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Defensive strategies of modular organisms

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[Plates 1 and 2]

Convergences concomitant with the occurrence of modular growth among systematically remote plant and invertebrate taxa not only reflect similar optimal ways of exploiting resources such as space, but also common defensive requirements among such organisms.

This paper analyses the kinds of unfavourable interspecific interactions, principally predation, epibiosis, and endobiosis, which are found among the major aquatic invertebrate groups that may be considered to be modular (Porifera, Bryozoa, and some of the Coelenterata and Tunicata). Most of the organisms are also non-locomotory, and in extreme cases, virtually immotile. The defence mechanisms of organisms exhibiting the opposing traits of (i) modular and unitary organization, and (ii) motility and immotility, are compared and contrasted. There is a more widespread occurrence of defence (i) by means of consolidated and unconsolidated skeletal reinforcement, and (ii) by actively and passively dispensed secondary substances, in less motile than in more motile organisms. These defensive modes represent alternatives to 'fight' and 'flight' responses seen within the more motile invertebrates. Lack of motility is of greater significance in correlating defensive modes than is modularity.

The balance between physical and chemical mechanisms used in defence can vary, even among closely related taxa. A more particular pattern of significance is the more widespread occurrence of defence by the use of passively dispensed chemical substances within modular, rather than unitary non-locomotory invertebrate groups. This may be a response to the increased risks of pathogenic infection which modular biota face through their susceptibility to frequent large scale wounding and partial mortality.

1. INTRODUCTION

(a) *Aims*

Striking convergences of form and perhaps function have accompanied the acquisition of modular growth by systematically remote non-locomotory taxa (figures 1–5 and 7–12, plates 1 and 2). These convergences may primarily reflect superior space-competitive abilities (Jackson 1977; Harper 1985) (figures 1–3), but some are more easily related to optimal exploitation of resources like light and food (Ryland & Warner, this symposium), or defence against the biological risks of predation, epibiosis or endobiosis. Remarkably similar or even identical secondary metabolites with defensive potential have been found among taxa as different as vascular plants and sessile invertebrates.

This paper aims (i) to identify (but not comprehensively review) the range of potential or actual defensive mechanisms found in non-locomotory modular invertebrates in response to

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TABLE 1. SUGGESTED RANGES OF DEFENCE AMONG SOME MAJOR GROUPS OF MODULAR AND UNITARY AQUATIC INVERTEBRATES CATEGORIZED ACCORDING TO WHETHER (GENERALLY) NON-LOCOMOTORY, LOCOMOTORY BUT SLOW MOVING, OR LOCOMOTORY BUT AGILE

(This scheme is neither definitive nor exhaustive in coverage; only reflecting evidence, views and suggestions as appear in the text. Some exceptions to the scheme are referred to in footnotes. Defence may not be the sole, or even the major function listed mechanisms. For each specific group, a mechanism is only referred to if it is believed to have the potential to serve in defence.)

group	modular cloner	unitary cloner	unitary non-cloner	defence by locomotion	defence by flexion	defence by reinforcement			defence by secondary substance							
						consolidated skeleton	unconsolidated skeleton	density of spines	passive metabolites	venoms	other					
non-locomotory																
Porifera (sponges)	+	-	-	-	PE	PEI	PI	PE	PEI	-	-	PEI	-	PEI	8	
Coelenterata	
Alcyonacea (soft corals)	+	-	-	-	PE	PI	PI	-	PEI	PE	PE	PEI	PE	PE	5	
Gorgonacea (sea fans)	+	-	-	-	PE	PI	PI	.	PEI	PE	PE	PEI	PE	PE	5	
Madreporaria (hard corals)	+	1	-	-	PE	PE	-	PE	-	PE	PE	-	PE	PEI	5	
Actinaria (anemones)	.	+	-	E	PE	-	-	.	-	.	.	-	PE	5, 8	PEI	
Polychaeta	.	.	.	2	5	PEI	5, 8	
Sedentaria (in part) (tube worms)	-	3	+	-	PE	PI	-	-	-	-	-	-	-	-	-	
Crustacea
Cirripedia (barnacles)	-	-	+	-	PE	PI	PI	-	-	-	-	-	-	-	-	
Mollusca
Bivalvia (in part) (non-locomotory spp.)	-	-	+	-	PI	PI	-	-	-	-	-	-	-	-	-	
Bryozoa (sea mats)	+	-	-	E	P	PI	-	PE	PEI	-	-	PEI	-	PE	6	

biological risks; (ii) to identify common trends that may exist among these; and (iii) to consider whether they are a function of modularity or of some other trait. Problems arise in the analysis of these traits because those most likely to be correlated with defensive requirements are not mutually exclusive. This is true for the main categories discussed here, namely, modular versus unitary, and locomotory versus non-locomotory habits.

(b) *Modular organization*

The concept of modularity, when less specifically defined, can accommodate a broad range of plants and invertebrates with similar growth patterns, although there is the view that it should be more restricted in definition (Boardman *et al.* 1973, Harper & Bell 1979; Larwood & Rosen 1979; Rosen 1979; Chapman & Stebbing 1980; Harper 1985). For the purposes of this paper, modular species are recognized more broadly as macrobiota growing by the addition of repeated blocks, units, or modules from growing points or fronts, that remain interlinked. The resulting continuous or intact clones, hereafter referred to as *individuals*, have theoretically indeterminate growth, size and longevity (figure 4). Organisms regarded as modular include macroalgae and vascular plants, and among the aquatic Invertebrata, all Porifera and Bryozoa and many of the Coelenterata and Tunicata (table 1).

(c) *Degree of motility*

Modular organisms are generally non-locomotory (unable to move from place to place under their own power) (table 1), and usually sessile, that is, they grow anchored to a substratum

DESCRIPTION OF PLATE 1

FIGURE 1. Strong tidal flow and intermediate conditions of illumination facilitate the development of a mixed assemblage of modular forms. A sponge, *Halichondria bowerbanki*, competes for space with various erect macroalgae. (The Fleet Lagoon, southern England, chart datum c.d. -4 m.)

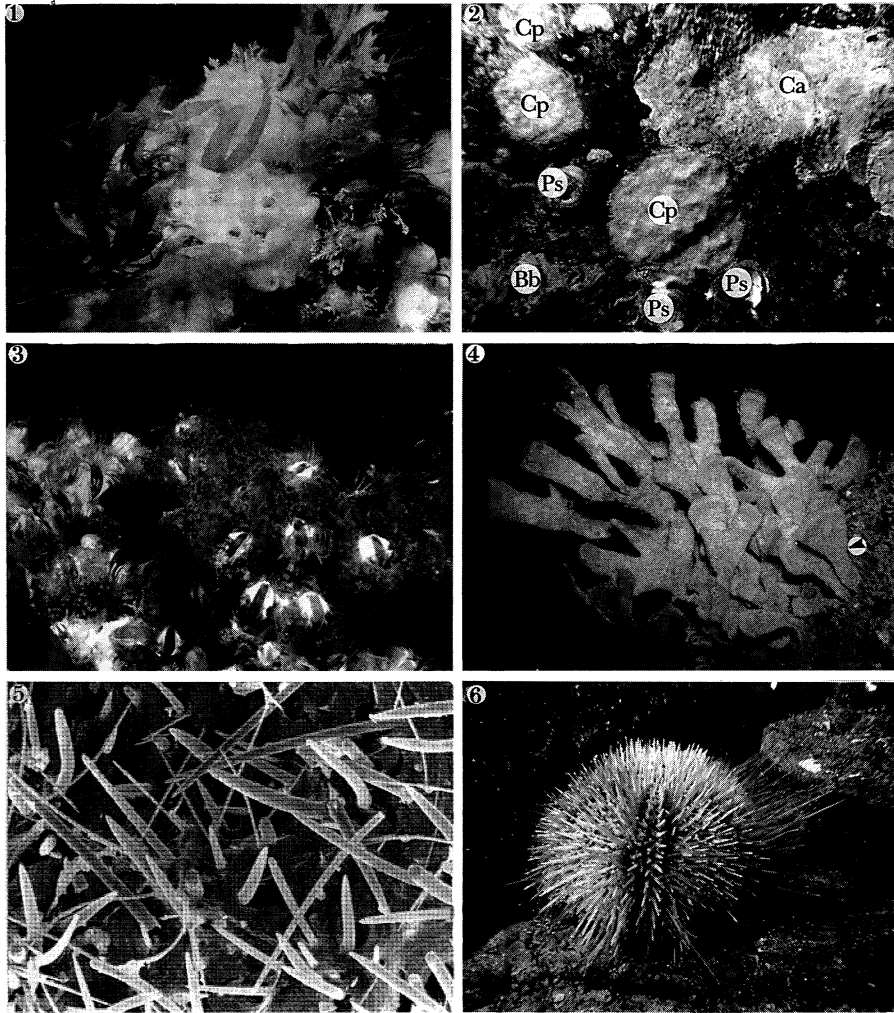
FIGURE 2. Thin, sheet-encrusting modular forms: *Cryptosula pallasiana* (Cheilostomata, Bryozoa) (Cp) and a coralline algal species (Rhodophyceae) (Ca) compete for space with unitary forms, the barnacle *Balanus balanus* (Bb) and the tubicolous polychaete *Pomatoceros* sp. (Ps). Space occupancy by such sessile biota is kept well below 100% by heavy grazing pressure from the echinoid *Echinus esculentus* (compare figure 6). The above species prevail by virtue of appropriate anti-predatory defences: all are characterized by heavy surface skeletal reinforcement (calcification), and the modular forms also by their ability to survive large-scale partial mortality. (Loch Fyne, Scotland, c.d. -12 m.)

FIGURE 3. Modular-cloning contrasted with unitary non-cloning. A recently established, originally monospecific cover of the barnacle *Semibalanus balanoides* (Cirripedia, Crustacea) is now being overgrown by a colony of the sheet-encrusting modular ascidian *Trididemnum tenerum* (Asciacea, Tunicata). A proportion of the barnacles survive the epibiosis in that whereas their non-vital calcified exoskeleton is overgrown, the orifice through which feeding and other vital exchange takes place is physically kept clear (arrow) by the movement of opercular plates or the cirral beat. (Kepple Pier, Firth of Clyde, Scotland, c.d. -3 m.)

FIGURE 4. *Flustra foliacea* (Cheilostomata, Bryozoa) grows to a combined, sheet-encrusting and frondose-erect gross morphology. By virtue of indeterminate growth, both elements are added to in annual increments (arrowed). Individual fronds have been known to survive for 12 years (Stebbing 1971), and the clone in its entirety has the potential to survive very much longer. (Swanage Pier, southern England, c.d. -4 m.)

