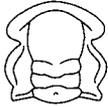


Symbiosis, competition, and physical disturbance in the growth histories of Pliocene cheilostome bryoliths

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Free-living (unattached) subspherical bryozoan masses (bryoliths) in Pliocene tidal channel deposits of the Imperial Formation of southeastern California show complex intra- and interspecific interactions during their accretionary growth. Ranging up to 10 cm in length, the bryoliths are composed almost exclusively of the anascan cheilostome *Biflustra commensale*. Approximately 50% of the bryoliths are nucleated on cerithiid or muricoid gastropod shells; secondary occupants (presumably pagurid crabs) determined the subspherical growth and associated epibionts of all of these specimens. Evidence for crab occupation includes the thick and relatively symmetrical bryozoan overgrowths that form short tubes extending from the aperture, thinning and pinchout of laminae on the undersides of bryoliths (wear facets), and the distinctive borings (*Helicotaphrichnus*) of symbiotic worms. In some instances, shells were infested by bryozoans and other encrusters before death of the gastropod, but these overgrowths are thin relative to hermit-associated bryozoan colonies. Episodic hermit abandonment, indicated by extensive erosion of the bryolith and/or its colonization by a more diverse epibiont assemblage including oysters and serpulids, was more frequent among bryoliths nucleated on the largest and most fouled gastropod shells; it was also more frequent among bryoliths in the relatively high-energy tidal channel thalweg than among those associated with oyster thickets on muddy channel margins. Bryoliths nucleated on other shell substrata are similarly thick, but have more irregular stratigraphies including more sedimentary inclusions, more borings, and fewer encrusting epibionts. Pebbles of crystalline basement rock are also encrusted by *B. commensale*, but only thinly. All of these bryoliths not inhabited by crabs are limited to the channel thalweg. As many as four distinct colonies of *B. commensale* could coexist on a single bryolith; lines of competitive standoff between colonies are marked by mineralized walls and topographic ridges on the bryolith exterior, and by teepee-like structures in cross-section. These standoffs were preferred sites of infestation by other epibionts and were remarkably stable in position on bryoliths with continuous hermit occupation. Bryoliths that suffered repeated abandonment by hermits, or that depended entirely upon chance reorientation, are characterized by highly unstable standoff positions, reflecting scramble competition under less predictable conditions. These circumstances were most common among large bryoliths and among those in channel thalwegs. □ *Bryozoa, symbiosis, competition, paleoecology, taphonomy.*

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Massive, free-living modular organisms that acquire a roughly spherical form fostered by reorientation during growth ('circumrotatory' colonies of Kissling 1973; macrooliths of Hottinger 1983) are not uncommon in the fossil record. This growth pattern has been recognized among coralline algae (rhodoliths of Adey & MacIntyre 1973), corals (coralloliths of Glynn 1974; Kissling 1973), and bryozoans (ectoprocaloliths of Rider & Enrico 1979; bryoliths of Reguant *et al.* 1991). A wide array of different growth histories, however, underlie these similar gross morphologies. Some coralloliths, for example, are initiated by frag-

ments of living coral (Lewis 1989 and references therein; Riegl *et al.* 1996), whereas for most groups the initial substratum is a shell or lithic clast that the colony eventually encases in a more or less concentrically built mass. The dynamics of the communities that encrust such substrata are still poorly known (Hottinger 1983; McKinney & Jackson 1989), but the growth form is promoted by episodic overturning of the mass by waves and currents (e.g., 'rolling stone' colonies on high-energy seafloors; Balson & Taylor 1982; Dade & Cuffey 1984; Scoffin *et al.* 1985; Bishop 1988; Lewis 1989; McKinney 1995a; Riegl *et al.*

1996; Cuffey & Johnson 1997), augmented or replaced on quieter seafloors by bioturbators (e.g., Glynn 1974; Piller & Rasser 1996). Extensive subtidal development of macroids is thought to require a delicate balance of low sedimentation rates (to avoid burial), intermittent high energy (to overturn episodically), and appreciable growth rate of the encrusting organism (Hottinger 1983), but concentric growth may also occur without episodic overturning, as long as wave and current energy is sufficient to feed and intermittently clear sediment from living tissue on their undersides (e.g., in rhodoliths and coralliths; Scoffin *et al.* 1985). Since their origin in the Jurassic, hermit crabs have been another important agent, at least in the early developmental phases of some bio-nodules. Gastropod shells carried by hermits can nucleate thick, concentric overgrowths by cyclostome and cheilostome bryozoans (Palmer & Hancock 1973; Moissette & Pouyet 1991; Taylor 1994; and references in Walker 1992), coralline algae (Zuschin & Piller 1997), and, less commonly, corals (Darrell & Taylor 1989) and hydrozoans (Blackstone & Yund 1989).

Here we report the detailed dynamics of circumrotatory colony growth in 2–10 cm-long bryoliths from Pliocene tidal flat facies of the Imperial Formation in southeastern California. Constructed almost entirely by a single species of the anascan cheilostome *Biflustra commensale*, cross-sectioning reveals the diverse and commonly complex growth histories of bryoliths, including the variable roles of hermit-crab symbiosis, intra- and inter-specific competition among epibionts, and physical reworking/disturbance, and the power of the internal stratigraphy of bryoliths to reveal these ecological dynamics.

Methods

Specimens were cleaned ultrasonically, stabilized by a coating of epoxy if necessary, and cut with a trim saw, in some instances producing a series of sections. Cut surfaces were ground using 600 grit and polished using 0.5 and 0.05 μm alumina, etched for a few seconds in dilute hydrochloric acid, and then replicated by taking an acetate peel. These peels, pressed between glass plates to flatten if necessary, were then used as negatives to produce enlarged ($\times 10$) photonegative prints on high-contrast paper.

The multilaminar structure of cheilostome bryoliths makes it especially easy to reconstruct their growth histories using the same reasoning as in stratigraphic analysis, and, in fact, we found the terminology and graphical methods of sequence stratigraphy especially useful. Holding the eye just a few degrees above the plane of a highly enlarged paper print, it is relatively easy to detect cheilostome analogs of erosional truncation, depositional onlap,

inherited vs. syndepositional topographic relief, and other divergences from simple layer-cake stratigraphy, in contrast to the subtlety of such features when polished cuts are viewed straight-on (cf. basic geometric arguments of Mitchum *et al.* 1977). Stratigraphically interesting growth features were mapped, producing interpreted cross-sections that could be checked against the original acetate peels and polished sections.

Material

All of the specimens are from a closely spaced series of stratigraphic horizons within the Camel Head Member, Imperial Formation (Woodard 1963), along tributaries of North Fork in the Fish Creek drainage of Anza–Borrego Desert State Park, southeastern California (Arroyo Tapido CA 7.5 minute topographic quadrangle; San Diego County). Bryoliths weather readily and locally in great abundance from their friable sandstone and mudstone matrix, permitting 143 specimens to be examined either in place or after collection. Of these, 20 were sectioned. All figured specimens and acetate peels are lodged at the Natural History Museum, London (BZ). A comparable set are held by the State Park in Borrego Springs, California.

Specimens range from 2 to 10 cm in their longest dimension. The majority (56%) have shapes indicating overgrown gastropod shells. Forty percent of these unambiguously gastropod-nucleated bryoliths involve the cerithiid *Liocerithium incisum* (Sowerby), and the remainder encrust fascioliid and buccinid shells. The whorls of the gastropod shells are filled with mud, sand, spar calcite or some combination of these; draft fills and geopetal structures are common. The remainder of the bryoliths (44% of the total examined) are irregular disks, hollow bowls, and oblate, quadrate, or nearly spherical masses. Sectioning revealed nuclei of disarticulated oyster and anomiid bivalve shells, sponge-bored mollusk fragments, gastropod columellae, small masses of encrusted medium-coarse sand, pebbles of local crystalline bedrock, and, in one instance, what appears to have been a cluster of agglutinated-sand tubes.

The relatively coarse texture of zooid walls under SEM suggests epitaxial cement overgrowth of bryozoan calcite. The originally aragonitic shells of gastropods were replaced by coarse calcite via solid-state transformation in a few sectioned specimens. In most instances, however, the aragonitic shell dissolved without replacement, permitting the still plastic mud-fill of gastropod whorls and of *Helicotaphrichnus* borings in the columella to shift or completely collapse; spar calcite fills the remaining void.

Similar but less rich assemblages of bryoliths nucleated on large gastropods were found in the Camel Head Member in badlands northeast of the Coyote Mountains, about 30 km southeast of the North Fork localities. Bryozoan-

encased pebbles of crystalline bedrock have also been found in fan-delta deposits of the Mio-Pliocene 'Latrania' facies (Andrade Member) of the Imperial Formation in the Coyote Mountains (Kidwell 1988).

Taxonomic identification and biogeographic significance

Most of the bryoliths are composed of a single species of anascan cheilostome, *Biflustra commensale* (Kirkpatrick & Metzelaar, 1922) (identification by Paul D. Taylor, personal communications, 1989, 1996). We place this species in the genus *Biflustra*, following Taylor (1994), who considered *B. commensale* to be a cosmopolitan species complex in Miocene to Recent assemblages. Cuffey & Johnson (1997) prefer to retain the species' original placement in the genus *Conopeum*, but Taylor (personal communication, 1997) cites the occurrence of a twinned ancestor, which is present in *Biflustra* and absent in *Conopeum*.

Cuffey & Johnson (1997) reported bryoliths of *B. commensale* in 2.4 Ma Pliocene deposits near Loreto, Baja California Sur, Mexico, providing important corroborative evidence for the existence of a north-flowing coastal current in the east Pacific prior to closure of the Panama Isthmus ~3.5 Ma (Weaver 1990). The bryoliths of *B. commensale* reported here (and in Gyllenhaal & Kidwell 1989) from the ~4 Ma Camel Head Member of the Imperial Formation (Johnson *et al.* 1983; Winker & Kidwell 1986) extend the known stratigraphic and geographic range of this species in the Gulf of California province. Pebble-nucleated specimens observed in the older Andrade Member of the Imperial Formation (pre-deltaic shallow marine facies, >4.3 Ma, <14–22 Ma; Winker & Kidwell 1996) extend the geological record even further. We have also encountered shell-nucleated bryoliths of *B. commensale* up to 12 cm length along the wrack-line of the northern Gulf of California near San Felipe, Baja California; these specimens are either Recent or Pleistocene in age.

