric (see Pl. 1), often showing distinct 'growth increments' (Taylor & Todd, 1990, fig. 6; Pl. 1, figs. 1-2 herein), which may vary in thickness.

As it is seeded onto a highly flexible and deformable periostracum so the Harper layer reflects this deformation in negative. For illustrations of the flexibility of the periostracum see Carriker et al. (1980, figs. 3-5) for *Crassostrea virginica* (Gmelin, 1791) and Harper (1992, fig. 2) for *Ostrea edulis* Linné, 1758. In fossil and Recent ostreoideans deformation structures of two different scales can be characterised, *rucks* and *pleats*. Rucks reflect ripples in the periostracum, best seen where induced by the projection of an epibiont from an otherwise flat surface (see Pl. 1, fig. 1). Their long axis runs normal to the direction of oyster growth and they may be lunate with 'horns' curling around either side of the obstruction, pointing in the direction of growth. Rucks are typically tens to several hundred μm in width. Pleats are much finer scale wrinkles (<1-15 μm wide) in the periostracum and may be accurately replicated in the surface of the underlying prisms (see Pl. 2, figs. 3, 4b). Pleats are moulded in negative by the Harper layer and are here termed, from their typical appearance, *cuts*. They may run parallel to rucks or radiate outwards from the high point of an obstruction over which the periostracum has been draped. In the latter case they often subdivide into thinner and thinner cuts away from the site of their inception.

The Harper layer may have a rugged profile if the periostracal sheet has advanced over an uneven substrate. Plate 1, fig. 1 illustrates the Harper layer of a Recent specimen of *Ostrea edulis*, which has been removed from its conspecific substrate. No trace can be seen of the periostracum; if still present it may have remained adhered to the immuring valve. Large rucks and finer-scale cuts running parallel to the commissure have been produced by the pushing over and bioimmuration of hydroid hydrocauli.

Examination of the Harper layer of *Deltoideum delta* reveals that the smallest cuts are less than 1 μm in width. As Harper (1992: 45) notes, intuitively one would expect periostracum to be unable to form pleats of a width less than twice its own thickness. This indicates that the maximum periostracal thickness on the left valve was <0.5 μm, a figure agreeing with that measured in Recent ostreids (Harper, 1991, 1992). This has been confirmed by measuring the corresponding pleats on the prisms of the left valve.

In fossils the Harper layer of the attachment area is frequently much better preserved than the prismatic layers of the right valve, or of the left valve outside this area, which are often bioeroded, weathered, or obscured by syntaxial diagenetic calcite. As such the fine periostracal pleating, as shown by the outer surface of the prisms (Pl. 2, fig. 3 herein, and see Carriker et al., 1980: figs. 3-7) is often unavailable for study. Examination of deformation structures in the Harper layer would appear to have great potential for the determination of periostracal thickness in extinct taxa.

The Harper layer and resultant preservational styles

Though the Harper layer is directly responsible for the high fidelity of preservation, it often completely enshrouds the epibionts so preserved. When the Harper layer is thin it is almost unnoticeable, allowing immured organisms to be examined clearly with a light microscope. However, when examined under the SEM, frustratingly such specimens often prove to be concealed by the electron-opaque cement (e.g. Pl.1, fig. 2). Luckily in areas of higher relief windows may develop in this layer, see Todd & Taylor (1992). These holes occur where the fracture plane between the Harper layer and the shell has been unable to follow the convolutions of the decayed periostracum and has broken through the cement. Through such windows one can examine the external moulds of epibionts, if unfilled, or their diagenetic or biogenic cement fills, if filled. This preservational (and developmental) style is here termed window preservation. Two end-members exist: open windows - those unfilled by biogenic or diagenetic cement, and closed windows - those which have been filled by the above. Many variations exist, for example Todd & Taylor (1992) have described Jurassic entoprocts preserved as open windows which are thinly lined by their partially phosphate (?) - permineralized cuticle. If absent or inadequately developed, then windows have to be made using a sharp needle in order to expose fully the epi-

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Plate 1

Pl. 1, fig. 2 and Pl 2, figs. 2-4 are back-scattered electron micrographs of uncoated specimens. The remainder are secondary-electron micrographs of coated specimens. All figured material has been deposited in the Natural History Museum, London. Recent specimens are housed in the Dept. of Zoology and fossils in the Dept. of Palaeontology. Registration numbers given where applicable. Umbo of bivalve to the top in all figures.