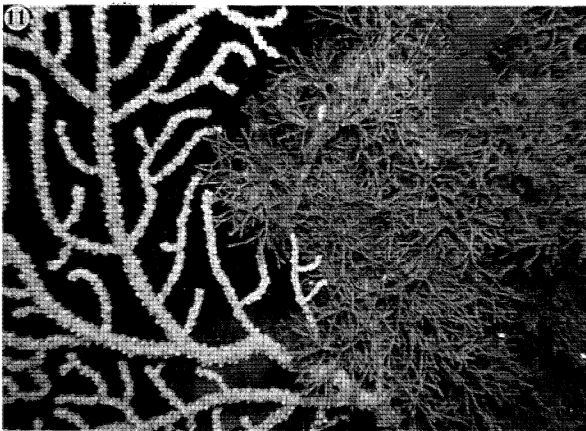
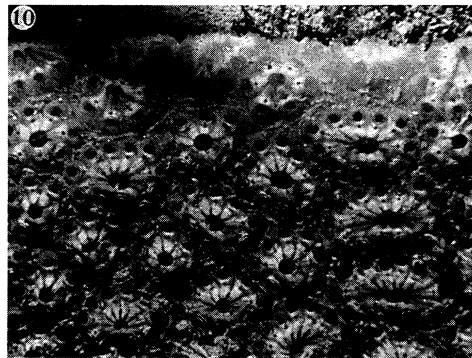
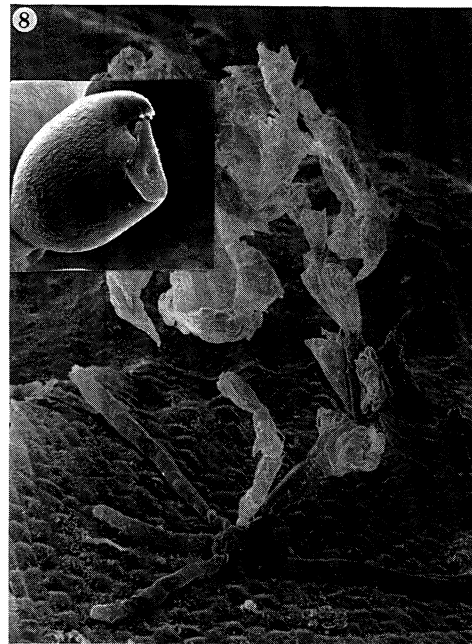
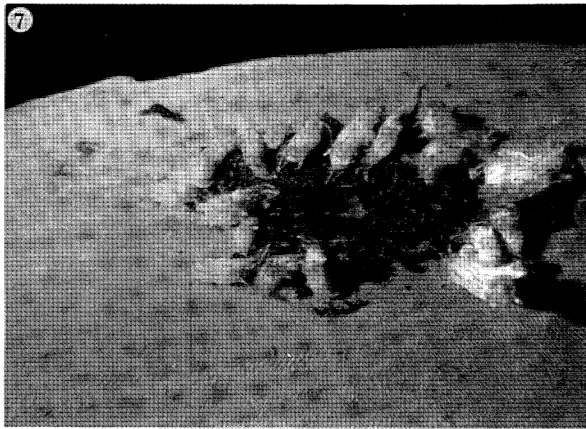
FIGURE 5. Detail of the surface of a thin, sheet-encrusting sponge *Microciona atrasanguinea* showing the barrage of pointed spines consisting of siliceous spicules (unconsolidated skeletal elements) and believed to provide defences against predation and epibiosis. (Scanning electron micrograph, sample from Swanage Pier, Dorset.)

FIGURE 6. *Echinus esculentus* (Echinodermata) grazing sessile invertebrates colonizing a vertical rock face (compare figure 2). The tube-feet, the means of locomotion of this slow-moving invertebrate, are clearly visible, as are the barrage of calcareous spines, which supplement the consolidated exoskeletal reinforcement as antipredatory defences. (Loch Fyne, Scotland, c.d. -12 m.)



FIGURES 1-6. For description see opposite.

(Facing p. 230)



FIGURES 7–12. For description see opposite.

consisting of rock, sediment, soil, etc. However, some that are non-locomotory and benthic, are non-sessile, lying unattached upon the substratum, whereas other non-locomotory forms are planktonic, drifting in air or water currents. Some modular invertebrates like the Siphonophora (Coelenterata) and Thaliacea (Tunicata) have secondarily re-acquired locomotion. Both of these taxa are pelagic but the bryozoans *Cristatella* and *Selenaria* and the ascidian *Diplosoma virens* are all benthic (Mundy 1980; Cook & Chimonides 1978; Ryland *et al.* 1984). Although incapable of true locomotion, some sessile and encrusting poriferans, scleractinians, bryozoans and ascidians appear to 'creep' by directional growth and die-back. Whereas many non-locomotory modular species are motile, in that they can effect appreciable gross or local body flexions, in common with the majority of plants, others are immotile. It is also true that not all non-locomotory invertebrates are modular. The anemones (Actiniaria, Coelenterata) (barely locomotory) are unitary and can clone, whereas most other unitary, non-locomotory forms do not clone, for example, most tube worms (Sedentaria, Polychaeta), barnacles (Cirripedia, Crustacea), and some bivalves (Lamellibranchia, Mollusca).

Among locomotory, unitary forms, the degree of locomotion is highly variable, for example, many reptant decapod crustaceans, prosobranch and opisthobranch molluscs, and also echinoderms, are relatively slow-moving; whereas errant polychaetes, natant decapod crustaceans, and cephalopod molluscs tend to be much more agile (table 1).

(d) *Categories of defence*

Interactions unfavourable to a *defender*, that is, predation, epibiosis, and endobiosis (often occurring in combination), are kinds of sequestration, that is, the *offender* (any micro-

DESCRIPTION OF PLATE 2

FIGURE 7. An extensive colony of the thin, sheet-encrusting bryozoan *Membranipora membranacea* (growing as an epibiont on *Laminaria digitata*) is being predated by a group of nudibranch molluscs *Polycera quadrilineata*. Zoooids (modules) beyond the immediate area of injury are unaffected, so that despite loss by partial mortality, the colony of this fast-growing species survives. The nudibranch is marked with clear orange and black spots on a white background, which is probably aposematic (see text). (Oxwich Bay, South Wales, c.d. - 3 m.)

FIGURE 8. Early colony of *Epistomia bursaria* (Cheilostomata, Bryozoa) growing on a rhodophyte. The first zooid (ancestrula) is clearly visible. From this, two erect shoots have arisen (one much smaller than the other). Feeding and reproductive activity are confined to shoots (Dyrynda & King 1982), each of which consists of alternating pairs of autozooids (feeding) and avicularia (zooids on shoots have partly collapsed during preparation; intact giant avicularium shown in inset). Avicularia probably function as do those of *Bugula* (see text). Four encrusting (and heavily calcified) runners have also been produced by the ancestrula. These will subsequently give rise to further runners and shoots. (Scanning electron micrographs prepared from specimens collected at Swanage Pier, southern England, c.d. - 4 m.)

FIGURE 9. A species of the nudibranch *Doto* climbs a shoot of the modular hydroid *Kirchenpaueria pinnata* on which feeding zooids are confined to side branches (Swanage Pier, southern England, c.d. - 3 m.)

FIGURE 10. Detail of the surface of the sheet-encrusting modular ascidian *Botryllus schlosseri* showing the replication of zooids (in constellations), resulting in such a high-density of vital orifices that any degree of epibiosis would constitute interference. *Botryllus* is known to deter direct and proximal settlement by the propagules of competitors (see text). (Swanage Pier, southern England, c.d. - 3 m.)

FIGURE 11. Partial mortality of this sea fan *Eunicella verrucosa* (Gorgonacea, Coelenterata) has exposed its gorgonian core (right, which persists long after polyp mortality). Whereas the living gorgonian keeps itself totally clear of sessile macroepibionts, the exposed endoskeleton supports a heavy epibiotic cover initiated by larval settlement and dominated by erect bryozoans. (Gulland Rock, southwest Britain, c.d. - 35 m.)

FIGURE 12. Sponge *Suberites domuncula* with an extensive laceration (cause unknown). This was healed completely within seven days. (Swanage Pier, southern England, c.d. - 2 m.)

or macrospecies) attempts to capture a primary resource, whether nutritional, or habitational space, already possessed by the defending modular macrobiont. This is in contrast with competition, in which the resource in question is presumed not to be possessed by either interacting individual.

Defensive arrays deployed against particular risks consist of 'physical' or 'chemical' mechanisms, or both. They might operate externally and before contact; or *at the surfaces* upon contact with an offender; or *internally*, if an offender penetrates the defender. Although defence is usually *intrinsic* (that is, the defender itself has its own defensive mechanisms), it is also sometimes *extrinsic* if it has a symbiont which acts as a defensive agent. Symbionts serve in the defence of many large immotile modular organisms.

A defence mechanism, as recognized here, is any mechanism that is capable of providing defence against biological risks, even though this may not be the sole, or even the major function of the mechanism in question. The main risks discussed below are predation, epibiosis and endobiosis. Mechanisms of defence are as categorized in table 1. In the text below, reinforcement and secondary substances are concentrated upon.

2. REINFORCEMENT

(a) *Categories of reinforcement and their occurrence*

'Panclonal' skeletal systems, internal or external, constructed or produced by the intermodular interaction of 'hard' acellular elements characterize all modular groups, as they do numerous unitary invertebrates. Such skeletal systems provide support or defence, or both. In *consolidated* reinforcement, skeletal elements are continuous or fused between modules (for example, the internal spongin fibre networks of some demosponges, or the siliceous frameworks of some hexactinellid sponges). Scleractinian corals produce rigid consolidated, external calcareous bases secreted by the overlying polyps, into which the polyps can usually withdraw. Modular hydroids (Coelenterata) and bryozoans possess external chitinous skeletal reinforcement, supplemented in many bryozoans by calcification. Except for athecate hydroids, inactive or threatened polyps (or polypides) withdraw into the protection of the exoskeleton. Such responses are analogous to the 'flight' escape reactions of locomotory invertebrates. Modular ascidians have mucopolysaccharide exoskeletons, ranging from delicate to heavy in constitution. The 'panclonal' (or 'colony-wide') closure of vital orifices (that is, siphons), to seal the organism within the protection of the exoskeleton, characterizes some ascidians, and constitutes an even more specialized kind of physical 'flight' than retraction alone.

Unconsolidated skeletal reinforcement is provided by spicules (granules or sclerites), not fused or continuous between modules (though sometimes linked by connective tissues). Calcareous or siliceous spicules characterize most poriferans. Alcyonacean soft corals contain calcareous spicules: individuals that are soft when dilated with water while feeding, may become rigid upon contraction as spicules 'interlock' to form a framework into which the polyps withdraw.