B. commensale is a common facultative symbiont of hermit crabs but also encrusts bivalve shells, live gastropods (Taylor 1994), and, at least in the Pliocene, lithic pebbles (Cuffey & Johnson 1997; this paper). Its massive, multilaminar colonies are produced by eruptive budding and spiral growth over the colony surface (Taylor 1994, and following). At the apertures of crab-occupied gastropod shells, *B. commensale* grows beyond the shell edge by tangential accretion, that is by stacking laminae that wrap around the apertural edge, rather than by axial accretion out into free space like most other Recent cheilostomes.

Several small colonies of the ascophoran cheilostome *Microporella* sp. (Paul D. Taylor, personal communication, 1996) occur on one gastropod-nucleated mass of *B. commensale* in our collection (channel-margin oyster-

bank facies at locality 81). Small colonies of *Microporella* were also found on disarticulated oyster shells, but far more rarely than *B. commensale* and never entirely encasing the shell substratum.

Stratigraphic context and sedimentology

The Camel Head Member of the Imperial Formation (Woodard 1963) has been dated as Pliocene in age by combined biochronology and magnetic polarity stratigraphy (~4 Ma; Johnson *et al.* 1983) and is part of the progradational record of the ancestral Colorado River along the western margin of the Salton Trough (Winker & Kidwell 1986, 1996). Together with the laterally interfingering and coeval Jackson Fork Member, the Camel Head Member constitutes the stratigraphically highest marine deposits in the western Salton Trough. This rift basin initially flooded in the middle Miocene and was still a narrow, actively subsiding bedrock-rimmed basin in the Pliocene, when the Colorado River first became the dominant sediment supply to the nascent Gulf of California (Winker & Kidwell 1986, 1996) (Fig. 1).

The Camel Head Member comprises four lithofacies which indicate a complex of very shallow subtidal to intertidal channels and flats (Winker 1987; Winker & Kidwell 1996) (Fig. 1). These are:

- 1 Massive reddish brown to gray claystone;
- 2 wavy-bedded sandstone–siltstone–claystone sequences with minor bioturbation and bidirectional paleocurrent features;
- 3 fine sandstone, typically in lenticular fining-upward cycles that average 5 m in thickness, with parallel and convolute bedding and coarse basal lags of clay intraclasts, lithic pebbles, and bryoliths; paleocurrents predominantly south-directed, north-directed mode is subsidiary; this facies contains the greatest diversity and largest specimens of bryoliths (e.g., localities 82, 84, and 85); and
- 4 oyster shells (*Dendostrea? vespertina* (Conrad)) in mudstone matrix, densely or loosely packed or dispersed, many articulated and attached to others in small clumps, but disarticulated valves also common; cerithiid gastropods and anomiid and pectinid bivalves locally common, usually with associated bryoliths (e.g., locs. 81 and 83).

This complex of intertidal facies interfingers laterally with fossiliferous coarse sands and conglomerates of the Jackson Fork Member, which in turn rests in faulted nonconformity on Cretaceous granites at the margin of the depositional Trough (Fig. 1). The Jackson Fork Member contains a diverse shallow subtidal to intertidal assem-

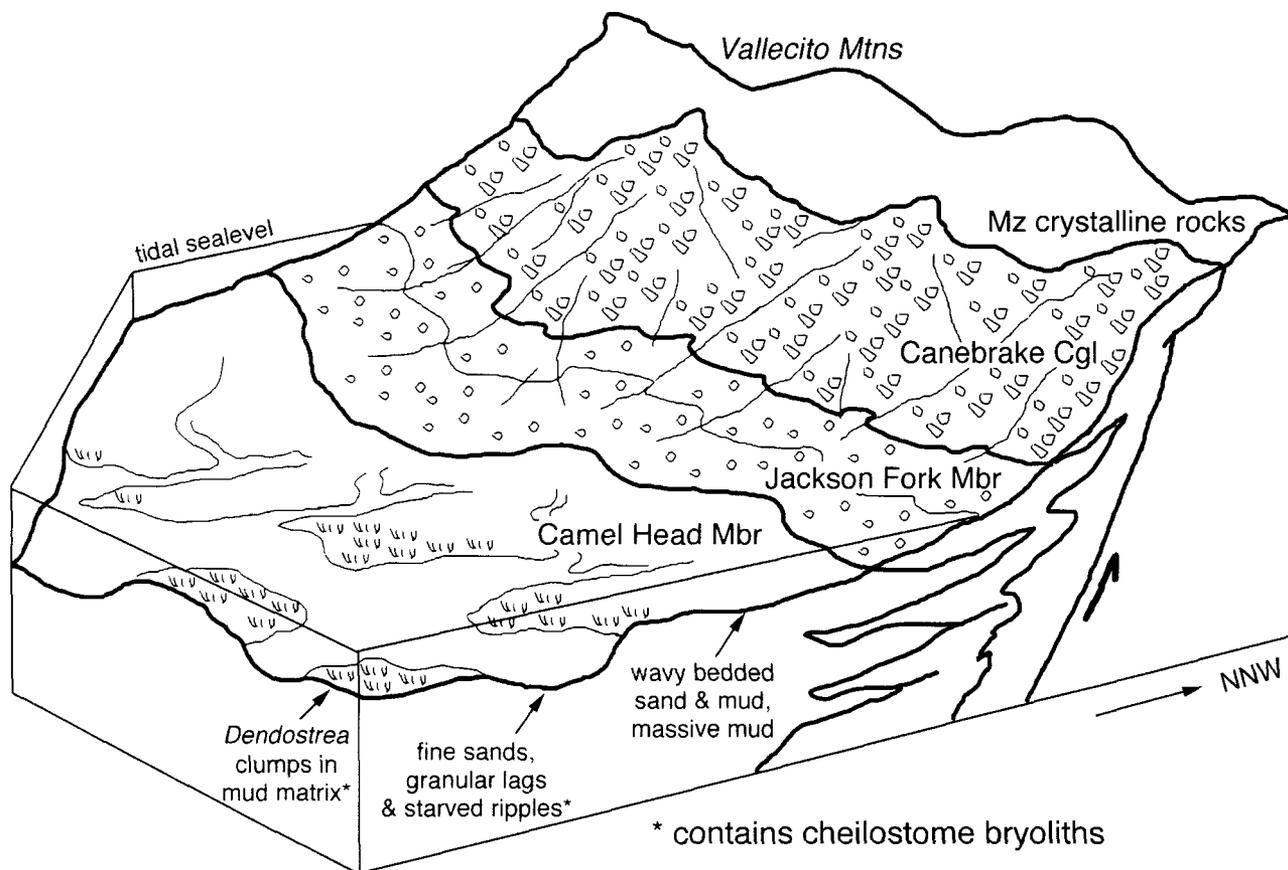


Fig. 1. Quartz-rich fine sands and muds of the Camel Head Member, constituting tidal-flat facies of the ancestral Colorado River delta, interfinger with locally derived lithic sands and conglomerates of Canebrake – Jackson Fork coastal alluvial fans along the western bedrock margin of the Pliocene Salton Trough, Anza–Borrego Desert State Park, California.

blage of infaunal bivalves, gastropods (cerithiid, nassariid, turritellid), spatangoid echinoids, and serpulid colonies, and brackets the high-tide paleoshoreline of small coastal alluvial fans.

Biostratinomy

Bryoliths are found only in association with tidal channels, either in the thalweg itself or in muddy oyster banks along channel margins. Each environment hosts a different assemblage of bryolith morphotypes and associated fauna.

Channel-hosted bryoliths. – Bryoliths occur in the basal meter of channel-sand bodies or are associated with particularly coarse-grained layers within multistory channel sands (lithofacies 3).

At locality 84, a 4.5 m-thick multistory body of fine sand is unfossiliferous with the exception of abundant bryozoan-encrusted oyster and gastropod shells in its basal 15 cm. Although some encrustations are small thin

patches, most shells are completely and thickly overgrowth by bryozoans; these bryoliths are commonly 5 cm in diameter (exceptionally 8 cm on large buccinid and fasciolariid gastropods). The bryolith-bearing bed is heavily bioturbated (in contrast to the current-bedded sands that dominate the rest of the channel), is very localized laterally even along the base of the channel, and is immediately overlain by a thin (5 cm) mud layer. The bryoliths appear to be indigenous to this bed, which appears to record a non-depositional channel thalweg that was eventually overrun by rapidly aggrading sand. (No bryoliths were collected from this locality, which is comparatively accessible to park visitors.)

The largest bryoliths collected in this study are from the foresets of starved dunes of cross-bedded granular sand (15–20 cm thick lenticular sets) in the lower meter of a medium- to fine-grained channel sand body at Locality 82. Fossils are dispersed (matrix-supported) throughout the foresets rather than concentrated exclusively along bedding planes, and include coarse shell hash (≤ 1 cm maximum dimension, mostly oyster fragments), disarticulated oyster valves (almost exclusively worn and broken,

and commonly encrusted), unattached articulated anomiid bivalves (mostly oriented convex-up), carbonized wood chips, mud intraclasts, large bryozoan-encrusted gastropods (mostly buccinids, to 7 cm), and large oblate and somewhat mamillary bryoliths (to 10 cm). Sectioning proved these latter types to be nucleated on various molluscan shell fragments, including severely sponge-bored oyster shells. In outcrop, some of the largest bryoliths had laminar extensions that appeared to have grown outward over adjacent granular sediment, and, in fact, a few 3–4 cm diameter bryoliths consist in section of thick (25–30 laminae) crusts wrapped 120°–220° around blebs of medium sand. These features indicate the thalweg of a channel that was located relatively near to Jackson Fork fans, with relatively strong tidal currents capable of reworking coarse lithic and skeletal grains into mobile dunes, at least episodically. Bryoliths collected from this facies appear to have grown locally under these conditions (see later discussion).