1. Harper layer secreted by an *Ostrea edulis* L. that has been removed from its substrate. Hydrocauli of thecate (?) hydroids are preserved through open windows. Note prominent rucks (r) and cuts (c). An *O. edulis* prodissoconch is bioimmured at bottom left. Magnification X 25.6. Recent, Ynys-Las, Dyfed, Wales, unregistered.

2. Thin Harper layer secreted by *Deltoideum* that has grown over a conspecific substrate from top left to bottom right, bioimmuring zooids of an arachnidiid ctenostome. A small closed window (w) partially exposes a zooid. Magnification X 16.8. Lower Kimmeridge Clay (*baylei* zone, Early Kimmeridgian), Wooton Bassett, Wiltshire, England. BZ 773.

3a. Zooid of arachnidiid buried in Harper layer of bioimmuring *Deltoideum* and exposed as a closed window. Magnification X 92.

3b. Close-up showing calcite infill is apparently continuous with external Harper layer (H) through the infilled orifice. Note cuticular gap (c) and stepped-faces of calcite crystallites. Magnification X 280. Lower Kimmeridge Clay (*baylei* zone, Early Kimmeridgian), Ferrybridge, Weymouth, Dorset, England. BZ 772.

4a. Trophon (= 'zooid') of *Buskia nitens* Alder, 1856, a stolonate ctenostome, embedded in Harper layer of a removed *Ostrea edulis* and exposed by a window. Note thin calcite lining within the former cystid wall. Magnification X 86.4.

4b. Close-up showing Harper layer, cuticular gap (c) and thin internal calcite lining, the crystallites having stepped faces. Magnification X 2.08K. Recent, Ynys-Las, Dyfed, Wales, unregistered.
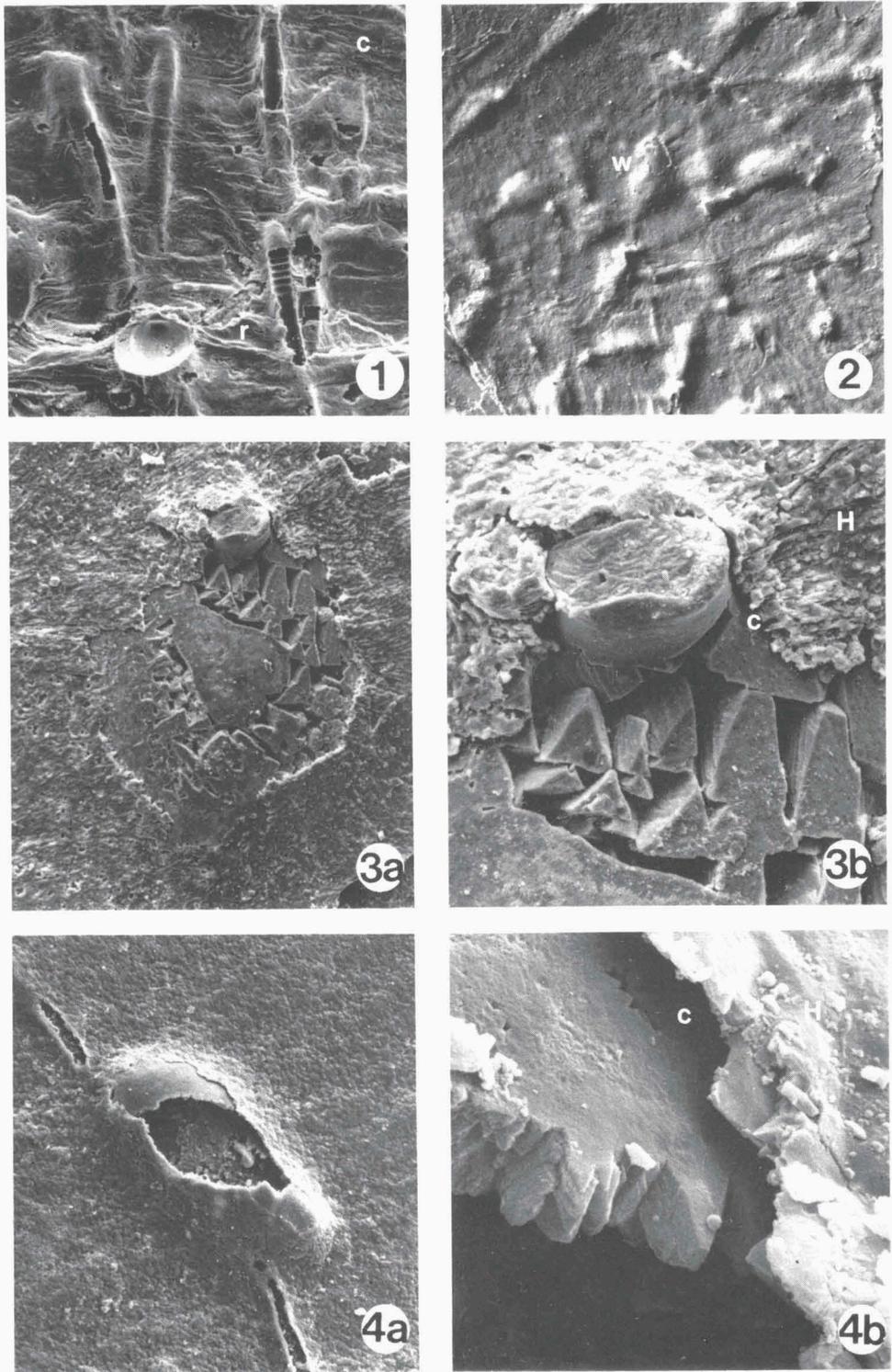
Plate 1