Combined reinforcement occurs in demosponges with both spongin networks and calcareous spicules. Some gorgonacean sea fans combine a tough endoskeletal consolidated core (gorgonin) with calcareous spicules in the enclosing polyp sheet. In many didemnid ascidians, the mucopolysaccharide test is supplemented by calcareous spicules.

Surface spines are common among non-locomotory modular invertebrates (for example, pointed spicules project through the epidermis in the form of spines in some sponges (figure 5)).

Consolidated skeletal elements also include spines as in many scleractinian corals and in bryozoans. Ascidians do not produce spines.

Coelenterate nematocysts might also be included in this reinforcement category, if we regard them as defensive, surface structures. They are chitinous and, when appropriately triggered, 'explosively' discharge an often penetrant and injurious filament, in many cases containing a toxic agent (see §3*d*). Avicularia are specialized non-feeding zooids characteristic of the cheilostomate bryozoans. Some support pincer-like structures which may function defensively (Cook, 1979; Winston 1984).

Many non-locomotory and slow-moving unitary invertebrates possess consolidated skeletons, usually external and calcified, (for example, tube worms, barnacles, many bivalve molluscs, decapod crustaceans, prosobranch molluscs, and echinoids (figure 6)). Unitary, sessile ascidians have mucopolysaccharide tests similar to their modular equivalents. Unconsolidated skeletal reinforcement is uncommon among non-locomotory forms, except for some barnacles; but spicules do occur within the slow-moving dorid nudibranch molluscs (which sequester their spicules from their sponge prey (Todd 1981)), and in most asteroid and holothurian echinoderms. Among locomotory groups, spines (at density) are more characteristic of slower-moving groups, for example, some reptant decapod crustaceans, and echinoids in general (figure 6). Nematocysts are ubiquitous and characteristic within all coelenterates, including unitary forms like anemones (Actiniaria). They also occur in aeolid nudibranchs, sequestered from their coelenterate prey (Todd 1981). Echinoderm pedicellariae are remarkably similar to some defensive bryozoan avicularia in form and perhaps function. They possess gripping pincers, and some are venomous (Russell 1984).

External reinforcement, if present, among more motile forms including the modular thaliaceans and some siphonophores, tends to be less substantial than in sessile forms. This is even more true for more agile locomotory organisms like errant polychaetes and natant decapods.

(*b*) *Skeletal reinforcement as a defence against predation*

Many modular, non-locomotory species exhibit intermodular functional delegation, more vulnerable vital systems (for example, feeding or reproduction) being confined to less vulnerable parts of the whole clonal individual (for example, centrally in sheet-encrusters, or upon the shoots of erect species). Attack may be prevented by barrages of spines. Thus small gastropod molluscs are unable to climb the spiny surfaces of the sponge *Microciona atrasanguinea* (personal observation) (figure 5). Such defences are usually passive in that they exist irrespective of threat, but some are active, for example, the sheet-encrusting bryozoan *Membranipora membranacea* produces peripheral spines in response to grazing pressure by nudibranch molluscs (Harvell 1984) (figure 7).

Jackson (1979) considers 'escape' from predation to be a major advantage of the erect gross morphology adopted by many colonial invertebrates. Some thecate hydroids and cheilostomate bryozoans (for example, *Dynamena* and *Bugula* or *Epistomia*, respectively) have combined runner-and-erect gross morphologies (figure 8). The runners, highly vulnerable to substratum-bound predators, are protected by heavy skeletal reinforcement. Feeding and reproductive activity is usually confined to erect 'shoots', the proximal sections of which can be difficult to climb, often being smooth and very slender. Nevertheless, there may be specifically coadapted predators like nudibranch molluscs of the genus *Doto*, which are specialized in their ability to

climb such features, (figure 9). Nematocysts and avicularia have the potential to prevent a surface-bound predator from reaching its feeding site. *Trivia* (Prosobranchia, Mollusca) sharply withdraws its foot when it comes into contact with *Alcyonium digitatum* (Alcyonacea, Coelenterata) (personal observation). Nematocysts may entrap or toxify the predator. N. Ravenscroft (unpublished) observed that the avicularia that line the shoots of *Bugula* (Cheilostomata, Bryozoa) can immobilize various climbing predators like crustaceans, mites and pycnogonids. The avicularia can maintain their grip for days, even causing predators to shed appendages or die (other examples are cited by Winston 1984) (figure 8).

If the predators can actually reach their attempted feeding site, skeletal features may prevent them from commencing to feed. The mass withdrawal of vulnerable polyps or polypides to within the skeletal framework, or the closure of orifices, may safeguard vital systems. Sharp spines may wound the feeding predator. Skeletal reinforcement, consolidated or unconsolidated, may render the surface impenetrable. For example, the exoskeletal morphology of scleractinian corals protects polyps from chaetodontid and other coral-grazing fish. Polyps raised on protuberances are more vulnerable than when recessed within foveolate skeletal structures. Best & Winston (1984) found exoskeletal strength of sheet-encrusting cheilostomate bryozoans, and hence vulnerability to penetration by grazing molluscs, to be highly variable.

Internal skeletal reinforcement, consolidated or otherwise, may curtail feeding and so limit potential damage: internal 'vital' structures may be impenetrable, and angular spicules may irritate the gut of the predator. Modular species are at an advantage in this respect in their ability to survive a large degree of partial mortality such that internal mechanisms may constitute a major line of antipredatory defence. Although metameric annelids and asteroid echinoderms, for example, can appreciably enhance their survivorship by regeneration, this potential does not approach that of modular biota. The prospect of such organisms 'sacrificing' a proportion of themselves as part of a defensive strategy would carry a high risk of outright mortality.

(c) *Skeletal reinforcement as a defence against epibiosis*

The physical (and chemical) nature of a substratum is a primary factor influencing larval settlement. The extreme delicacy of the surfaces of some species (for example, the modular ascidian *Diplosoma listerianum*) render them unsuitable for epibiosis. Spines can also prevent colonization, both by larval settlement and lateral overgrowth. The spines of *Microciona atranguinea* ensnare larvae of *Bugula* (Cheilostomata, Bryozoa) (personal observation) (figure 5). As an 'active' equivalent to this mode of defence, the sheet-encrusting bryozoan *Electra pilosa* produces a peripheral barrage of spines when 'threatened' by lateral overgrowth of adjacent biota (Stebbing 1973). In addition to advantages in terms of anti-predation, the adoption of an erect gross morphology can also be considered an 'escape' from epibiosis initiated by lateral growth (Jackson 1979), particularly when proximal sections are slender, since sheet-encrusters tend to grow around rather than up such substrates (figures 1, 8, 9). On the other hand, runner networks of genera such as *Sertularia*, *Bugula* and *Epistomia* are not harmed by being overgrown since they are heavily skeletalized, and are not sites of vital exchange (feeding, etc.).

In consolidating its surface by skeletal reinforcement, an organism usually becomes more susceptible to epibiotic colonization. It presumably gains, however, from better self-support, or better resistance to other kinds of attack like predation, or both. Symbiotic epibionts, however, may prevent further epibiosis of their host by having defences of their own.

(d) Skeletal reinforcement as a defence against endobiosis

Surface skeletal reinforcement, particularly when consolidated, may be important in deterring the entry of both potential micro- and macroendobionts (Ratcliffe 1986).

3. SECONDARY SUBSTANCES

(a) General

Defensive secondary substances may be categorized into those that are essentially physical in their action and effect (for example, colour, adhesion or lubrication) and those that are chemical (for example, signal, noxious, or toxic). Both can be subdivided into those passively dispensed, that is, irrespective of threat; and those actively so, that is, in response to a stimulus associated with a specific threat.

(b) Secondary substances that act physically

A number of poriferan taxa (for example, *Myxilla*) produce substantial quantities of mucus, which accumulates throughout the individual, and is released in quantity from sites of injury. Scleractinian corals and zoanthids are also major producers of mucus. This is secreted from epithelia and flows as a film over the coral surface. Sponge and coelenterate mucus can have lubricant or adhesive physical effects but may also carry, for example, noxious or toxic substances. Epithelial mucus is not known to be produced by Bryozoa or Ascidiacea. It is doubtful, however, if mucus serves as a defence against macropredators, except by hindering the approach of substratum-bound climbers (for example, gastropod molluscs or pycnogonids) by adhesive or lubricating effects. Noxious or toxic substances carried within mucus may be antipredatory.

Surface mucus is more likely to be a defence against epibiosis, especially inhibiting larval settlement. Larvae of *Bugula* (Cheilostomata, Bryozoa) settling on *Myxilla* become incapacitated when their ciliary mechanisms become clogged by mucus (personal observation). This action may also affect larvae which might settle on scleractinian corals. Surface mucus is also likely to provide a major defence against micro-endobiosis (Ratcliffe 1986). Antonius (1981) believes this is so for scleractinian corals.

Of the unitary groups, surface mucus is particularly common among anemones (Actiniaria, Coelenterata) and gastropod molluscs. It is also produced by echinoderms (Russell 1984) and other groups.

Pigments can provide defensive colour or pattern, carotenoids being widespread among modular sessile groups, as they are among invertebrates in general. Strong, unpatterned pigmentation is characteristic of many modular species, patterning being less common. Aposematic coloration is common among some modular groups. Potential predators may associate the bright colours of many toxic species with their unsuitability as prey; though not all toxic species are distinctive in this way, *Flustra foliacea*, for example, (figure 4) being a dull plain brown.

Anemones are one unitary immotile group in which aposematism is significant (as a forewarner of nematocyst protection). The same is true for nudibranch molluscs with noxious or toxic chemical protection (Todd 1981) (figures 7, 9) and many echinoderms with skeletal reinforcement or toxicity (figure 6).

(c) *Secondary substances that act chemically: passively dispensed substances*

Many modular, non-locomotory invertebrates are known to accumulate secondary substances of relatively low molecular mass that are passively dispensed, that is, whether present within the organism, on the surface, or actually released from the organism, their occurrence exists irrespective of specific threats (contrast with venoms, discussed in (d)). Many of these substances have the potential to exert noxious or toxic effects. Evidence is growing that their occurrence in marine species is on a scale comparable to that known for plants, not only marine macroalgae but also vascular plants (Whittaker & Feeny 1971; Rice 1974; Rosenthal & Janzen 1979). Alkaloids and terpenoids, for example, are particularly prevalent in both (Halstead 1978; Scheuer 1978, 1983; Hashimoto 1979; Rosenthal & Janzen 1979; Russell 1984), and there are striking examples of the very same substances being common to higher plants and modular invertebrates (for example, the monoterpenoids citral and geraniol occur both in vascular plants and the cheilostomate bryozoan *Flustra foliacea* (Christopherson & Carle 1978)).