Locality 85 is another channel-hosted body of fine sand but is located nearer to the basin margin than localities 82 and 84 and includes several discrete beds of Jackson Fork-type conglomerate. These conglomerates are the primary source of skeletal material within this channel. One fossiliferous conglomerate is a 50-cm thick debris flow (maximum clast size 4 cm; medium sand matrix); pebbles and gravel are distributed throughout the bed, but those along its upper surface support modest encrustations by bryozoans and serpulids, which apparently colonized these grains after emplacement in the channel. A second conglomerate is a 10 cm-thick grain flow with bryozoan-coated pebbles, spherical bryozoan–serpulid colonies (to 3 cm), disarticulated and broken oyster valves, articulated but unattached balanid barnacles, limpet gastropods, and rounded clasts of sandstone and crystalline rock. These grains are graded, with lithic clasts (both clean and encrusted) along the erosional base of the bed, followed by flat-lying and imbricated skeletal material, which is capped by exclusively granular to medium sand. It is likely that these fossils are ecologically exotic to the Camel Head channel, having been transported there along with lithic clasts from adjacent Jackson Fork fan deltas under flood conditions.

Channel-margin bryoliths. – Oyster banks with mud matrix (lithofacies 4) are common in the Camel Head Member. The oyster accumulations, which consist of closely spaced clusters of a few dozen articulated specimens rather than a densely packed or intergrown framework, lie immediately above channel sand bodies, and grade upward into wavy-bedded muds and sands such as those produced on flats between tidal channels. The oyster clumps and low banks are consequently interpreted as autochthonous aggregations that colonized the margins of active channels where water energies were sufficient to

maintain fine sediment in suspension and deliver food, but insufficient to smother the site with bedload.

Bryozoans and serpulids sparsely encrust many disarticulated and articulated specimens of oysters as well as associated pectinid and anomiid bivalves, but circumrotatory encrustations on bivalves are generally rare and only a few laminae thick (e.g., localities 83 and 86, where the ornamentation of the encrusted valves is still quite clear). At Locality 81, the oyster bank assemblage contains an exceptionally high density of bryozoan-encrusted oysters and abundant, heavily encrusted cerithiid gastropods (2.5–3 cm long bryoliths); larger bryoliths on fasciolariid and buccinid gastropods are also present (5–6 cm) here. The 1 m-thick oyster bed with mud matrix at locality 81 rests on the relatively coarse-grained channel sand, the base of which yields the large circumrotatory colonies at locality 82. The oyster bed is capped by a 6 cm-thick, poorly sorted granular sand with a fossil assemblage that closely resembles that of channel thalwegs. This includes bryozoan- and oyster spat-encrusted lithic pebbles, lightly to heavily encrusted fasciolariid gastropods (3.5–6 cm; bryozoans commonly fouled in turn by serpulids, oysters, and solitary corals), and large oblate mamillary bryoliths (4.5–5.5 cm, which sectioning reveals are nucleated on oyster valves, whole fasciolariid gastropods, and worn gastropod columellas). The implied proximity of this oyster bank (locality 81) to a high-energy tidal channel (locality 82) perhaps explains why this particular oyster bank has coarse-grained intercalations (storm washover of the channel banks) and why the oyster-bank assemblage itself is especially rich in circumrotatory bryozoans and other encrusters (hydrodynamics favoring greater water circulation and thus food supply).

Growth histories and biotic interactions in gastropod shell-nucleated bryoliths

External morphology and sectioning indicate that approximately one-half of the bryoliths encrust gastropod shells. Bryozoan growth might have been associated with (a) live gastropods, (b) dead shells occupied by pagurid crabs, (c) dead unoccupied shells, or (d) a series of these conditions.

Criteria for differentiating these relationships have been summarized by Walker (1992) for gastropod shells having very thin or patchy encrustations, and by Walker (1992) and Taylor (1994) for shells completely encased by thick encrustations. Bryozoans that encrust the shells of living gastropods are present only on the exterior of the shell, and in some instances one or more laminae of zoecia become intercalated with shell layers as the gastropod grows over earlier whorls of its shell. For thick encrustations, the most reliable evidence for association with her-

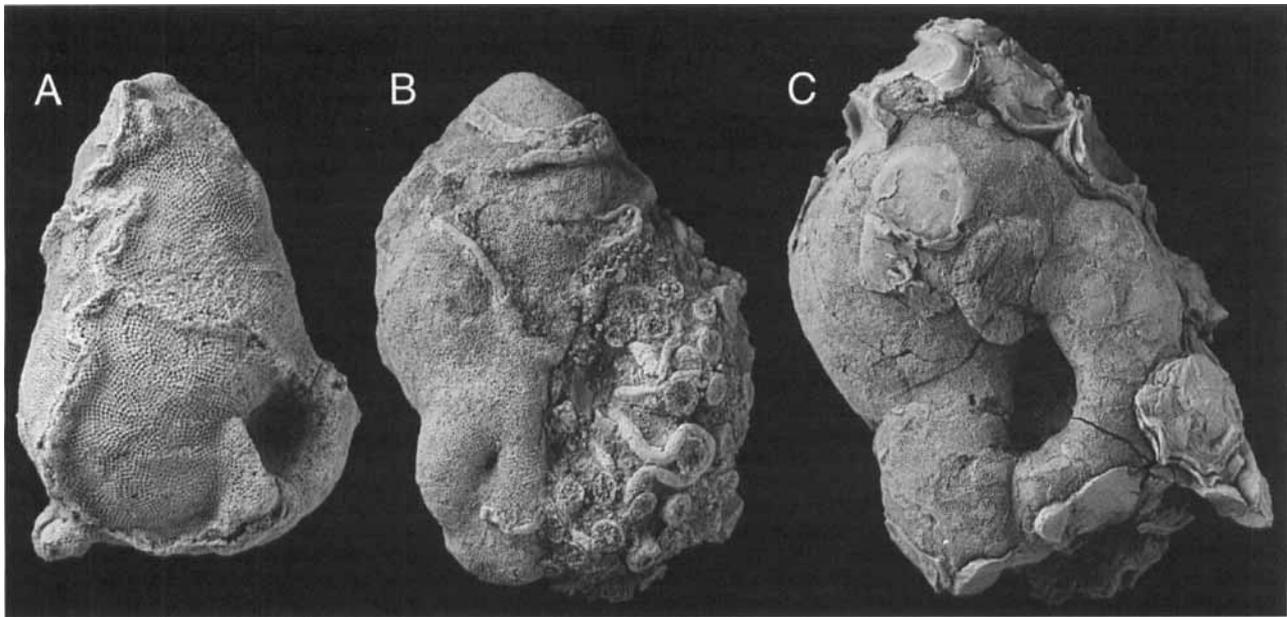


Fig. 2. Examples of gastropod-nucleated bryoliths associated with hermit crabs. □A. Bryolith nucleated on cerithiid gastropod shell, showing spiral growth pattern of *Biflustra commensale* on the surface, and a short apertural tube produced by tangential growth around the aperture. Sinuous ridges mark competitive standoffs of multiple, co-existing bryozoan colonies (specimen 81-I, 2.8 cm long; BZ 4500). □B. Bryolith nucleated on buccinid gastropod shell, with encrusting serpulid worm tubes and the solitary corallites of *Astringia*; their arrangement inside the aperture is consistent with hermit-occupancy (cf. Walker 1992; specimen 81-S, 4.6 cm long; BZ 4501). □C. Bryolith nucleated on buccinid gastropod shell, with encrusting oysters distributed at a distance from the aperture; this is consistent with a decline in colony condition away from the hermit crab (specimen 81-U, 5.6 cm long; BZ 4502). Photos courtesy of the Natural History Museum, London.

mit crabs is (1) growth of the colony as a tube extending outward from the aperture of the gastropod shell, and (2) the helicospiral coil of this tube, which is possibly determined by the form of the crab abdomen. Very even overgrowths and bilaterally symmetrical outgrowths (Cook 1964) are also highly characteristic and contrast with strongly asymmetrical (lopsided) growth on unoccupied, immobile dead shells. Barnacles and serpulids are common associates of thick bryozoan colonies, but none of these or other co-occurring species have obligate relationships with hermits. The sole exception is *Helicotaphrichnus commensale* (Kern *et al.* 1974), which is a spiral bore-hole or capped groove produced by spionid polychaetes which is known only from the columella of crab-occupied gastropod shells (Blake & Evans 1973; Walker 1992). Finally, because hermit crabs often drag their home across the seafloor, the underside of the bryolith may have fewer epibionts or be worn into a flattened surface ('pagurid facet' of Walker 1992). In thickly encrusted shells, dragging can cause local erosion of laminae; this facet migrates with helical growth of the bryozoan colony, producing a series of patchy discontinuities rather than a single, laterally continuous unconformity in section (Taylor 1994).

Applying these criteria, all of the gastropod-nucleated bryozoan colonies in the Neogene collection exhibit evidence of hermit crab occupation at some phase in their development.

Bryoliths nucleated on cerithiid gastropod shells

These narrowly conical masses, reaching ~3 cm maximum length, are the most common gastropod-nucleated bryoliths in the collection; they constitute a total of 32 specimens, of which 9 were sectioned (Fig. 2). Based on cross-sectional views and on specimens where the bryozoans have been partially removed, the shell nucleus is the high-spined cerithiid gastropod *Liocerithium cf. judithae* Keen, 1971 (previously referred to as *Cerithium incisum* Sowerby; Durham 1950). These bryoliths are restricted to the channel-margin (oyster-bank) facies of the Camel Head Member.

The exterior of most cerithiid-nucleated bryoliths is quite smooth and regular, reflecting the morphology of the shell nucleus and providing clear evidence of the spiral growth that typifies *B. commensale*. Several larger specimens have a network of walls, marking standoffs between competing, genetically distinct colonies (Fig. 3); in the most striking examples, these standoffs produced sinuous ridges 1–2 mm high (e.g., specimen 81-I, Figs. 2A, 3A). The exteriors of ~15% of cerithiid-nucleated bryoliths are encrusted by small specimens of the oyster *Dendostrea vespertina*.