biont. Acid-etching has so far only proved entirely successful in revealing those epibionts diagenetically replaced by pyrite.

Assuming body-wall permineralization not to have taken place, then an extrapallial cement infill can be distinguished from a diagenetic calcite infill (for the latter see Taylor, 1990b, pl. 1, figs. 1, 2, 4; text-fig. 1) by the presence of a cuticular gap. This represents the position of the decayed cuticle of the bioimmured organism, and separates the internal cement which nucleated upon it from the surrounding Harper layer. Diagenetic calcite infills precipitate from pore waters and typically form after the decay of the cuticle and soft-parts. Hence they form a cast bioimmuration of an external mould (Taylor, 1990a: 5-6; Taylor & Todd, 1990), no trace of the cuticle being preserved.

To illustrate closed window preservation a *Deltoideum*-immured zooid of an arachnidiid ctenostome is illustrated (Pl. 1, fig. 3a, b). Harper layer cement has apparently entered what was presumably the empty cystid of a zooid through its open orifice. It has nucleated on the inside of the cuticle (= cystid wall), forming crystallites with stepped-faces. Subsequently the chitinous cuticle has decayed leaving a cuticular gap. To further demonstrate the non-diagenetic origin of the cement infill, *Buskia nitens* Alder, 1856, a Recent 'stoloniferan' ctenostome is illustrated, preserved in a similar manner (Pl. 1, fig. 4a, b). This specimen grew upon the exterior of a left valve of *Ostrea edulis* and was immured by another specimen of the same oyster. In this case the cement has crystallized upon the inside of the cystid wall as a thin layer (4-8 µm thick). The window has broken through this to reveal an unfilled void and cement crystallites with stepped-faces identical to those of the Jurassic example. This specimen can be considered as showing a somewhat intermediate state between open and closed window preservation.

Complex preservational styles (sensu Allison, 1988) can result from bioimmuration by bivalves. These may involve combinations of Harper layer infiltration, soft-part permineralization by calcite, pyrite or phosphate (e.g. Todd & Taylor, 1992) and later diagenetic infilling by the same minerals. These aspects will not be further dealt with here.

Bioimmuration by a growth lamella

Comarginal lamellae (= spurs, Nakahara & Bevelander, 1971; = scales, Carriker et al., 1980) composed of prismatic calcite are widespread amongst pteriomorph bivalves. They are present in the Ostreoidea, Pterioidea, Pectinidae, Anomioidea, Limidae and Pinnidae (Vermeij, 1987; pers. obs.). They are produced by periodic retraction of the mantle (see Nakahara & Bevelander, 1971), which potentially allows the underside of the lamella to be colonized by epizoans. With the re-extension of the mantle a layer of periostracum is often draped over the inside (bottom) of the previous lamella for a variable distance before it pulls away into free space. Prisms of calcite nucleate on the inside of this periostracum to form a new prismatic sheet, the ventral (free) part of this sheet representing a new lamella. Epizoans living on the underside of the old lamella may become immured by the new lamella where the two remain closely adpressed. For a schematic summary of this process see Fig. 3.