Invertebrates, like plants, can accumulate closely related metabolites that are species-specific either individually or in combination (for example, the terpenoid chemistry of sponge groups is sufficiently characteristic for their use in chemotaxonomy (Bergquist & Wells 1983)). These kinds of substances can accumulate sufficiently to constitute a significant proportion of an animal's biomass (for example, the alcyonacean coelenterate *Lobophytum crassospiculatum* contains up to 5% dry mass of diterpenoids (Coll *et al.* 1985)). The occurrence of such metabolites at concentration is patchy among the non-locomotory modular invertebrates. In part at least, this reflects a research bias, but there are well-screened groups for which absence is probably genuine. Passive secondary substances are nearly universal among poriferans (Minale 1978; Bergquist & Wells 1983), whereas among coelenterates they are abundant in alcyonaceans and gorgonaceans and probably scarce among scleractinians (Hashimoto 1979). They are not reported for the pelagic Siphonophora. The substances concerned are quite different from the higher molecular mass polypeptides that occur within venomous nematocysts (Russell 1984). The few bryozoans that have been investigated are rich sources of secondary substances (Christopherson & Carle, 1978; Carle *et al.* 1982; Wulff *et al.* 1982). Perhaps least is known about modular ascidians. Although vanadium and sulphuric acid have been claimed as chemical defensive agents that are widespread among both modular and unitary representatives of this group (Stoecker 1978, 1980); as yet, evidence for the presence of organic equivalents is limited.

Although such potentially defensive metabolites also occur in unitary invertebrates, those that are typical of modular biota, like alkaloids and terpenoids, are not well represented, except in organisms that sequester them via the food chain. Among the major non-locomotory, or nearly non-locomotory unitary groups, anemones (Actiniaria, Coelenterata), tubicolous polychaetes, barnacles (Cirripedia, Crustacea) and bivalve molluscs are not particularly known for such substances, and only unitary ascidians are claimed to be (Stoecker 1978, 1980). Among locomotory unitary forms, slow-moving groups are mostly characterized by defensive metabolites, for example, some opisthobranch molluscs sequester them from their diet which is often based on modular organisms (for example, *Phyllidia* acquires sesquiterpenoids from the sponge, *Hymeniacidon* (Todd 1981)). Many echinoderms produce saponins with antipredatory actions (Russell 1984). Defensive metabolites are less common among faster-moving invertebrate groups.

Defensive potential is dependent on potency and levels of dose: a function of concentration and duration of exposure. At very low doses, a barely perceptible substance may have a signalling role (compare with aposematism in (b)). At intermediate doses, it may have noxious roles (that is, unpleasant but causing no damage), and at higher doses, it may be sublethally or lethally toxic. Concentrations are likely to be greatest internally, less at the surface of the organism, and, if release takes place, very much less in the surrounding water column. Although within some species metabolites may be generally distributed, in others, there is appreciable localization. Gradients of antimicrobial activity occur along fronds of *Flustra foliacea* (Al-Ogily & Knight-Jones 1977) (figure 4), and levels of palytoxin (one of the most potent marine toxins known) within colonies of the zoanthid coelenterate *Palythoa* are greatest in female zooids, and particularly in their developing eggs (Hashimoto 1979). Although one would expect internal and surface metabolites to be released at the sites of injury it does not follow that they are released from intact uninjured individuals. This phenomenon, however, has been demonstrated for a sponge (J. Thompson, in Russell 1984), and also by *in situ* experimentation on the alcyonarian soft coral *Sarcophyton*, which is known to release detectable levels of a monoterpene (Coll *et al.* 1982a).

Whereas noxious or toxic doses of a substance may well be generated within or on the surface of an organism, it is difficult to believe that the same levels of potency could be achieved by external release into the surrounding water column other than within the confines of a tide-pool. It is certainly difficult to envisage this in the kinds of current-scoured localities where modular invertebrates proliferate (figure 1).

(i) *Passive chemical defence against macropredators*

Noxious doses of secondary substances, whether present externally, on the surface, or within internal tissues, may provide antipredatory defence by evoking aversive responses from potential predators. Predatory invertebrates often select their prey from a distance by chemoreception, a fact well established by food preference tests (for example, Chadwick & Thorpe 1981). Coll *et al.* (1985) have shown that purified soft coral metabolites (impregnated into pellets) cause fish to reject at the 'tasting' or 'mouthing' stage.

In view of their more prolonged and intimate contact with the prey, climbing, substrate-bound predators are more likely to be toxified by noxious or toxic doses of surface metabolites than are non-climbers. The action of surface metabolites (before feeding) or of internal metabolites (after the onset of feeding) may be external in their effects on predators (via gills, sensory organs, etc.) or internal (via the gut). Ichthyotoxic substances are common within sponges, alcyonacean soft corals, and occur in bryozoans (Green 1977; Bakus, 1981; Coll *et al.* 1982b; Dyrinda 1985). More chronic antipredatory effects like reduced fecundity, and indeed carcinogenesis, may select against predator populations feeding on chemically protected prey, as is well recognized for plants (Keeler & Tu 1983).

Passively dispensed secondary metabolites serve in the antipredatory defence of several unitary invertebrate groups, all locomotory, including nudibranch molluscs and echinoderms (Todd 1981; Hashimoto 1979; Russell 1984).

(ii) *Passive chemical defence against epibiosis*

Since invertebrate larvae widely use chemoreception to select their settlement surfaces, signal doses of metabolites, whether on the surface or released from an organism constituting a

potential settlement site, may inhibit settlement of motile propagules. Whereas most studies have been concerned with positive chemotaxis, Grosberg (1981) has demonstrated the converse: larvae of many species do not settle on surfaces more heavily colonized by the sheet-encrusting ascidian *Botryllus schlosseri* (figure 10), possibly because *Botryllus* releases inhibitors. In this and in other cases, settlement may be prevented by the initiation of an avoidance response or by sublethal toxification, for example, incapacitation of ciliary mechanisms leading to disorientation.

Such metabolites would be most important for species at risk from epibionts, that is, those with reinforced surfaces. Burkholder (1973) suggested that the strong antimicrobial activity shown by gorgonacean coelenterates may reflect larvicidal defence. Although gorgonaceans are rigid, they are usually notably devoid of epibionts (figure 11). The same was proposed for the bryozoan *Flustra foliacea* (Al-Ogily & Knight-Jones 1977), for which larvotoxicity was subsequently demonstrated (Dyrynda 1985) (figure 4). Bandurraga & Fenical (1985) have separated and identified specific larvicidal factors (saponins) from the alcyonacean *Muricea fruticosa*.

Similar defences against epibiosis by larval settlement occur among unitary, non-locomotory invertebrates. Larvotoxic agents occur on the surface of the unitary ascidian *Ascidia nigra* (suggested by Stoecker (1978) to be sulphuric acid or vanadium, as in modular species). In contrast, tubicolous polychaetes and cirripede crustaceans, also at risk, are probably free of such chemical defences. Motile invertebrates that are incapable of maintaining skeletalized surfaces free of epibionts by flexion, scraping, or other physical means like spines and pedicellariae, are also vulnerable. Periodic moulting solves this for Crustacea and echinoderms may use passively dispensed metabolites in conjunction with pedicellariae and spines (Russell 1984).

Secondary substances may also inhibit colonization by lateral overgrowth. Some modular species release, or present at their surface, metabolites suppressing the progress of such colonizers, for example, the growing fronts of some thinly encrusting sponges are preceded by bands of necrosis within their opponents (Bryan 1973; Jackson & Buss 1975; Ayling 1983). Assays have shown that some tropical sponges and ascidians contain agents that are toxic to competing bryozoans (Jackson & Buss 1975). Alcyonacean coelenterates administer doses of toxic secondary metabolites to neighbouring scleractinian corals, sufficient to retard respiratory and growth rates, or even to kill them (Coll *et al.* 1985).

Defences against epibiosis initiated by lateral overgrowth are unnecessary for locomotory invertebrates, since even the slowest movers can move away faster than any rate of lateral overgrowth by potential epibionts.

(iii) *Passive substances as defences against endobiosis*

Toxic secondary metabolites are involved in defence against endobiosis throughout the Invertebrata (Ratcliffe 1986). However, most modular species differ from unitary ones in their greater susceptibility to pathogenic microbial invasion, associated with the tendency for partial mortality often following large-scale wounding (figure 12). Despite the disruption of surface defences, many species are able to maintain themselves free of microepibionts and endobionts (Burkholder 1973), and it may be no coincidence that antimicrobial activity is the most widely documented characteristic known for purified secondary substances (see, for example, Burkholder 1973; Amade *et al.* 1982).

(d) Actively dispensed substances: venoms

In contrast to most passively dispensed substances, actively dispensed venoms are typically of relatively high molecular mass, for example, polypeptides. Although these substances are often primarily concerned with feeding (Halstead 1978), venomous systems can also be defensive in some organisms. Many coelenterate nematocysts are venomous, containing often highly toxic polypeptides (Halstead 1978; Hashimoto 1979; Russell 1984). For many species, their sole function is prey capture, their defensive role being secondary or insignificant, although those not located near the oral disc of feeding polyps are more likely to be defensive. Nematocysts may be the main line of anti-predatory defence for siphonophores (Halstead 1978; Hashimoto 1979; Russell 1984). A crude venomous system is encountered in 'aggressive' scleractinian corals which toxify their neighbours that are competing for space, with digestive enzymes released from extruded mesenterial filaments (Lang 1973). Venomous systems remain little known for the other modular groups.

Nematocysts provide the same sort of protection for anemones, as they do for modular coelenterates. Among slow-moving locomotory groups, aeolid nudibranchs are also venomous; some of them sequestering undischarged nematocysts from their coelenterate prey whereas others secrete acidic venoms (Todd 1981). Among the prosobranchs, species of *Conus* are highly venomous (Halstead 1978; Hashimoto 1979; Russell 1984). The spines and pedicellariae of some echinoderms are also known to produce venoms (Russell 1984). The use of venomous systems for defence may be less common among the more agile locomotory invertebrate groups. However, many cephalopods produce venomous saliva which may be used for antipredation in addition to their major function of prey capture (Russell 1984).

4. DISCUSSION

Common themes of defence are shared by sessile invertebrates that combine immotility with modularity. Some defensive mechanisms, notably the use of passively dispensed secondary substances of relatively low molecular mass, are strikingly similar to those of other modular groups, that is macroalgae and vascular plants. Rather than being a function of modularity, these common themes are a function of being immotile. A trend can be identified of the increased application of defensive options *not* dependent on motility (movement by flexion or locomotion) as the latter declines.

Highly motile invertebrates like errant polychaetes, natant decapod crustaceans and cephalopod molluscs are more able to 'fight' potential predators by body flexions alone, or are quick enough to escape by locomotion as a 'flight' option. They can also easily escape epibiosis initiated by lateral overgrowth by locomotion. They can deter larval settlement by body flexions or by abrasion between their body surfaces and their surroundings as they move.