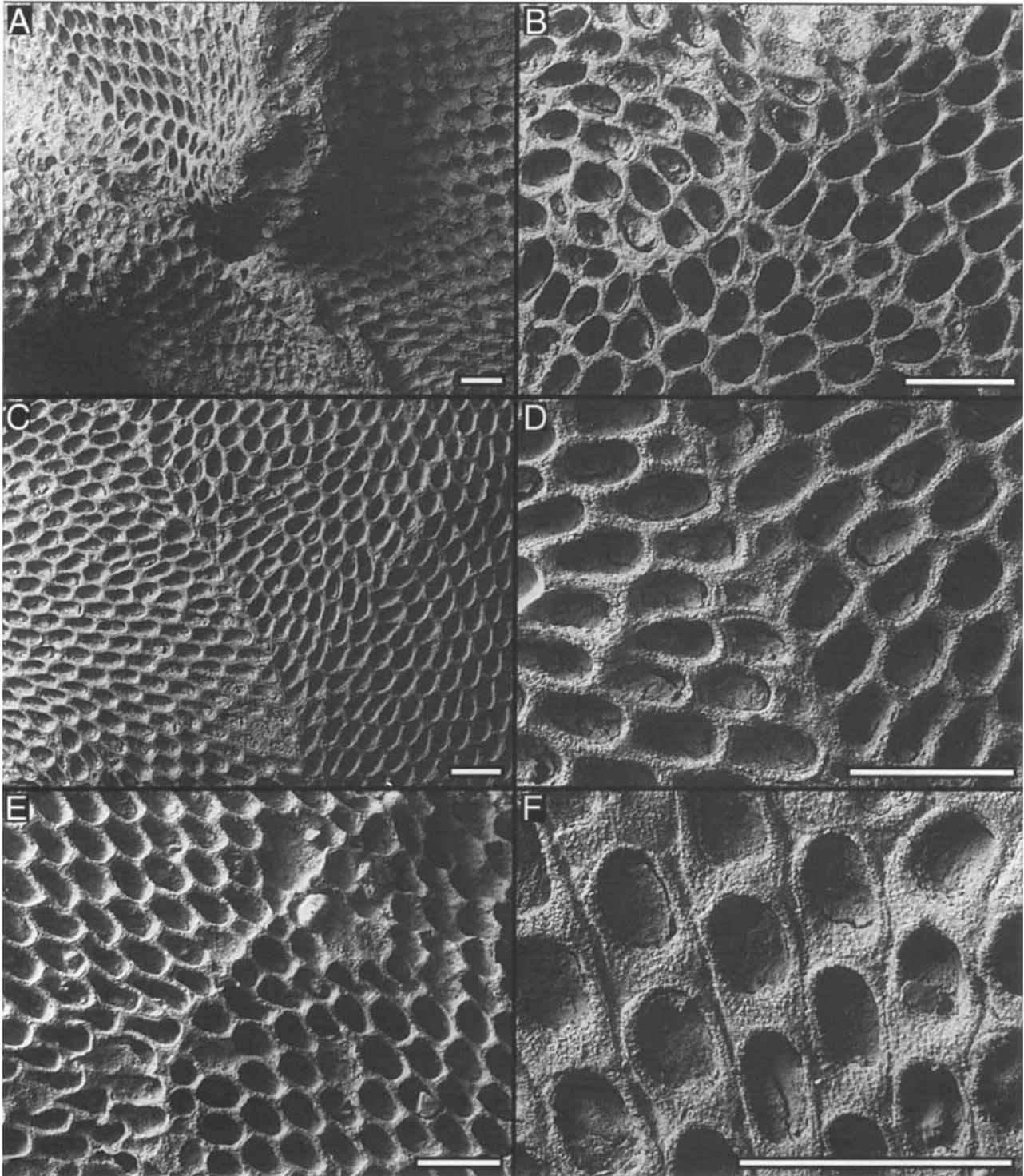


Fig. 3. SEM views of standoffs between competing colonies of *B. commensale* on the exterior of cerithiid gastropod-nucleated bryoliths. Scale bars 500 μm . □A. Standoff ridges between three colonies, with borehole of acrothoracican barnacle at the triple-junction; in cross-section, growing fronts of laminae would be upturned and separated by a sand-filled fissure (specimen 81-1). □B. Standoffs marked by thickened walls rather than ridges; in cross-section, laminae of competing colonies would abut without any gap (specimen 81-R2; BZ 4503). □C–D. Standoff wall between two colonies (specimen 81-R2). □E. Standoff wall between two colonies (specimen 81-R1; BZ 4504). □F. Unabraded colony of *B. commensale* on muricoid gastropod-nucleated bryolith (specimen 81-V; BZ 4505). SEM courtesy of the Natural History Museum, London.

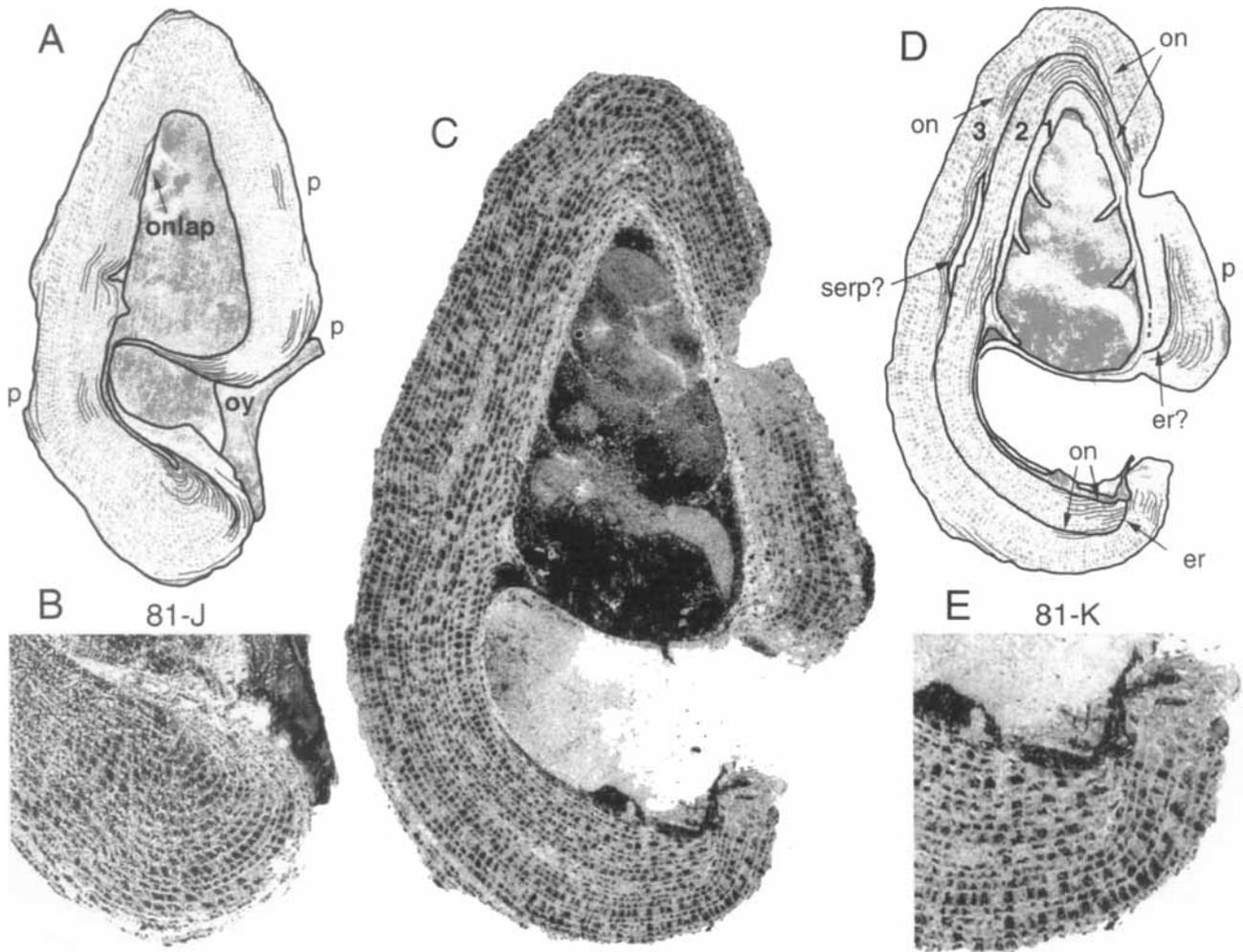


Fig. 4. Prints and interpreted line-drawings from acetate peels of cerithiid-nucleated bryoliths; channel margin oyster bank facies. □A. Conformable bryolith growth on specimen 81-J, 2.9 cm long; BZ 4506. □B. Tangential growth of laminae to form apertural tube, specimen 81-J. □C. More complex growth history, with initial bryozoan laminae formed during life of gastropod (sequence 1) and two successive phases of hermit-associated growth, interrupted by erosion of aperture and colony decline permitting epibiont encrustation (probably phase of hermit abandonment) (specimen 81-K, 2.1 cm long; BZ 4507). □D. Sequence stratigraphy of bryolith 81-K. □E. Repair history of apertural tube, specimen 81-K. Abbreviations: on=onlap; er=erosional truncation; p=pinchout; 1, 2, etc.=internally conformable depositional sequences in growth history; St=standoff between competing colonies of *B. commensale*; b=boring, commonly of acrothoracican barnacle; oy=oyster; ag=agglutinated tube; serp=serpulid worm tube; sed=sedimentary inclusion; He=trace of the polychaete boring *Helicotaphrichnus commensale*.

Formation of apertural tube.—On the bryolith exterior, the location of the aperture is indicated by a depression or sediment plug. Sectioning reveals that the bryozoans built tube-like extensions from the aperture by tangential growth, a behavior consistent with crab-occupancy in modern bryoliths.