In this way a runner ctenostome bryozoan of the family Arachnidiidae has been
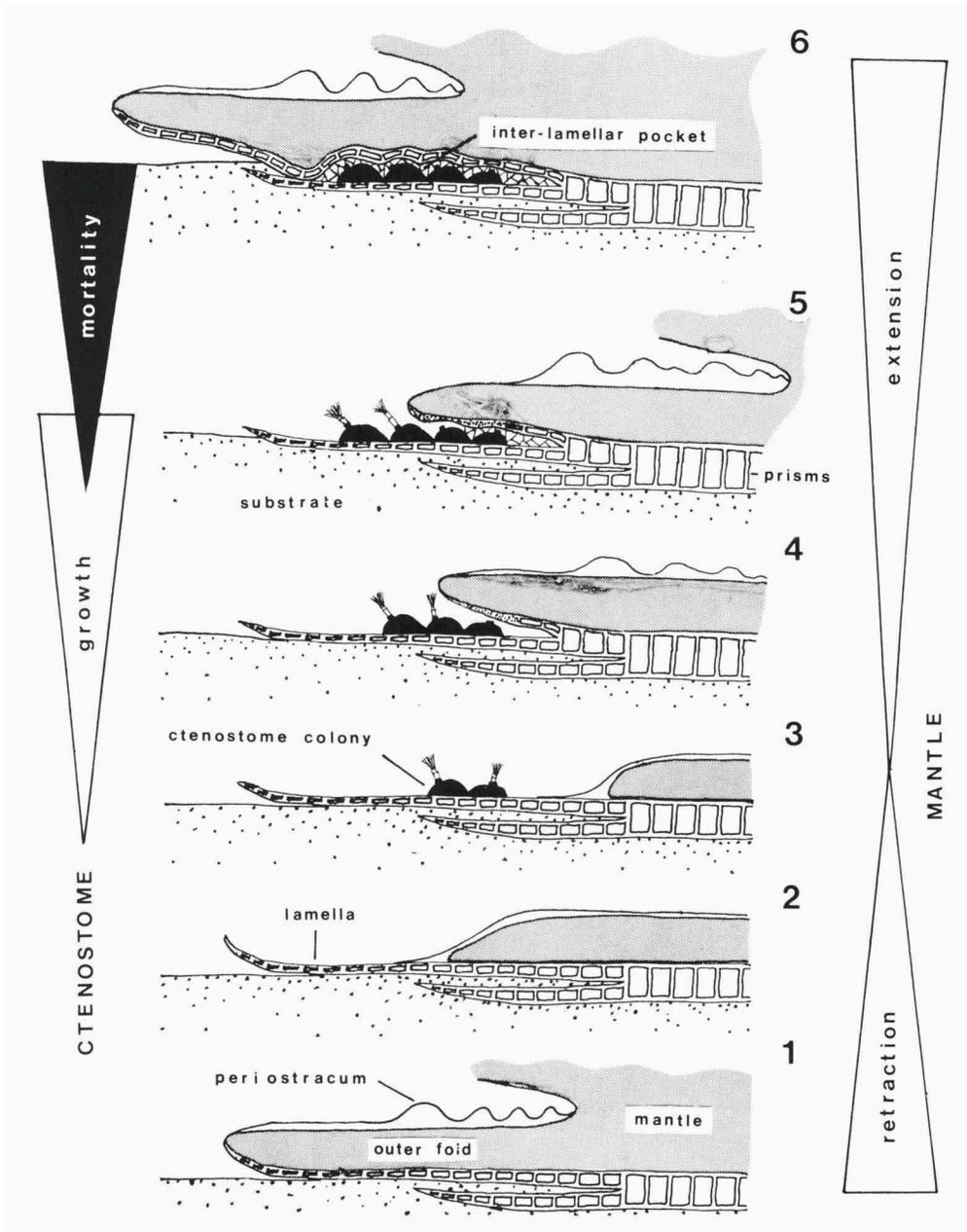
Fig. 3. Schematic summary of lamellar bioimmuration in a reclining left valve of *Deltoideum*; 1: lamella fully formed; 2: mantle retraction; 3: ctenostome bryozoans settle on lamella; 4: mantle extension, new lamella begins to form; 5: ctenostome zooids begin to be encapsulated in cement; 6: ctenostome colony entirely encapsulated in cement within inter-lamellar pocket, new lamella fully formed.