Slow-moving, locomotory biota (that is, some reptant decapod crustaceans, prosobranch and opisthobranch molluscs and echinoderms as unitary examples; and the modular thaliacean tunicates and some siphonophoran coelenterates) are less able to use motion in 'fight and flight'. Their alternative means of 'fighting' predators include increased skeletal reinforcement, particularly at their surface (for example, reptant decapods, prosobranch molluscs and echinoderms), and spines are a common elaboration of this within reptant decapods and echinoderms. Passively dispensed noxious or toxic secondary substances of relatively low

molecular mass are more common (for example, within nudibranch molluscs and echinoderms) than in more agile organisms. The same is true for actively dispensed venoms of relatively high molecular mass (for example, among prosobranch and nudibranch molluscs, echinoderms, siphonophoran coelenterates). Such invertebrates are more at risk from epibiosis by larval settlement than are fast-moving ones, although their motility is still sufficient to avoid colonization by lateral overgrowth. Particularly at risk from epibiosis are species with skeletal surface reinforcement, but among crustaceans, moulting counteracts epibiosis, while molluscs may rely on abrasion, and rigid-surfaced echinoderms may be protected by a combination of spines, pedicellariae and passively dispensed larvicidal agents (many rigid-surfaced species can sustain a degree of epibiosis with little adverse effect). Cryptic camouflage as an alternative to 'flight' by locomotion is a common antipredatory defence among the less locomotory invertebrate groups in general. The siphonophores, pelagic coelenterates that are both modular and locomotory, may rely on nematocysts as their major line of defence against predators (although their tentacular nematocysts are primarily for feeding).

Sessile groups, including those that are modular, exhibit an extreme condition with respect to motility: by definition all are non-locomotory, and in many cases, movements are limited to internal flexions such that alternative mechanisms prevail. Skeletal reinforcement is widespread among tubicolous polychaetes, cirripede Crustacea, Porifera, Coelenterata, Bryozoa, and both unitary and modular Ascidiacea. In many cases, the degree of reinforcement clearly far exceeds requirements for support. Spines are common among all non-locomotory modular groups except ascidians, but are less common among unitary ones. Cheilostomate bryozoans possess avicularia, which in some cases have defensive functions analogous to those of echinoderm pedicellariae. Venomous nematocysts, exclusive to the Coelenterata, constitute a major defence within that group. Passively dispensed metabolites which may be noxious or toxic to predators (among other roles) are common within the Porifera, Coelenterata, Bryozoa, and probably the Ascidiacea, but are not so within tubicolous polychaetes and barnacles. In conjunction with the above, the bright pigmentation of many species may serve in aposematism. More generally, different members of modular invertebrate groups show an emphasis on different defences. For example, whereas consolidated skeletal reinforcement, mucus, and venomous nematocysts constitute major aspects of the defensive array of scleractinian 'hard' corals, within the alcyonaceans the defensive array consists of unconsolidated reinforcement and, especially, passively dispensed metabolites, nematocysts being of reduced significance.

'Flight' options that require movement do exist among non-locomotory taxa in the form of a mass withdrawal of vital feeding structures to within the skeletal framework, or the closure of vital orifices. These are seen within representatives from all unitary and modular non-locomotory groups. Cryptic camouflage occurs in some groups, but others have distinct patterning and pigmentation, possibly aposematic, for example, signalling toxicity to potential predators.

Non-locomotory invertebrates are highly vulnerable to epibiosis, whether initiated by larval settlement or lateral overgrowth. Some tolerate a cover of epibionts, keeping only 'vital' orifices and surfaces clear; others remain totally clear (for example, by using 'fight' options like body flexions). Although surface reinforcement tends to increase risks of epibiosis, its supplementation by spines may help to deter it. Venomous systems are unlikely to be of significance in deterring settlement, but passively dispensed substances are effective within representatives from all major modular groups, together with unitary ascidians, but not tubicolous polychaetes or barnacles.

In defence against endobiosis, surface and internal barriers (skeletally reinforced or otherwise), antimicrobial, passively dispensed metabolites, and cell-mediated defences, are all common among motile invertebrates, and they probably also feature within all of the immotile groups. Passive chemical defences, however, are particularly widespread among modular as opposed to unitary non-locomotory groups (and unitary groups more generally). This may reflect the increased risks of microbial invasion associated with the proportionally massive injuries and partial mortality that occur commonly within the lifespan of species from all four major modular groups, particularly those with encrusting forms (Hughes & Jackson 1980, 1985; Jackson & Coates, this symposium).

By virtue of their immotility and often large size, many modular species support a diversity of associated biota, many of which provide extrinsic, symbiotic defence (for example, a heavy cover of sessile epibionts may provide camouflage or other antipredatory or anti-epibiotic mechanisms, whereas locomotory epibionts may provide antipredatory defence for their non-locomotory hosts). Microendobionts may synthesize the defensive metabolites accumulated by their hosts.

The ability to survive a high degree of partial mortality is itself a further form of defence for modular species (figures 2, 7, 11 and 12). The replication of vital systems within modules across a continuous (or intact) clone, spreads the risk of fatal damage occurring. Should some vital systems within the clone be irrevocably damaged, then only the particular modules dependent on them would die. Whether the interference is predatory, epibiotic, endobiotic, or indeed abiotic, the intact clone will survive as long as it contains the minimal modular configuration necessary for this (this configuration may be species-specific). A few unitary groups are also capable of partial mortality, for example, annelids and asteroid echinoderms, but their potential to survive is orders of magnitude below that of modular groups.