In the simplest growth histories, the apertural tube grew as a single, uninterrupted series of laminae that wrapped around the leading edge of the tube and lapped out along the interior of the tube (Fig. 4A–B, specimen 81-J). In many instances, laminae extended down into the interior of the gastropod's outermost whorl, coating it with one (Fig. 4C–D, specimen 81-K) or more laminae

(Fig. 5A–B, specimen 81-Oa). This tangential growth characterizes the entire circumference of the aperture. Apertural tubes lengthen as the bryolith grows (Fig. 6A), but are always much less than a full whorl in length (only a few millimeters of apertural extension). Even these short tubes were prone to breakage during growth, judging from the number of apertures where an early phase of tangential growth is truncated and re-lapped by successive laminae (Fig. 4D–E, specimen 81-K). Several different causes are possible, including mechanical erosion during a phase of abandonment by the hermit, and damage by duraphagous predators of the hermit crab host.

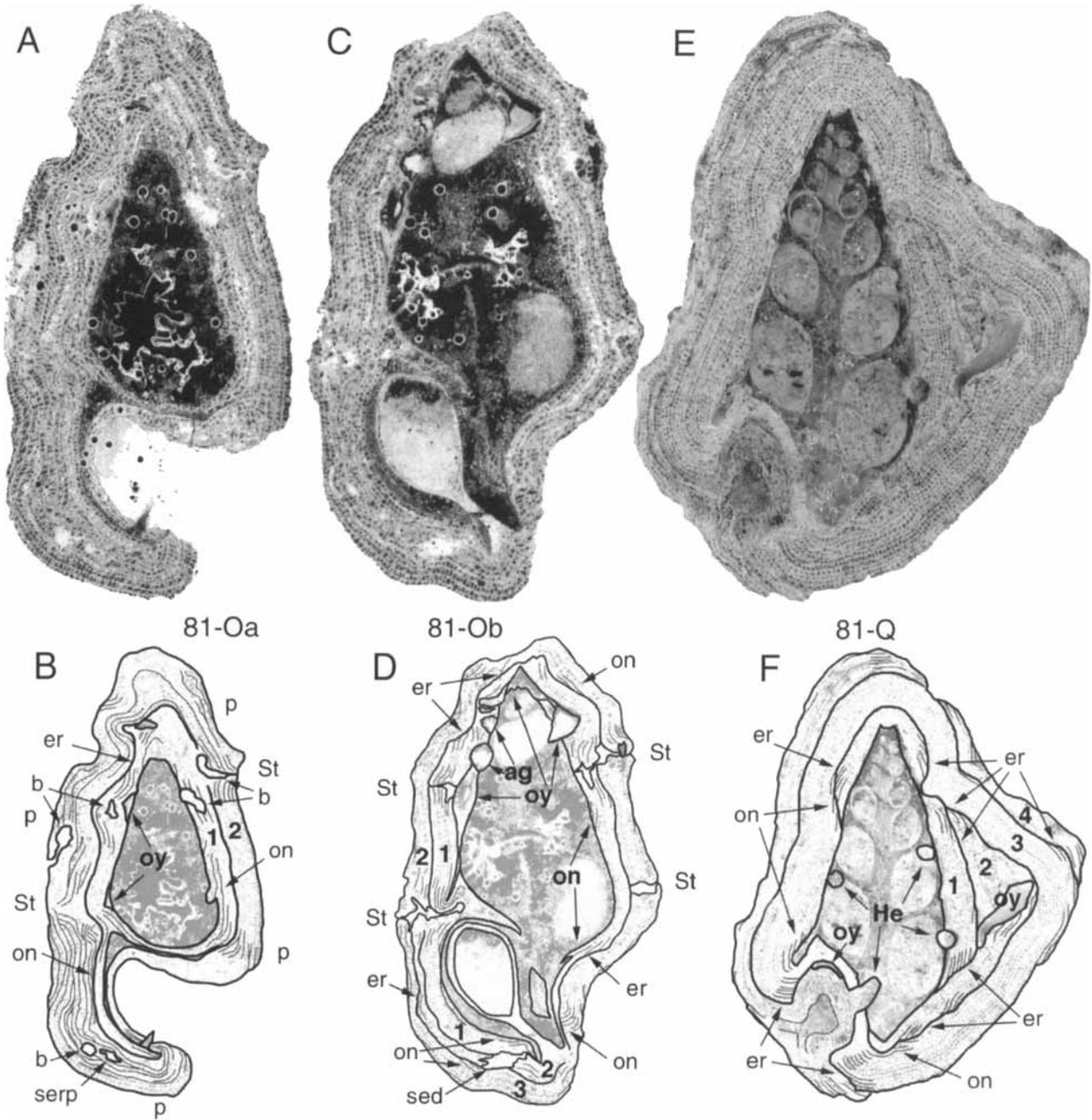


Fig. 5. More complex growth histories among cerithiid-nucleated bryoliths, channel margin oyster bank facies. □A, B, C, D. Prints and interpretations of two serial sections (a and b) through specimen 81-O (2.5 cm long; BZ 4508), showing relatively thick bryozoan growth associated with living gastropod (sequence 1), other gastropod-associated epibionts, and continued multiple colonies of *B. commensale* during hermit occupation (sequence 2). □E, F. Iterative history of bryozoan growth, erosion, epibiont encrustation, and bryozoan re-colonization on specimen 81-Q (3.0 cm long; BZ 4509), indicating repeated abandonment and reoccupation by hermits.

Bryozoan settlement and growth associated with hermits. – Lap-out directions of the oldest tube-related bryozoan lamina indicate that the tube-forming colony settled on the upper edge of the aperture (as held by the hermit), with successive laminae expanding both toward the apex (apical direction of onlap; Fig. 4A, specimen 81-J) and

toward the aperture (apertural direction of onlap; Fig. 4C–D, specimen 81-K). The initial hermit-associated laminae in some instances extended around the apex (Fig. 4C–D, sequence 2 in 81-K) and some distance across the shell underside (Fig. 4C–D, sequence 2 in specimen 81-O). In most instances the initial laminae also reached the

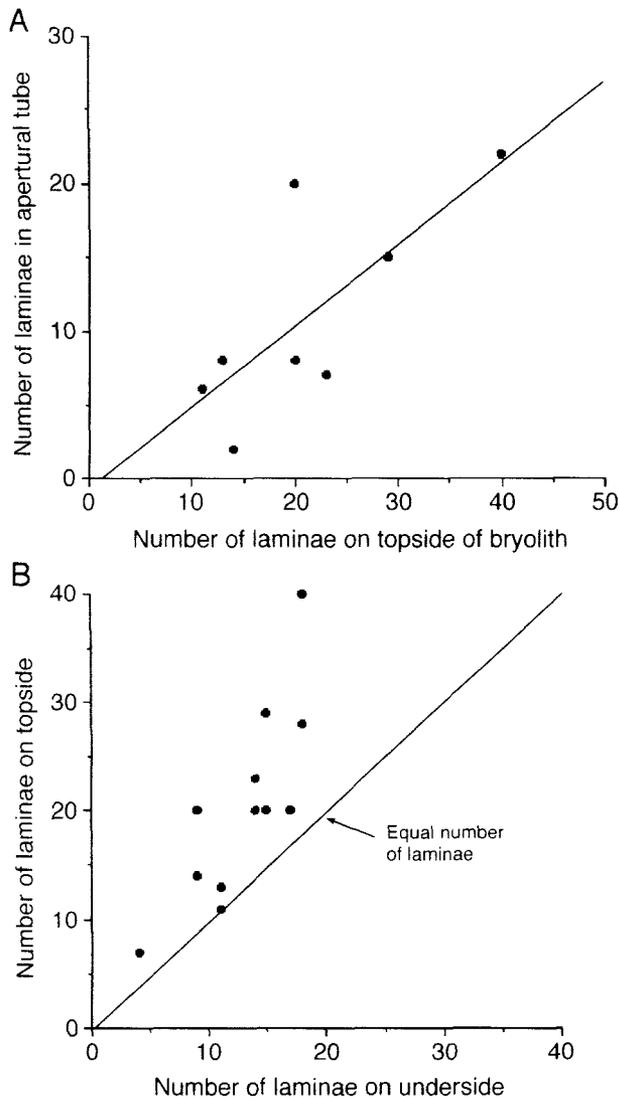


Fig. 6. □A. Apertural tubes comprise 2–22 stacked laminae and increase with overall growth of the bryolith despite erosional breaks in most tubes ($p < 0.05$). □B. Difference in thickness of multilaminar growth on underside versus topside of hermit-occupied bryoliths, as measured by number of laminae in cross-section. Cerithiid-nucleated specimens only.

very edge of the aperture and even wrapped over it, extending a short distance into the interior of the apertural whorl itself (Fig. 4A–B, specimen 81-J). Laminae generally did not extend well into the whorl interior until later stages in bryolith growth (e.g., sequence 3 of specimen 81K in Fig. 4C–D). Inside the aperture, laminae tend to have exceptionally small zooecia, resembling the non-feeding kenozooids observed in modern hermit-associated colonies of *B. commensale* (e.g., Taylor 1994; Fig. 4C, specimen 81-K).

Of the sectioned bryoliths, those with relatively smooth exterior surfaces mimicking the cerithiid shell (and no

standoff ridges) have relatively simple histories of concentric, multilaminar overgrowth by *B. commensale* (specimens 81-J and 81-K in Fig. 4). The thickness of the bryozoan overgrowth is slightly asymmetric, being thinner on the underside of the gastropod as it would have been carried by the hermit crab (aperture pointed down). The asymmetry in bryolith thickness increases with bryolith growth but is never very severe, consistent with general criteria for hermit occupation (Fig. 6B). Thinning was accomplished primarily by (a) depositional lap-out of laminae as they wrap toward the underside, especially around the shell apex (e.g., in sequences 2 and 3 around apex of 81-K, Fig. 4D; in sequence 2 of 81-Ob in Fig. 5C–D), and to a lesser degree by (b) erosional truncation or pinchout of individual laminae or sets of laminae on the lowest part of the underside (i.e. development of a pagurid facet; e.g., possible significance of pinchouts on underside of specimen 81-J, Fig. 4A), and (c) thinning of individual laminae on the underside (surviving zooecial walls appear to be shorter in some specimens).