preserved as an external mould within a lamella of the left valve of *Deltoideum*. Surprisingly, SEM examination shows it to be very accurately moulded by an isolated patch of Harper layer cement varying from <1-20 μm thick. This has preserved the fine pustulose ornament and transverse wrinkling of the zooids' cuticle (Pl. 2, figs. 1a, 4a-c). This is despite the lamella having been produced in the post-cementational phase of growth. Evidently extrapallial fluid leaked through the newly secreted periostracum of the growing lamella where it was deformed by growing over the zooids. Here a small inter-lamellar 'pocket' was produced in which the cement grew and externally moulded the enclosed zooids. Indeed in *Deltoideum* it appears that carbonate-charged extrapallial fluid leaked through the periostracum of the left valve (and possibly through inter-prismatic gaps in newly secreted shell, Harper, 1992: fig. 9) throughout its growth. This would account for the very variable size of the attachment area, which frequently extends over the whole of the left valve in this species (Machalski, 1989; pers. obs.). The ability to produce cement apparently throughout post-cementational growth also allowed facultative re-cementation to occur. This is demonstrated by the attachment of shell fragments to the outside of the left valve (e.g. Machalski, 1989: fig. 5a). In similar cases SEM examination has shown the fragments to be attached by Harper layer cement. It is probable that such re-cementation occurred when free periostracum extending from a reclining *Deltoideum* contacted and grew over shell fragments lying on the sediment surface.

So far as I am aware nothing has been published on the factors that may control how and when a cementing oyster 'lifts off' from its substrate. Indeed a variety of identifiable cementing strategies are developed within the Ostreoidea, one of the

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Plate 2

1a. Three zooids of arachnidiid ctenostome preserved as mould bioimmurations within a growth lamella of *Deltoideum*. Part of the overlying lamella, upon which the zooids grew, is seen at left. Magnification X 31.2.

1b. Close-up of part of same specimen showing distal part of zooid, including peristome moulded by Harper cement (H). This overlies extensively bioeroded prismatic layer (p). Note very fine pustular ornament of cuticle has been preserved (as dimples). Magnification X 224. Early Kimmeridgian, Cricqueboeuf, Normandy, France. BZ 774.

2. Stoloniferous organism (possibly a hydroid) bioimmured by lamella of *Neopycnodonte cochlear* (Poli). The broken overlying lamella under which the organism grew, is seen at top. Note disturbance of growth increments produced by pushed-over erect elements. Magnification X 10.4. Coralline Crag (Pliocene), Ramsholt, Suffolk, England, L 1885.

3. Basal mould of arachnidiid zooid preserved by passive deformation in prismatic layer of *Deltoideum*. Fine deformation is due to wrinkling of the periostracum onto which the prisms were seeded. Magnification X 80. Ringstead Waxy Clay (Sandsfoot Grit Fm.), (*rosenkrantzi* zone, Late Oxfordian), Ringstead Bay, Dorset, England. BZ 775.

4a. Branching grooves of colonial organism preserved by active deformation of periostracal sheet. Preserved in prismatic layer of *Deltoideum*. Magnification X 20.8.