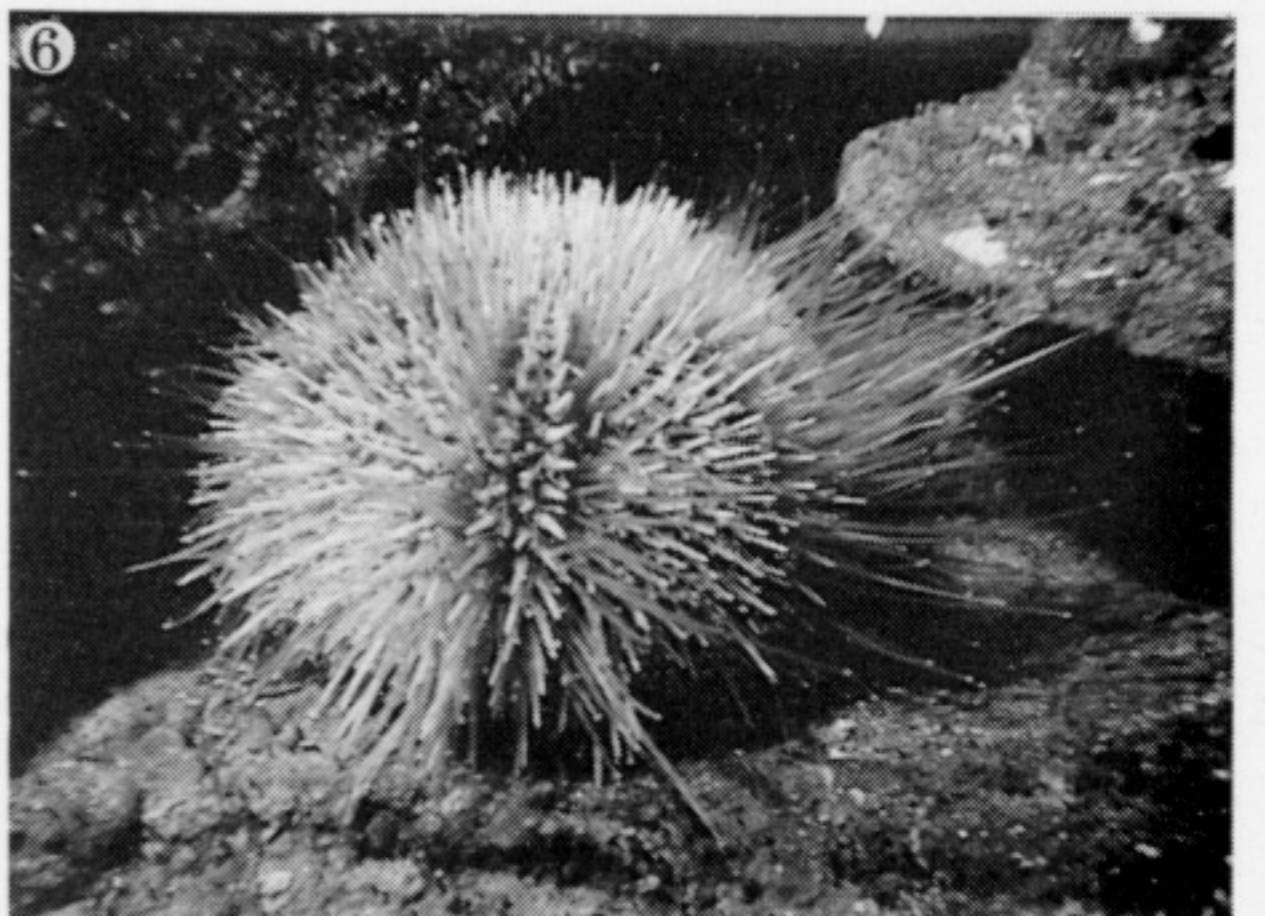
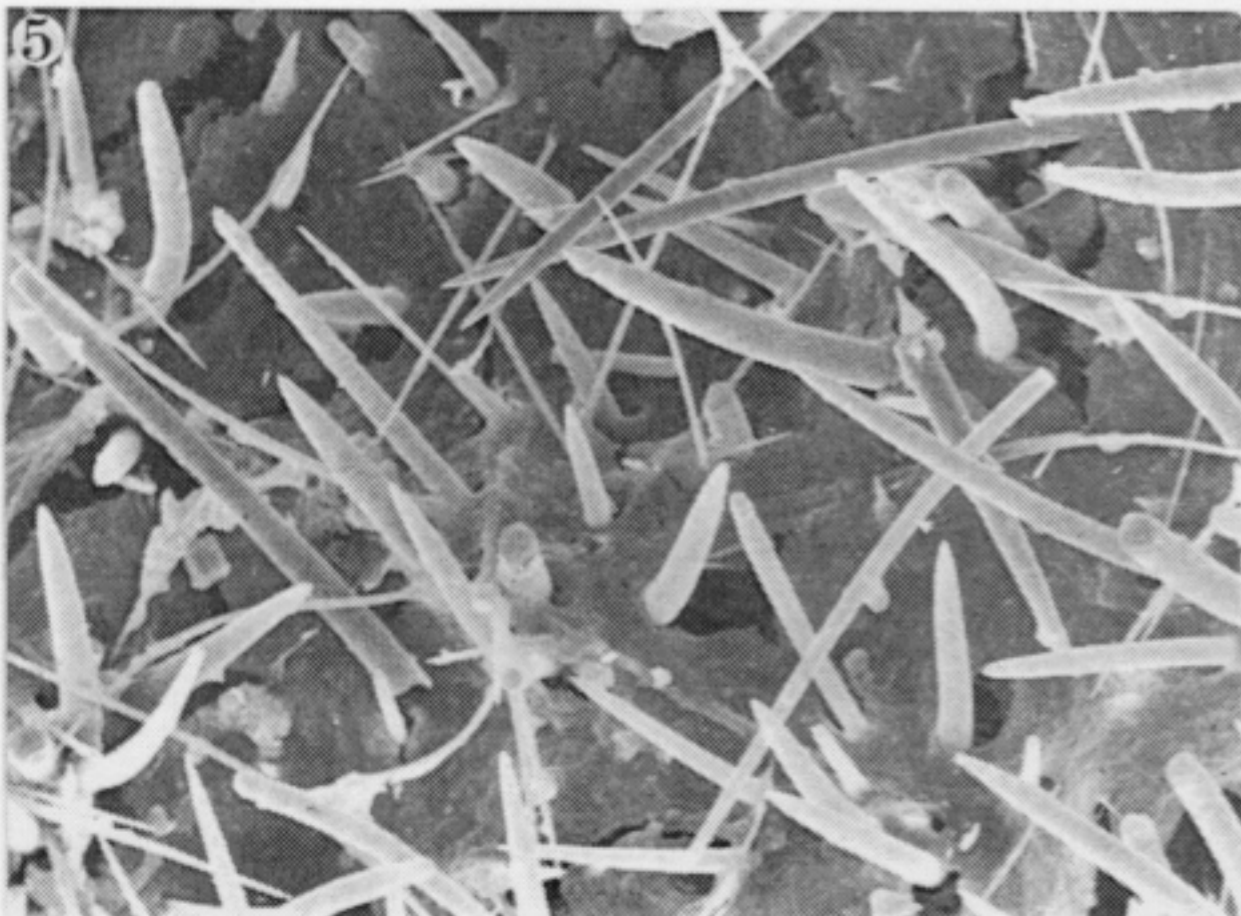
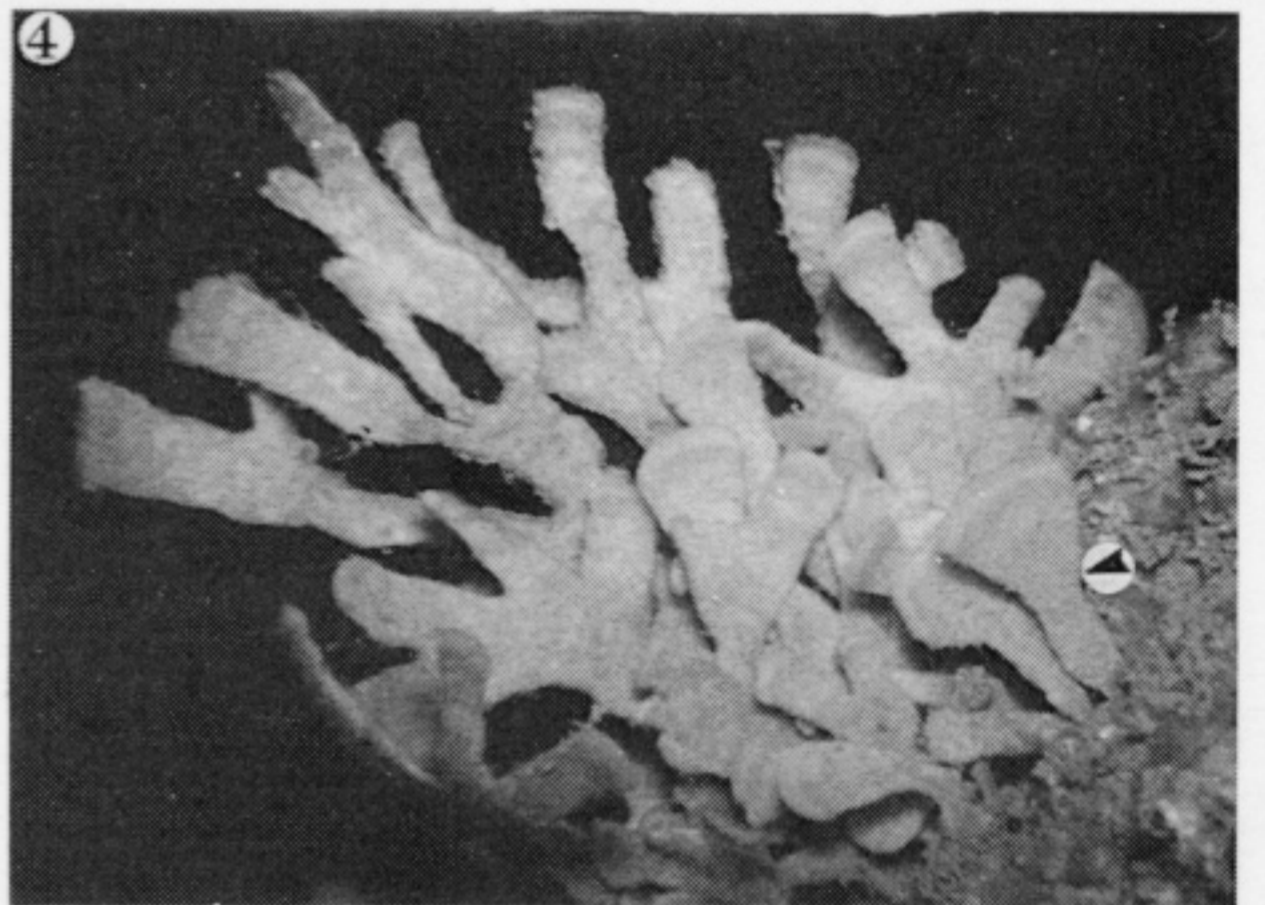
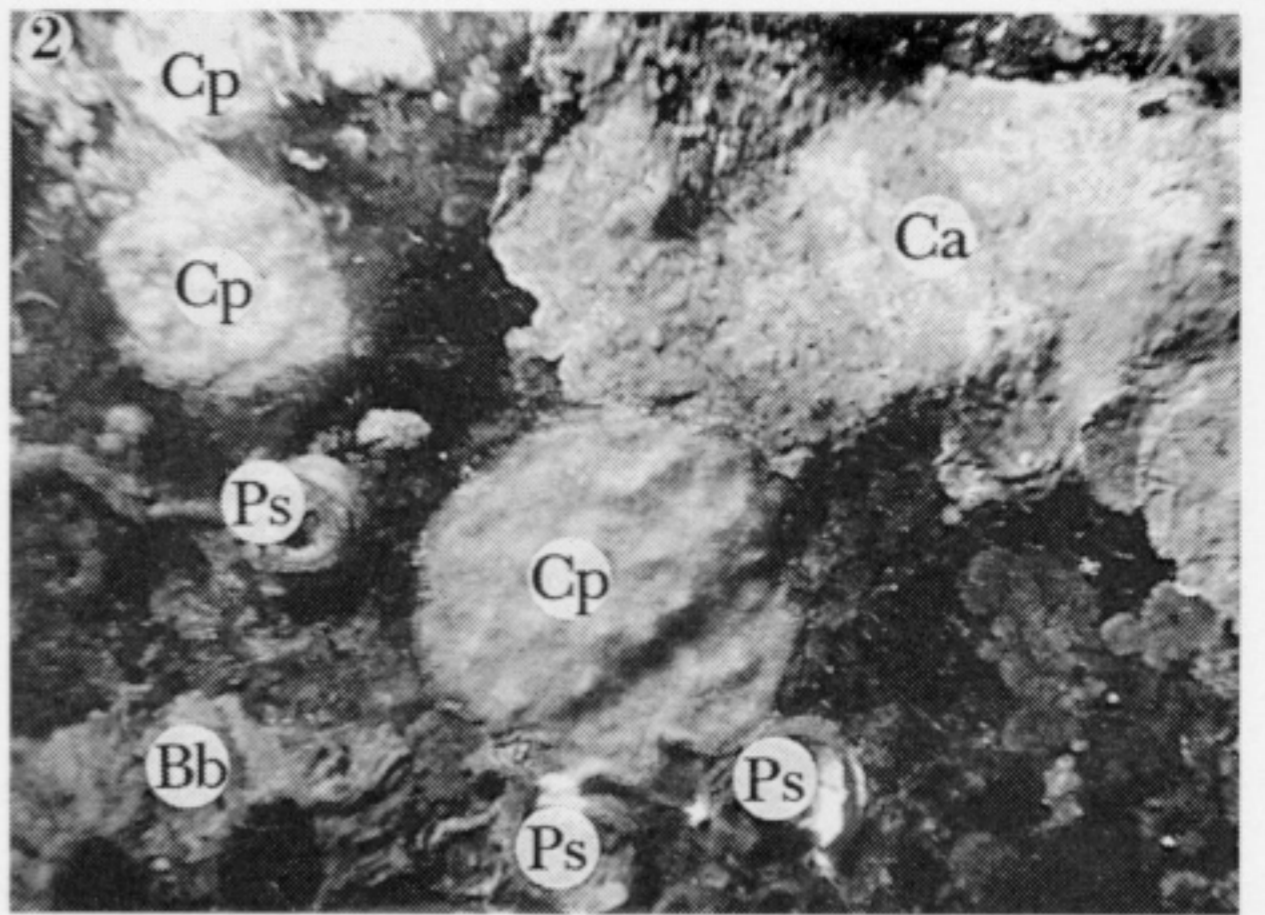
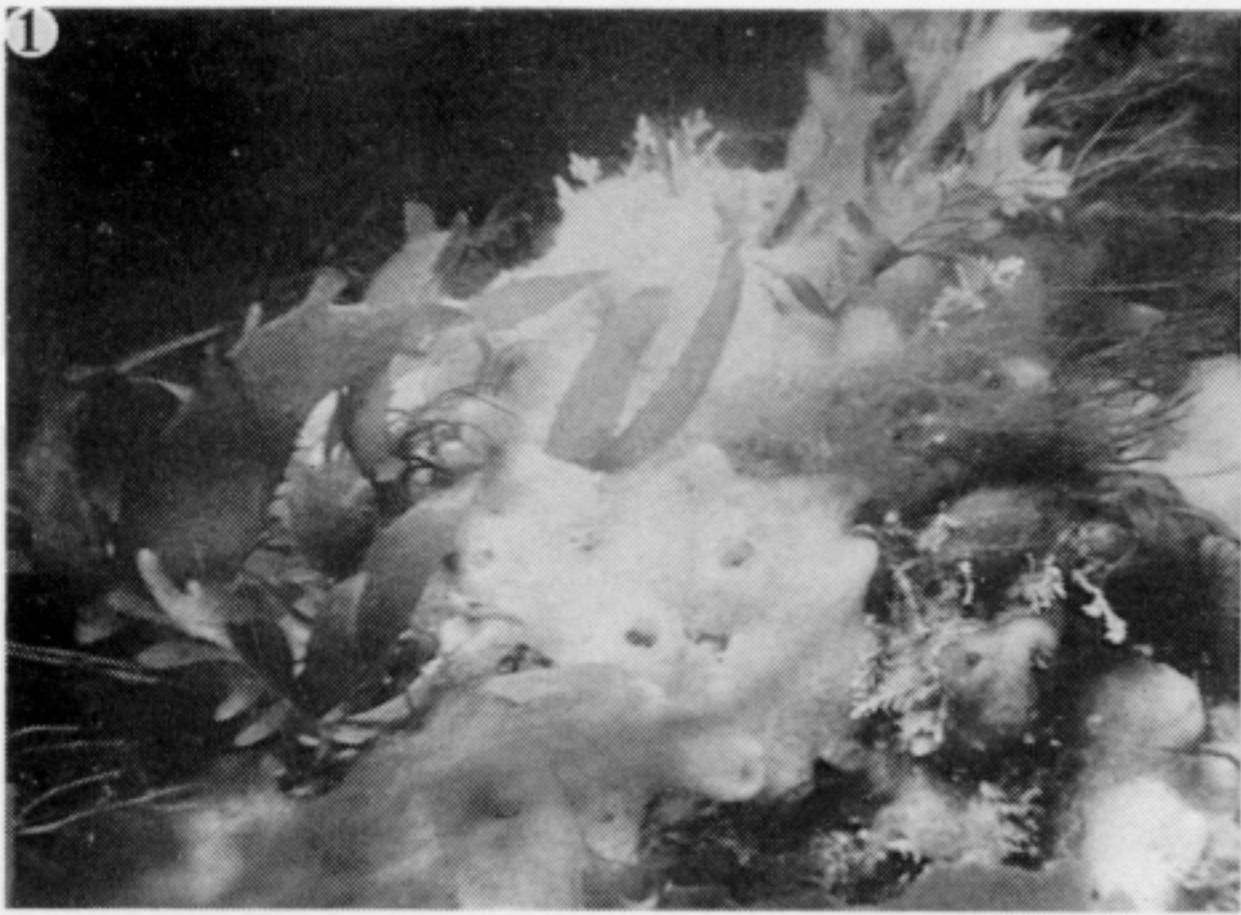