Bryozoan growth on living gastropods. – In several specimens, *B. commensale* grew on the shells of living gastropods, as demonstrated by zooecia that were overgrown by later whorls of the gastropod shell (sequence 1 in specimen 81-K, Fig. 4C–D; sequence 1 in specimen 81-O, both sections, Fig. 5A–D). These fouling colonies are usually only one or two laminae thick near the aperture and thicken toward the apical areas, opposite to the aperturally thickened colonies associated with hermits; they also exhibit aperture-directed onlap (e.g., within sequence 1 of specimen 81-O, both sections, Fig. 5A–D), further indicating initial settlement near the shell apex and colony expansion aperturally as the gastropod shell itself grew. In a few specimens (e.g., sequence 1 of 81-K in Fig. 4C–D), the individual laminae of fouling colonies appear to be thinner than the constituent laminae of hermit-associated colonies, but it is not clear if this is due to stunted growth or surficial degradation.

The presence of fouling bryozoans on living gastropods appears to have had no negative effect on the settlement and growth of bryozoans after death of the gastropod, when the shell was hermit-occupied. Concentric hermit-related laminae on the *B. commensale*-fouled specimen 81-K (Fig. 4C–D), for example, are no more complicated than those on unfouled specimen 81-J (Fig. 4A). It is possible that the hermit-associated colony is the same as the fouling colony, having survived the transition from a living gastropod to a hermit crab host, but this cannot be proven. In specimen 81-O, for example (Fig. 5A–D), two standoffs continue uninterrupted from pre-hermit sequence 1 up into hermit-associated sequence 2, but other standoffs are strongly offset or disappear entirely.

Biotic effects of non-bryozoan epibionts. – In contrast, the presence of non-bryozoan epibionts on the shell before

bryozoan settlement, or at any time during the history of the bryolith, appears to have led to more frequent or prolonged abandonment of the bryolith by hermits. These specimens tend to have more complicated internal stratigraphies, including one or more strongly erosional unconformity, and also tend to have had multiple bryozoan colonies competing on the bryolith surface (based on competitive standoffs).

In specimen 81-O, for example, most of the shell exterior was fouled by oysters, agglutinated worm tubes, and (finally) bryozoans while the gastropod was still alive (Fig. 5A–D). The irregular topography created by these foulers is progressively muted but never eliminated entirely, and the bryolith contains an unusual number of sedimentary inclusions, lap-outs, and irregular truncations (including the final exterior surface), suggesting repeated and ultimately permanent abandonment by hermits. In specimen 81-L (not figured), the shell was clean at death (unfouled), leading to a very simple, smoothly conformable hermit-associated bryolith. However, the first unconformity in this bryolith was heavily colonized by serpulids, oysters, and boring barnacles, and the subsequent stratigraphy of the bryolith is highly complex: the topography produced by non-bryozoan epibionts and by the standoffs of newly established bryozoan colonies persisted, and accretionary growth was interrupted by two additional unconformities, each recolonized by non-bryozoan epibionts, suggesting repeated abandonment by hermits and bryozoan morbidity. Specimen 81-Q (Fig. 5E–F) underwent four phases of erosion, each with encrustation or boring and each presumably marking a distinct phase of hermit abandonment (including permanent abandonment, i.e. truncation of sequence 4; hermit occupation persisted at least through sequence 3, based on *Helicotaphrichnus* boring).

The observation that initially simple bryoliths may acquire progressively more complex stratigraphies upon settlement by non-bryozoan epibionts, and that these complex stratigraphies do not later revert to simple ones, suggests that these epibionts decrease the desirability of the bryolith for the hermits, and thereby negatively affect bryozoan growth through repeated hermit abandonment.

Borers of bryoliths. – Borings are much less common than encrustations on cerithiid-nucleated bryoliths and tend to have very limited occurrences. *Helicotaphrichnus* was observed in only one of the sectioned specimens, where it exhibits the unusual behavior of spiralling around the outer edge of the gastropod whorl rather than only along the columella, and of penetrating not only the shell but the inner layers of the bryolith itself (specimen 81-Q in Fig. 5E–F). The only other identifiable borings in cerithiid-nucleated bryoliths are from rare acrothoracican barnacles. One pierced a bryolith from the interior

of the gastropod shell (specimen 81-L, not figured), but all others penetrated from the exterior of the bryolith (e.g., specimen 81-Oa, Fig. 5A–B) or from disconformity surfaces within it. Most of these borings coincide with standoff ridges, suggesting that the borers were taking advantage of a narrow no-man's-land between competing bryozoan colonies (e.g., specimen 81-I, Fig. 3A; specimen 81-Oa, Fig. 5A–B).

Status at time of burial. – Only two specimens from the collection of cerithiid-nucleated bryoliths ($n=32$) show unambiguous evidence that the shell had been permanently abandoned by hermits; for example, as indicated by oysters that completely plug the aperture (Fig. 4A, specimen 81-J). All other cerithiid specimens show phases of temporary abandonment at most, suggesting a shortage of housing of this size in the oyster-bank facies.

Bryoliths nucleated on larger gastropod shells

Forty-eight bryoliths, of which five were sectioned, are nucleated on relatively large buccinids (*Solenosteira* cf. *capitanea* Berry, *Solenosteira* cf. *anomala* (Reeve)) and, less commonly, fascioliids (*Fasciolaria* cf. *princeps* Sowerby) (as figured in Hanna 1926 and updated using Keen 1971). The aperture, siphonal fasciole, anterior canal, and one or more whorls of these muricoid gastropods can generally be detected even through thickly encrusting bryozoans.

These bryoliths are relatively large (5–6 cm) and all show tangential overgrowth of the aperture, indicating hermit-occupancy. Apertural tubes are quite short, as in cerithiid-nucleated bryoliths. Overall, these bryoliths have a higher incidence of non-bryozoan epibionts on their exteriors than the cerithiid-nucleated bryoliths (~30% vs. 15%). Oysters (*D. vespertina*) are the most common non-bryozoan epibionts, amounting to one or many individuals per bryolith (25% specimens affected; Fig. 2C, specimen 81-U). Clusters of the solitary coral *Astrangia* sp. (12% of specimens, especially at loc. 83; identification verified by Ann F. Budd, personal communication, 1990), serpulid polychaetes, and calcitic byssal plugs from anomiid bivalves are also present, especially in specimens from channel thalwegs (specimen 81-S, Fig. 2B). Boreholes of acrothoracican barnacles are commonly associated with these epibionts.

Although all were hermit-occupied, the growth histories of these bryoliths vary depending on whether they occur in channel thalweg sands or channel margin oyster banks.

Bryoliths nucleated on muricoid shells in oyster bank facies. – These bryoliths were clearly hermit-occupied, given their well-wrapped apertures (specimens 81-S and

81-U, Fig. 2B–C). Many specimens (e.g., specimen 81-U, Fig. 2C) are heavily encrusted by small oysters, especially on their upper sides, contrary to the preference that most epibionts show for settling around the aperture on living crab-occupied shells (e.g., Walker & Carlton 1995). In addition, the oysters become intergrown with *B. commensale*, indicating more closely matched competition than seen on smaller cerithiid-nucleated bryoliths. This is consistent with Taylor's (1991) observation of epibionts increasing in abundance away from the aperture of crab-occupied bryoliths of the modern Otago Shelf, owing to decline in condition and growth rates of the bryozoan colony. Several of the encrusting oysters and low areas on the exterior of some of these bryoliths (e.g., specimen 81-V, not figured) also support small colonies of *Micro-porella* sp.

Bryozoan overgrowths (maximum of ~15–25 laminae) are comparable in thickness to those on cerithiid-nucleated bryoliths but are more evenly symmetrical, presumably because the more rotund form of the muricoid gastropod shells provided less surface area for development of a pagurid facet (e.g., specimen 81-A in Fig. 7A–B). Apertural tubes are the sites of greatest wear (erosional thinning). Standoffs form distinct ridges on these bryolith exteriors and sand-filled 'fissures' in cross-section; laminae abut or bow upward along these fissures (Fig. 7). Standoffs on bryoliths from this facies maintained fairly stable positions through bryolith growth. For example, the four distinct colonies that characterize the surface of specimen 81-A (Fig. 7A–B) can be traced continuously downward to the gastropod shell nucleus.

Bryoliths nucleated on muricoid shells in channel-thalweg facies.—These bryoliths resemble those from oyster banks, except that the encrustations are generally thicker, and thus the shape of the gastropod shell is more obscured (fascioliid-nucleated specimen 82-B, Fig. 7E–F) and in some instances the final bryolith is nearly spherical (buccinid-nucleated specimen 81-C, Fig. 7C–D).