4b. Close-up showing marginal ramparts and fine deformation due to periostracal wrinkling. Magnification X 128. Ampthill Clay (*rosenkrantzi* zone, Late Oxfordian), Middlegate Quarry, South Ferriby, South Humberside, England. Unregistered.
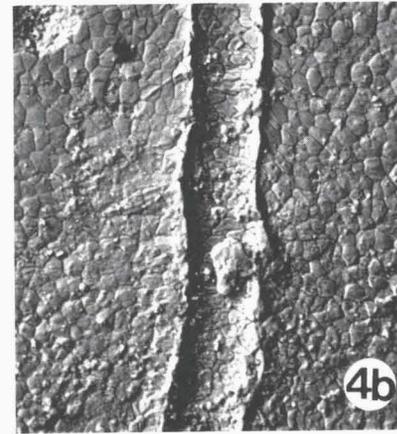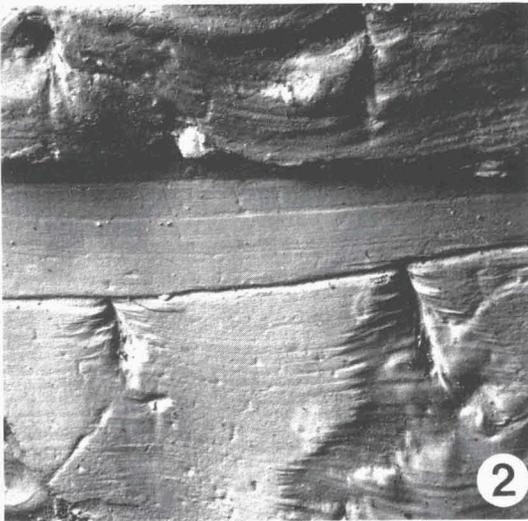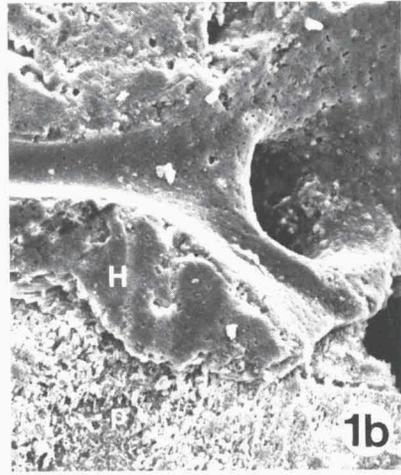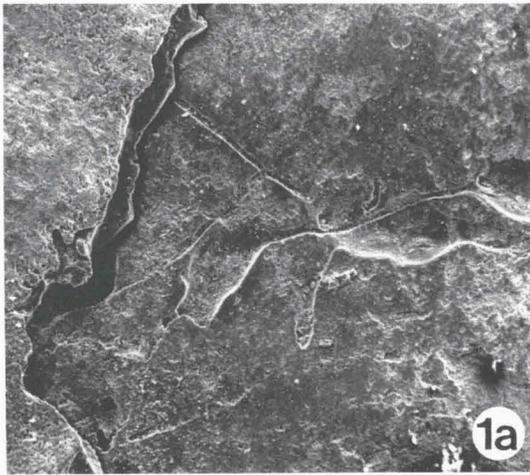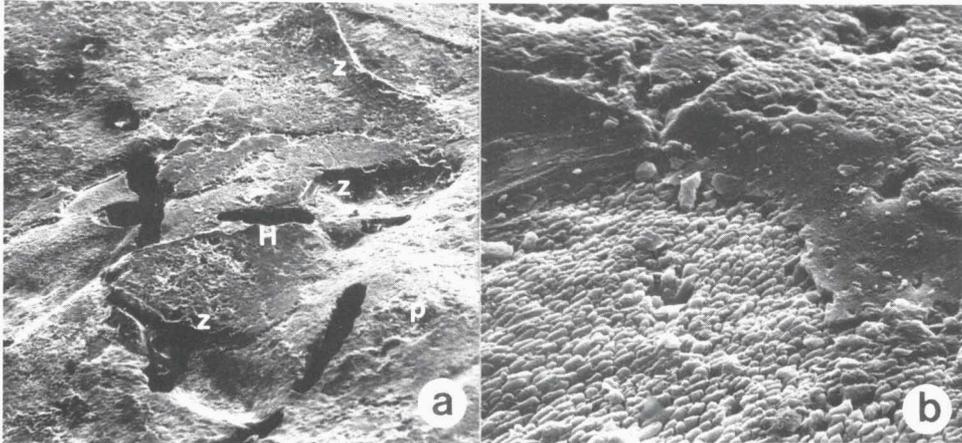
Plate 2

Fig. 4a. Oblique view of *Deltoideum* lamella with external moulds of arachnidiid ctenostome zooids (z) preserved in Harper cement (H) overlying prisms (p). The overlying lamella has been removed; growth direction of shell from top right to bottom left. Dark slit-like holes are *Talpina* borings. Magnification X 43.2.