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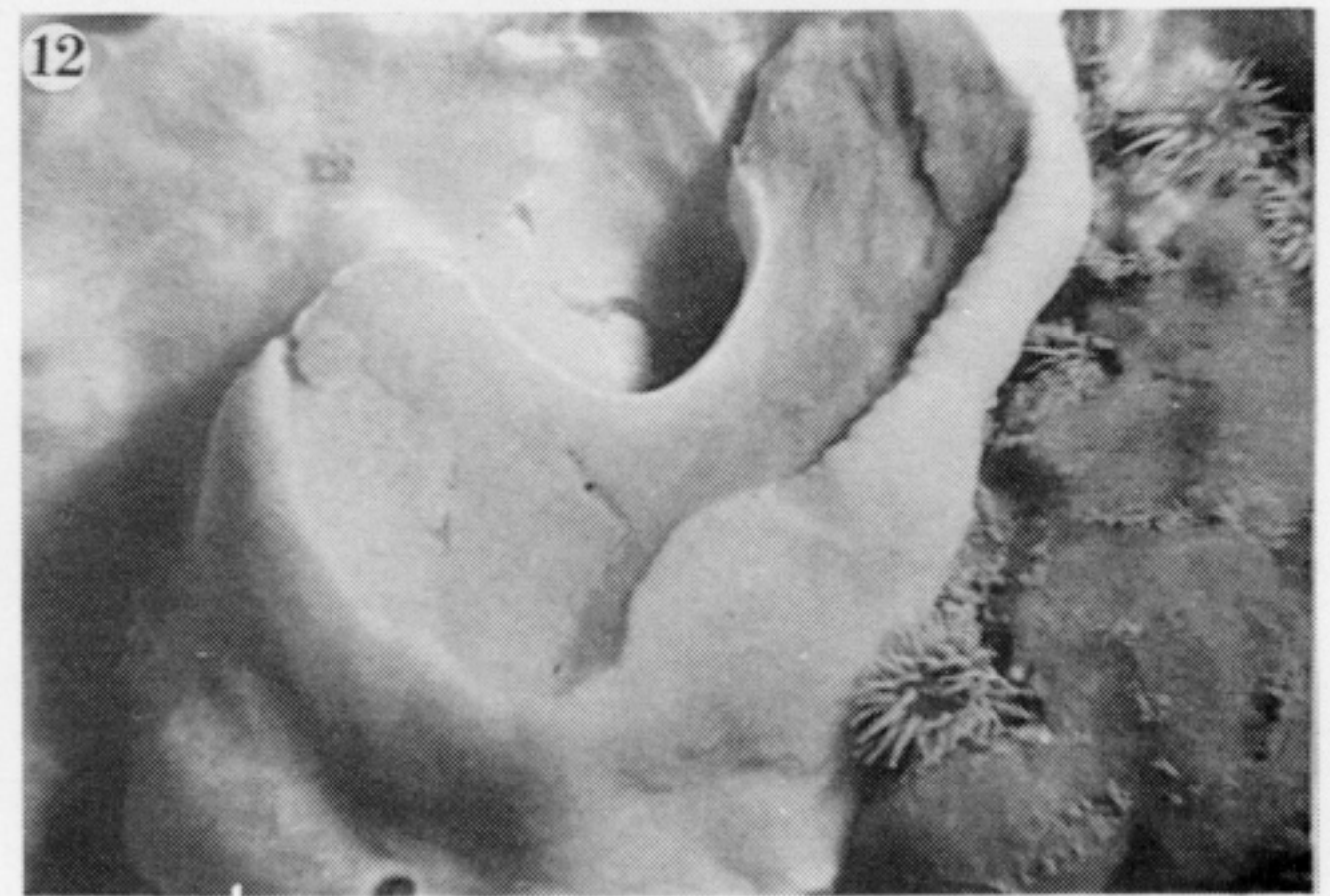
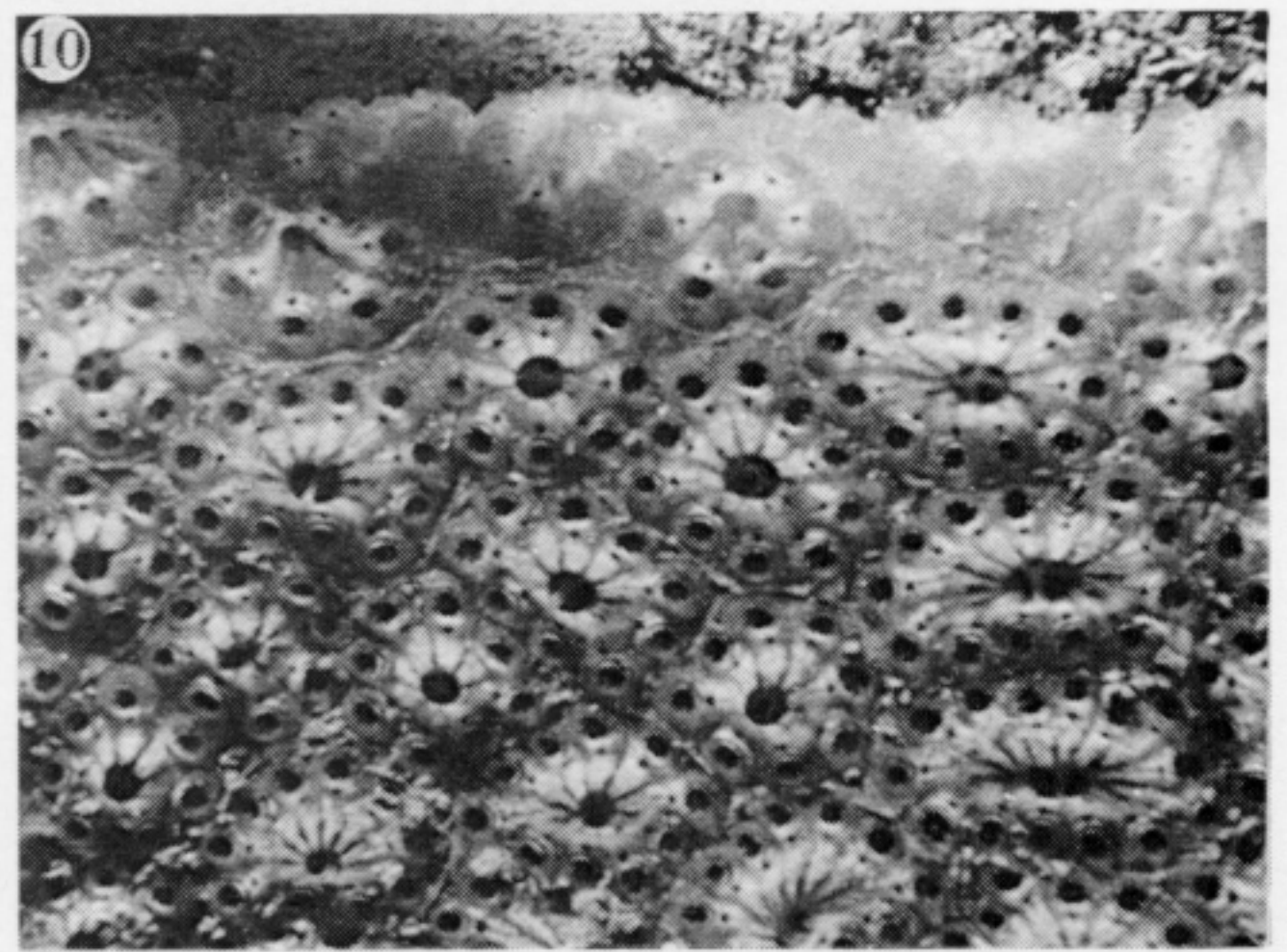
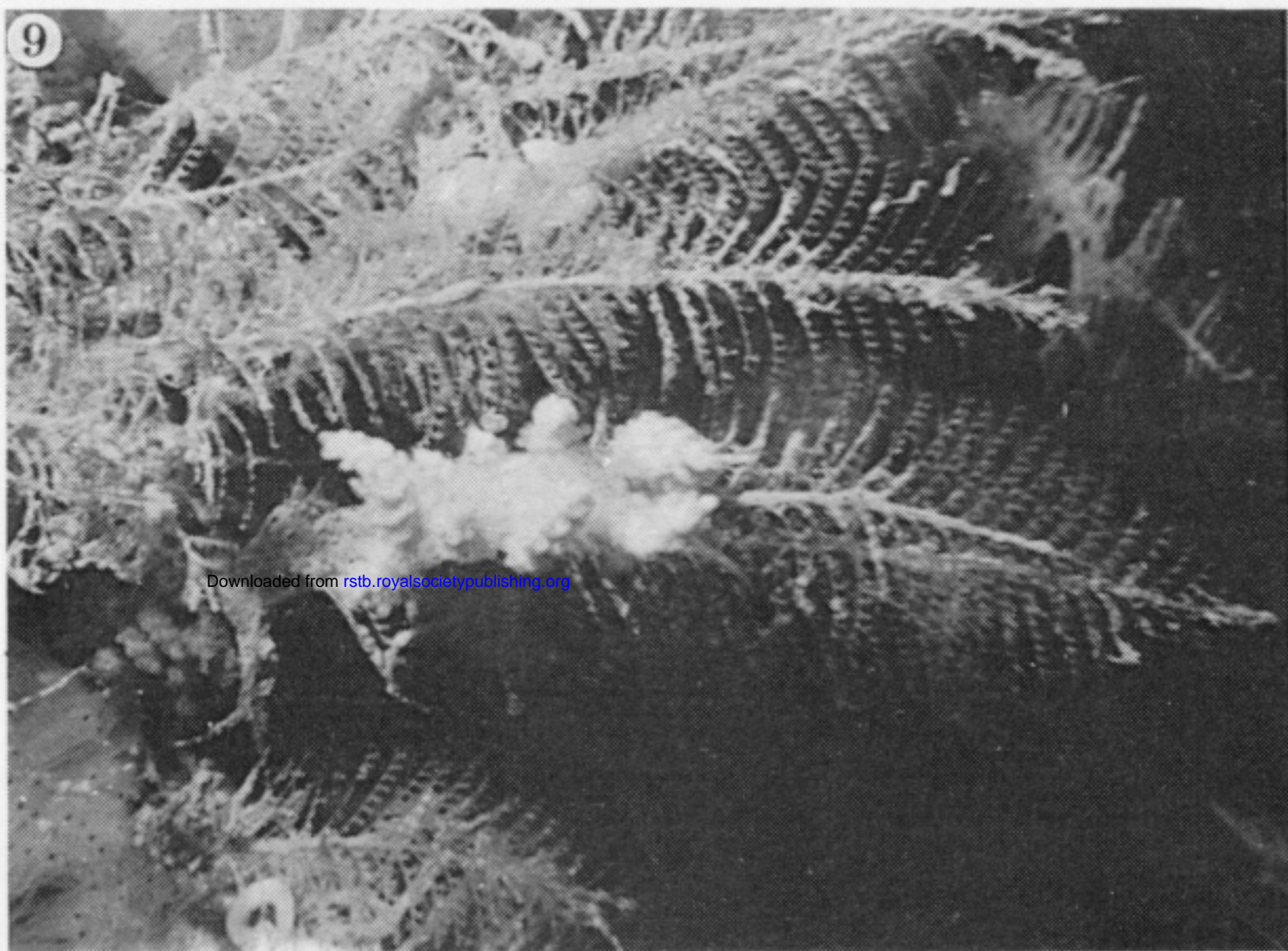
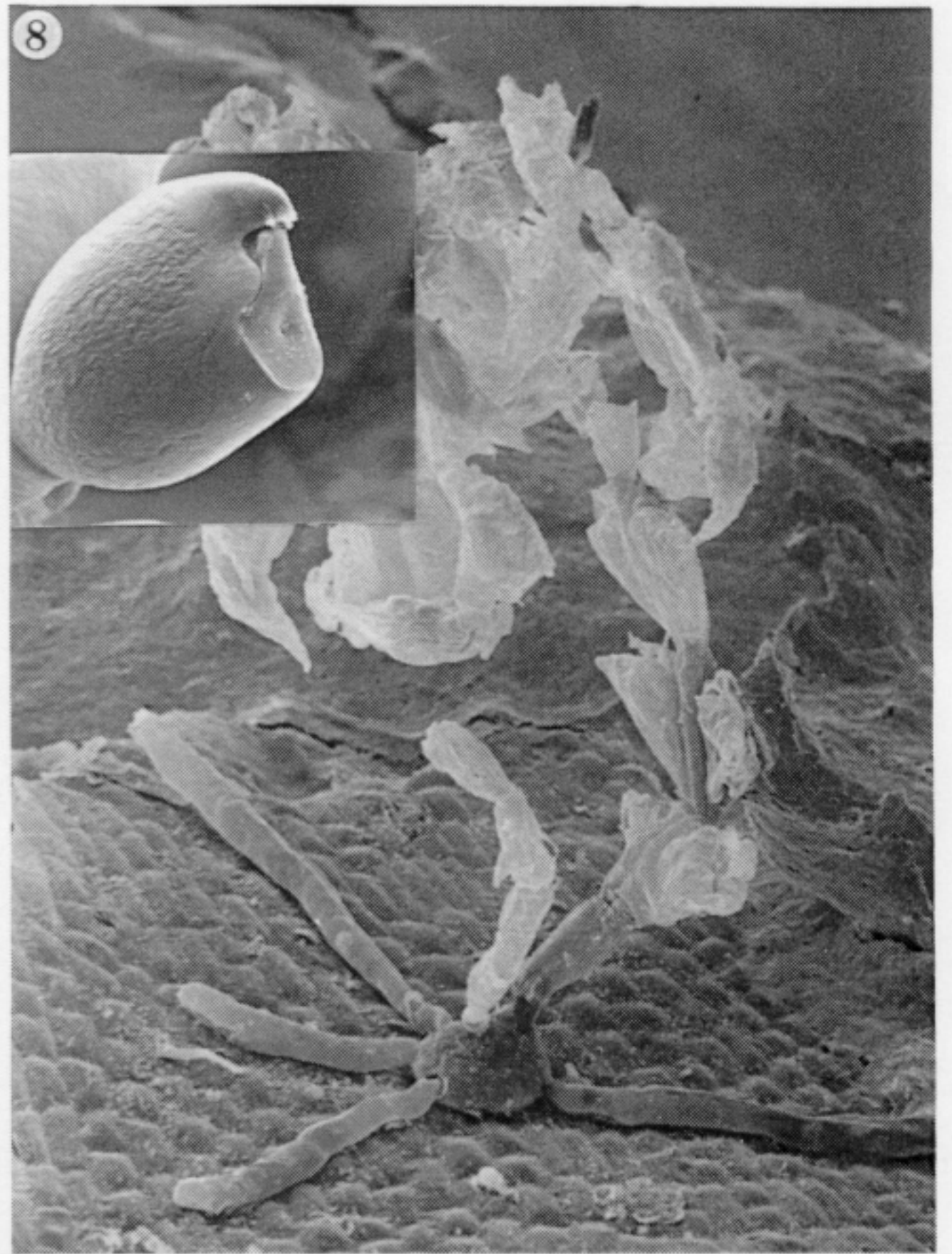