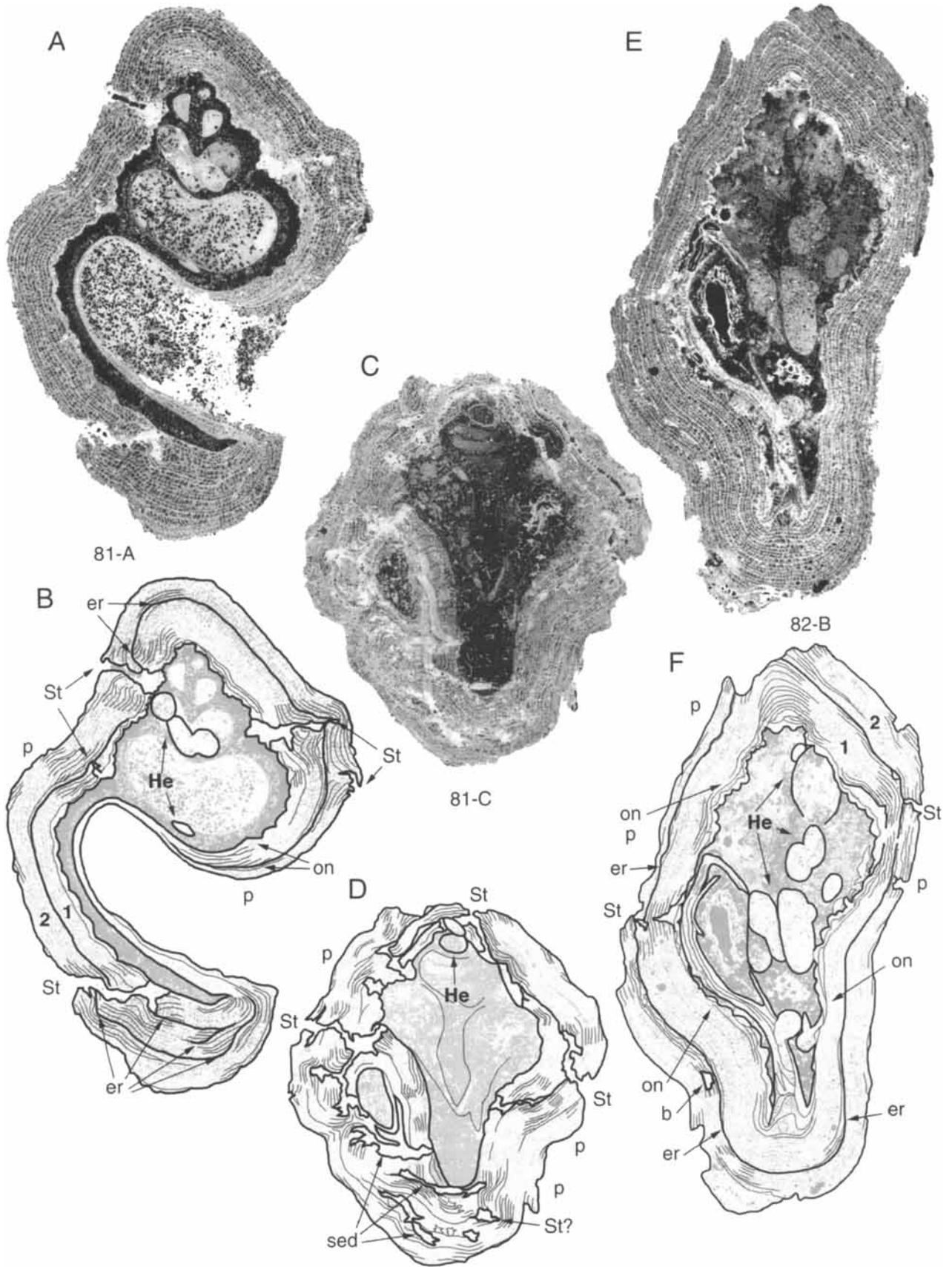
Epibionts are common on the exterior surface of the buccinid-nucleated bryoliths and are most abundant on the largest specimens. Specimen 81-S (Fig. 2B) has a dense bouquet of serpulids and solitary corals growing out of its aperture in a manner diagnostic of hermit crab association (e.g., Walker 1992); we also found bryoliths totally encased in serpulids (locality 85), with serpulids and corals largely overgrown by *B. commensale* (specimen 81-T), and with dense serpulids entirely overgrown by *B. commensale* (float specimens W from the vicinity of locality 82). The great irregularity of the exterior surfaces of these bryoliths suggests complex internal stratigraphies, as seen in sectioned specimen 81-C (Fig. 7C–D; and buccinid-nucleated specimen 82-G, unfigured), which contains no evidence of non-bryozoan epibionts but many truncated and irregularly wavy laminae and abundant sedimentary

inclusions. Some of these inclusions mark standoffs of highly unstable position and number, whereas others are possibly poorly defined borings; sediment also occurs in lenses along local unconformities and between otherwise conformable-looking laminae. The aperture was nearly but not completely occluded by tangential growth of *B. commensale*, indicating persistent if not continuous hermit occupation.

Three fascioliid-nucleated bryoliths from channel sands were sectioned, and all had apertures sealed by bryozoans, indicating that they had been permanently abandoned by hermits. In contrast to rotund buccinid-nucleated specimens, these elongate bryoliths have well-developed pagurid facets on their long undersides, especially at the shell shoulder where the bryolith would be expected to have most frequent contact with the seafloor (specimen 82-B, Fig. 7E–F). These facets have both non-depositional and erosional features (lap-out of laminae at apex, thinning and pinchout of laminae on underside, erosional beveling at sequence boundaries including bryolith exterior). Overgrowths are relatively thick (30 laminae on specimen 81-B, 28 laminae on 82-C, 28 laminae on 82-B), more nearly conformable, and standoffs are less common than on buccinid-nucleated bryoliths. All three sectioned specimens have *Helicotaphrichnus* borings in their columella, and two specimens (81-B, 82-B) have abundant acrothoracican borings in their outermost laminae (these do not appear in the plane of the cross-section of 82-B in Fig. 7E–F).

None of the sectioned fascioliids (or buccinids) show evidence of fouling during the life of the gastropod. The ridged external ornamentation of the gastropod is not filled by zooecia but instead by a microcrystalline material, possibly microbial micrite replacing the original periostracum (e.g., white outline of shells in specimens 81-A and 82-B, Fig. 7A–B and E–F). The initial laminae of *B. commensale* thus did not encrust directly on the shell. In some specimens, portions of the micritized shell-coating detached from the bryolith upon dissolution of the aragonitic gastropod shell and now 'float' in the void-filling spar, as do the collapsed fill of *Helicotaphrichnus* borings that would originally have run through the shell columella (e.g., Fig. 7E–F).

Fig. 7. Bryoliths nucleated on large muricoid gastropods. □A, B. Buccinid-nucleated bryolith from channel-margin oyster bank showing extensive damage to apertural tube during growth and long-lived standoffs (specimen 81-A, 3.3 cm long; BZ 4510). □C, D. Buccinid-nucleated bryolith from channel-thalweg facies, showing extremely complex stratigraphy with abundant sedimentary inclusions and instable standoffs (specimen 81-C, 3.5 cm long; BZ 4511). □E, F. Especially thick bryolith nucleated on fascioliid gastropod shell, showing well-developed pagurid facet on shoulder, collapse of mud-filled *Helicotaphrichnus* borings following dissolution of aragonitic gastropod shell, and geopetal spar (specimen 82-B, 4.2 cm long; BZ 4512).



Growth histories and biotic interactions of bryoliths nucleated on non-gastropod substrata

These constitute a total of 63 specimens and include the largest bryoliths we have found in the Imperial Formation (10 cm). Most have pustulose to mamillary external surfaces, and range in shape from disks to bowls to oblate and nearly spherical masses. The substratum is not identifiable without sectioning, and all are from sandstones of the channel-thalweg facies. Of the seven specimens sectioned, three are nucleated on oyster shells (specimens 82-BM and 81-F, Fig. 8B–C, Fig. 9B–C), one on a gastropod columella, two on sponge-bored shell fragments (oyster *D. vespertina*), and one on a set of agglutinated-sand tubes (specimen 82-A, Fig. 8A, Fig. 9A). These bryoliths are commonly bored and rarely have non-bryozoan encrusters.

Each of the sectioned masses began as a one-sided encrustation, went through a circumrotatory phase of relatively symmetrical and concentric growth, and then reverted to lop-sided growth when the bryolith presumably crossed a critical size threshold for mobility. The surface on which laminae eventually failed to accumulate is assumed to be the ultimate underside of the mass; this typically constituted ~25–40% of a bryolith's circumferal area.

Despite phases of lop-sided growth, these bryoliths progressed through a fairly consistent succession of forms toward a subspherical form, with a progressive decrease in the frequency of overturning. The two largest bryoliths sectioned (specimens 81-F and 82-BM, Fig. 8B–C), for example, began as one-sided growths on flat or concave oyster shells. After the shell edges were overgrown, the bryozoans initiated a ridge along the shell circumference, creating a bowl shape. These ridges grew taller and slightly inward during a free-rolling phase on the seafloor, eventually producing a hollow hemispherical bryolith (quite a few specimens were found in this stage of development, especially at locality 84). The central void, like the lagoon of an atoll, captured sediment, which eventually stabilized the bryolith in a concave-up orientation; the coarse-grained sand and mud-chips in specimen 82-BM (Fig. 8B) suggest 'catastrophic' fill during a storm rather than a gradual process. Overgrowth of this sedimentary fill (a small volume in specimen 81-F, but large in 82-BM, Figs. 8 and 9) led to a subspherical form that then became increasingly oblate, with growth directed outward from the sides of the bryolith. In specimen 82-BM (Figs. 8B and 9B), laminae pinched out or were eroded from both the top and under sides of the oblate mass, indicating that the bryolith was still subject to occasional flipping and sliding along the seafloor even after it ceased to roll freely.

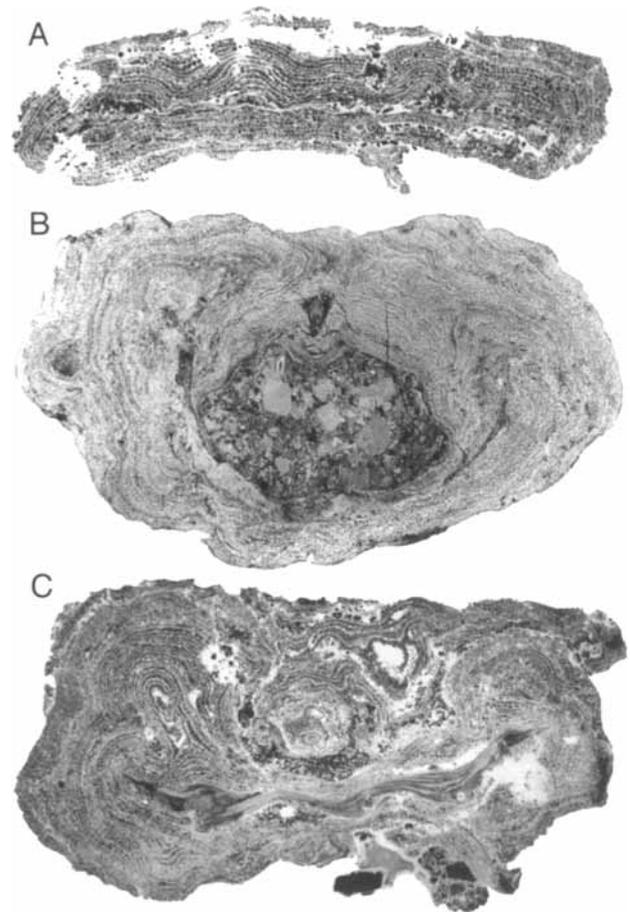


Fig. 8. Bryoliths nucleated on other substrata, all from the channel-thalweg facies (line-drawings in Fig. 9). □A. Heavily bored bryolith nucleated on agglutinated tubes (and originally aragonitic shell fragment?) (specimen 82-A, 4.2 cm long; BZ 4513). □B. Relatively uninterrupted growth on convex oyster shell, showing early 'atoll' form that is eventually roofed by the bryozoan and transformed into oblate spheroidal mass (specimen 82-BM, 7.5 cm long; BZ 4514). □C. More irregular, interrupted growth on flat oyster shell, still exhibiting an 'atoll' phase before reaching final quadrate spheroidal shape (specimen 81-F, 4.5 cm long; BZ 4515).