Fig. 4b. Close-up of zooid in top right corner of Fig. 4a. It is compressed and only partially moulded by cement. The very uneven surface of the underlying prisms is typical for those seeded onto immuring periostracum. Magnification X 624.

most characteristic being a 'pie-dish' morphology (see Cooper, 1992) where a, generally thin, left valve lifts-off near-perpendicularly from the substrate. This morphology, so clearly distinct from that of *Deltoideum*, is well-seen in Cretaceous pycnodonteine gryphaeids. These include species and morphotypes of *Pycnodonte (Phygraea)* (e.g. Bottjer et al., 1978), *Velostreon umfolozianum* Cooper, 1992 as well as the Recent *Parahyotissa (Numismoida) numisma* (Lamarck, 1819) (see Harry, 1985). This morphology is much less commonly developed in ostreids, but a similar growth-form is characteristic of *Pseudoperna* (e.g. Stenzel, 1971: fig. J1030). Whether or not 'lift-off' is a response to crowding in these typically gregarious taxa remains to be tested. However, it seems likely that the role of exogenous as well as possible endogenous factors in controlling valve 'lift-off' varies considerably throughout the superfamily.

Clearly much additional work is needed to discover whether or not Harper layer cement is produced throughout growth in other fossil and Recent cementing bivalves. There are some indications that this may not be the case. An example is provided by a left valve of the gryphaeid *Neopycnodonte cochlear* (Poli, 1795) from the Coralline Crag (Pliocene) of Suffolk, England (Pl. 2, fig. 2). This has bioimmured a stoloniferous organism, possibly a hydroid, in a manner identical to that described for the arachnidiid zooids above. In this case the external mould produced is quite coarse and Harper layer appears to be lacking. However, post-depositional dissolution of the cement cannot be discounted. Future observations on Recent specimens of this species should be able to clarify the matter.
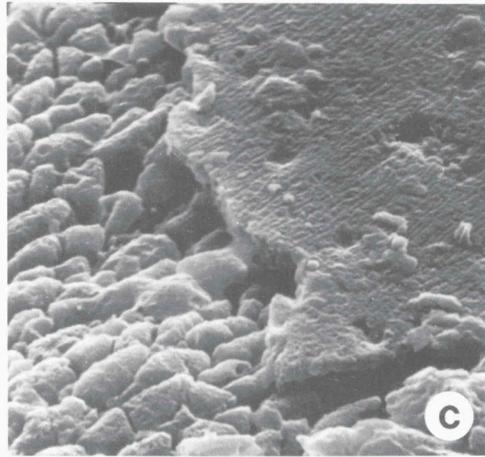
Fig. 4c. Close-up of the cement and prisms. Note the transverse cuticular wrinkling of the zooid and its pustulose ornament moulded by the cement. Magnification X 3.18K. Early Kimmeridgian, Cricqueboeuf, Normandy, France; BZ 774 (see also Pl. 2, fig.1).

Deformation of the periostracal sheet prior to prism growth

In ostreids a wide flange of periostracum may exist at the ventral margin for some time prior to the initiation of prism growth upon it, though no details have yet been published (Harper, 1992 and pers. comm.). In the development of the prismatic layer prisms start growing as unorientated blobs, later aggregating to form irregular clusters. Only upon close lateral contact do the growing prisms assume their characteristic form, a thin conchiolin sheath being squeezed between them (Galtsoff, 1964; Carriker et al., 1980). Galtsoff (1964: figs. 93-98) has shown that in *Crassostrea virginica* (Gmelin, 1791), once calcite precipitation begins, coalescence of the growing prisms to form a complete layer takes four or five days. Harper (1992: fig. 9) has illustrated that, in *Ostrea edulis* Linné, prism growth occurs unevenly, with inter-prismatic spaces remaining at some distance behind the advancing front of calcification.

Settling of epibionts on such a thin, flexible periostracum prior to appreciable prism growth inevitably leads to its deformation. From such deformation, on both left and right valves, a similar delay in prism growth can be shown to have occurred in *Deltoideum*. In this taxon two types of deformation can be distinguished, based on their pattern and inferred mode of production. Such traces must be carefully distinguished from shallow borings or etchings, which of course show no features of shell deformation. The process and patterns of periostracal deformation will here be only briefly outlined, as they are the subject of continuing study.

Passive deformation

Arachnidiid ctenostome bryozoans frequently grew upon the unmineralized periostracum of *Deltoideum* of Late Oxfordian and Early Kimmeridgian age in Eng-

land and Normandy. They are preserved as external moulds of their flexible, basal, zooidal surface (e.g. see Jebram, 1985) where this ballooned into the periostracum, demonstrating the particularly elastic nature of the latter. Around the deformation very fine pleats may be reproduced perfectly by the prismatic layer which subsequently grew on the inner side of the periostracum (see Pl. 2, fig. 3). It is a moot point whether these external moulds should be considered trace or body fossils.