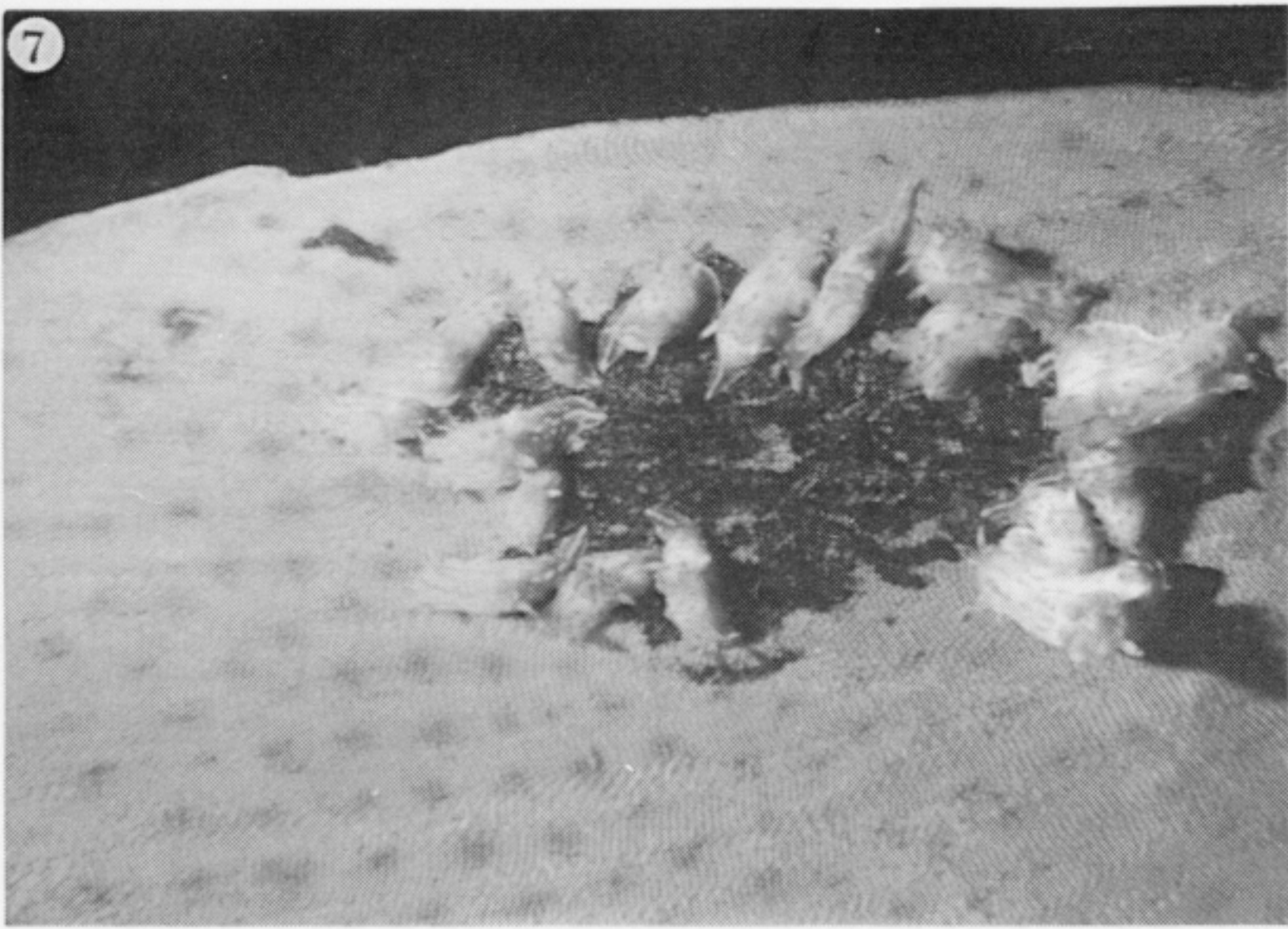
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FIGURES 1–6. For description see opposite.



FIGURES 7–12. For description see opposite.