Active deformation

On the same shells as those bearing arachnidiid traces, sparsely branched linear grooves may be developed. These run at an angle oblique to the commissure and have thin marginal 'ramparts'. Again fine-scale wrinkles may be developed within and on either side of the groove (Pl. 2, fig. 4a, b). The groove was produced by the growth of a thin, tubular, branching organism. Other lines of evidence indicate this organism to be colonial and a probable obligate commensal on *Deltoideum*. Its growth kept pace with the edge of the periostracal sheet into which its anterior end bent. This partial embedment actively produced the marginal ramparts. A fuller discussion of the nature of active deformation structures and their causative organisms is currently being prepared (Todd & Palmer, in prep.).

Importance of bivalve preservation traps

Unmineralized hard-substrate epibionts, though abundant in Recent seas, are almost unknown as fossils. Furthermore such faunas are not represented amongst the increasing number of Konservat-lagerstätten being described. Nor are they likely to, for 'the very conditions that promote soft-part preservation may also act to limit the nature or availability of the original assemblages' (Conway Morris, 1985) and such conditions frequently involved seafloor dysoxia. The process of bioimmuration provides the only way such assemblages are likely to be preserved.

Shell-cementing bivalves, and ostreoideans in particular, are, together with serpulids, the most important post-Palaeozoic bioimmurers, being widely distributed, often abundant, rapidly growing and bioimmuring with great fidelity (see Todd, in press). In effect the attachment areas of large oysters sample the epibionts growing on hard substrates (Taylor, 1990a: 7) and can provide information on the composition of such faunas, though such studies have yet to begin. In addition, potentially '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' (Taylor, 1990a: 6). I have discovered a few clear examples of such succession involving oyster bioimmuration.

Deltoideum, is an ideal bioimmurer for both studying the processes leading to the preservation of soft-bodied organisms, as well as the organisms themselves. It is large, diagenetically stable and may cement by the whole of its left valve. When it occurs it is often abundant, forming clumps or pavements.

Large collections of *Deltoideum* from the Late Oxfordian and Early Kimmeridgian

of Britain and France are providing detailed insights into the composition of the soft-bodied epibiont communities that lived on benthic islands in muddy substrates. Arachnidiid and other ctenostome bryozoans were particularly diverse and abundant. Species of the phylum Entoprocta, previously unrecorded as fossils (Todd & Taylor, 1992), were sometimes common though inconspicuous - much as they are today. Colonial hydroids and probable algae, as well as a number of unidentified forms, were also present. Amongst mineralized organisms, myriads of the small, attached, inarticulate brachiopod *Discinisca* have been found. Many have their long chitinous setae preserved (Taylor & Todd, 1990: fig. 6) and some may have phosphatized soft-parts.

Lamellar bioimmuration is a process likely to be widespread in Recent and fossil epifaunal bivalves with closely adpressed lamellae. Unfortunately, in fossils identifiable bioimmurations are likely to be restricted to mineralized epibionts. A notable exception to this being in those cementing taxa which were able to produce cement throughout their growth. A concerted search for lamellar bioimmurations might reveal the potential for cement production during post-cementing growth in a variety of fossil bivalves.

Perhaps the most unexpected result of this study is the discovery of periostracal deformation structures which, through their timing of emplacement, morphology and growth pattern, can be unequivocally related to their producers. In one case this is an unmineralized bryozoan of the family Arachnidiidae which is otherwise abundantly preserved by *Deltoideum* as attachment area bioimmurations and, more rarely, lamellar bioimmurations in the same deposits. Overall, close examination of many thousands of epifaunal bivalves of Mesozoic age, and smaller numbers from the Cenozoic, has shown epibiont-produced periostracal deformation structures to be not uncommon. Indeed at some horizons they may be found on almost every individual of what may be an abundant taxon. These structures are not confined to cementing or even pleurothetic taxa. Though their discovery is dependent on good preservation, with close observation they are likely to be discovered throughout the fossil record. Potentially they can provide much information about soft-bodied epizoans, particularly at horizons where cementing taxa are absent and hence the more typical bioimmurations are lacking. In addition, as this study has shown, one can gain important details of the host bivalve's biology such as the presence and extent of free periostracum and the relative timing of its mineralization. Although I predict such periostracal deformation structures to be widely distributed in Recent bivalves I am unaware of any published reports; they remain to be discovered.

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