In specimen 82-BM (Figs. 8B and 9B), *B. commensale* did not encrust directly over the sedimentary fill of the atoll-shaped bryolith, but instead roofed it by inward-arching, tangential growth from the walls of the bowl. Zooids on the underside of this roof thus faced downward into the area of sediment accumulation, suggesting that the final phase of sedimentary infill was by draft currents; the presence of two very small oysters encrusting the underside of this roof suggest that this part of the colony was in poor condition. In specimen 81-F (Figs. 8C and 9C), the central area of the atoll is filled by a distinct colony of *B. commensale* (isolated from others by standoffs) which faces outward and thus apparently settled directly on sedimentary fill.

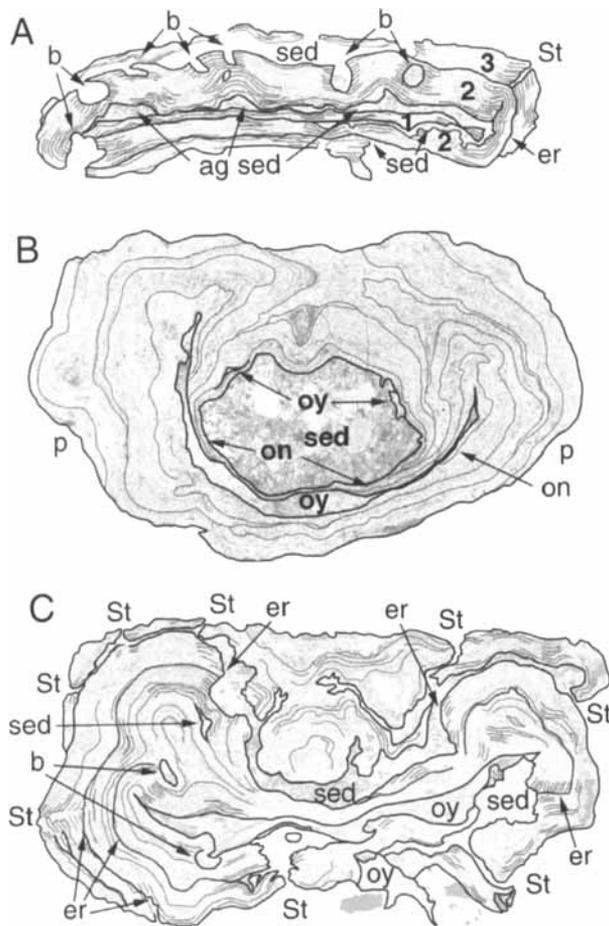


Fig. 9. Interpreted stratigraphy of bryoliths not inhabited by hermits in Fig. 8. □A. Specimen 82-A. □B. Specimen 82-BM. □C. Specimen 81-F.

Most of the largest bryoliths contain several distinct colonies. Specimen 81-F is especially complex, comprising at least two colonies even in its initial phase of development and an increasing number of colonies as it grew, based on the standoffs visible in a single section (Fig. 8C). Even the small bryolith 82-A goes from one colony in sequence 1 to perhaps two in sequence 2 and definitely two in sequence 3 (Fig. 8A). Standoffs in some of these bryoliths shifted positions dramatically over time and not exclusively at unconformities. Most of the sectioned specimens have abundant sedimentary inclusions (pods filling topographic irregularities of the bryolith; lenses between laminae and along unconformities) as well as abundant polydoridae and acrothoracican borings, which are present both along unconformities within the mass and over the exterior surface (e.g., specimen 82-A in Fig. 8A). Encrusting epibionts are rare. The specimens illustrated in Figs. 8 and 9 show the great variability in growth histories of bryoliths nucleated on non-occupied shell substrata, ranging from the relatively conformable internal stratigraphies produced by single-colony bryoliths to complex stratigraphies

with multiple unconformities, sedimentary inclusions, and multi-colony standoffs.

B. commensale also encrusted pebbles of crystalline rock derived from adjacent coastal fans of the Jackson Fork Member. These encrustations are usually only one or two laminae thick and may be partially overgrown or intergrown with serpulid worm tubes. Because the bryozoan laminae tend to exfoliate from these smoothly rounded substrata, specimens are more difficult to find and extract than encrusted shell, and thus material is inadequate for confident paleoecological analysis. The specimens are most definitely not lopsided in form, however, unlike the commonly one-sided growth seen in rock-nucleated bryoliths of *B. commensale* from Pliocene deposits near Loreto, Baja California Sur (Cuffey & Johnson 1997; SMK, personal observations).

Discussion

Two very different pathways to subspherical shapes are thus evident among these Pliocene bryoliths – one via hermit crab occupation of gastropod shells, and the other via wave-, current- and biotic overturning of dead-shell substrata (Fig. 10). These pathways are not randomly distributed across environments (Fig. 11) but instead vary with the kinds of domiciles available to hermit crabs (primarily small cerithiid gastropods on channel-margin oyster banks, versus large muricoid gastropods in channel thalwegs) and water-energy levels (determining whether overturning is sufficiently frequent to permit the formation of bryoliths without crab occupation). Although *B. commensale* clearly was not an obligate associate of hermits, its overwhelming preference for settling on numerically rare gastropod shells in the oyster-bank facies demonstrates the significant ecological advantage of the association to the bryozoan, of which circumrotatory growth and the formation of subspherical masses were simply byproducts.

Sequence-stratigraphic-type analysis of these laminar bryoliths permits a detailed examination of the dynamics of bryozoan growth under this range of circumstances, including the roles of symbiotic relations between hermits and bryozoans, and intra-specific and inter-specific interaction among bryozoans and other epibionts. Some patterns in bryolith growth patterns are fairly predictable from what is known in modern systems. For example: (1) the bryoliths with the greatest frequency and irregularity of global unconformities and sedimentary inclusions are those on (a) substrata without hermit crabs, totally subject to physical reworking, and (b) a subset of 'less desirable' gastropod domiciles, here the relatively globose buccinids or any gastropod shells made irregular by fouling epibionts; (2) the bryoliths with the largest numbers of bryozoan colonies and other epibionts tend to be the larg-

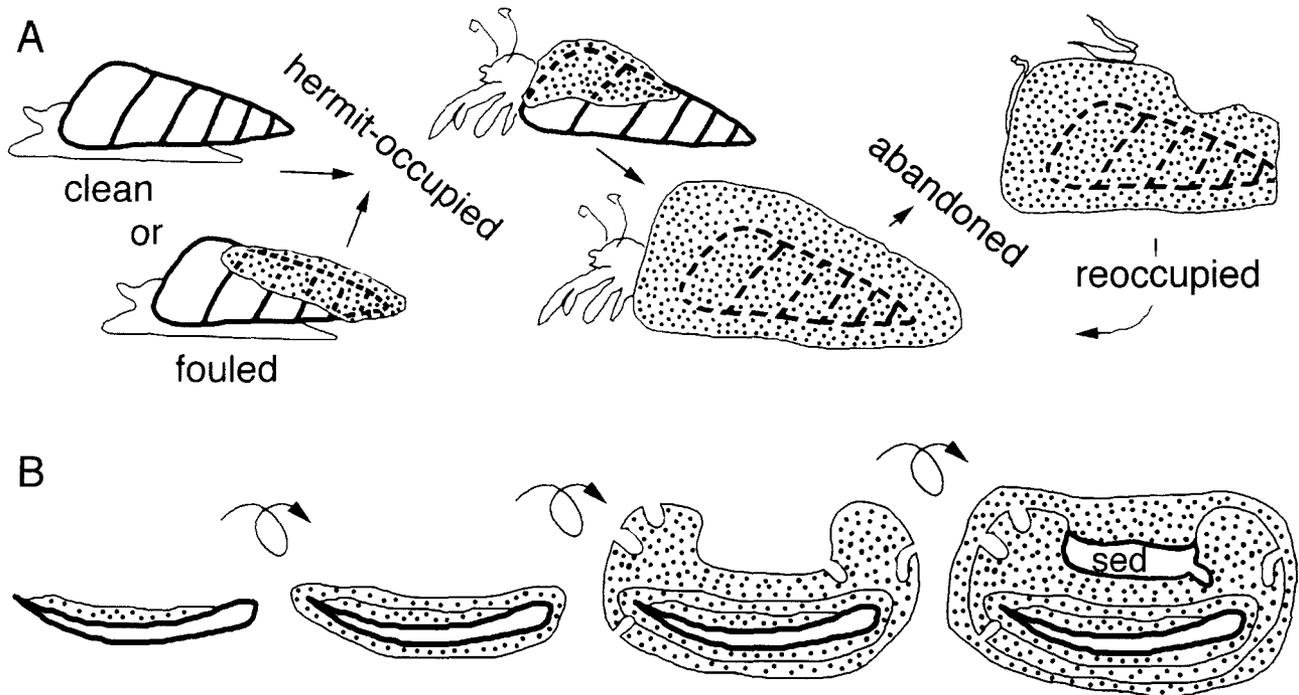


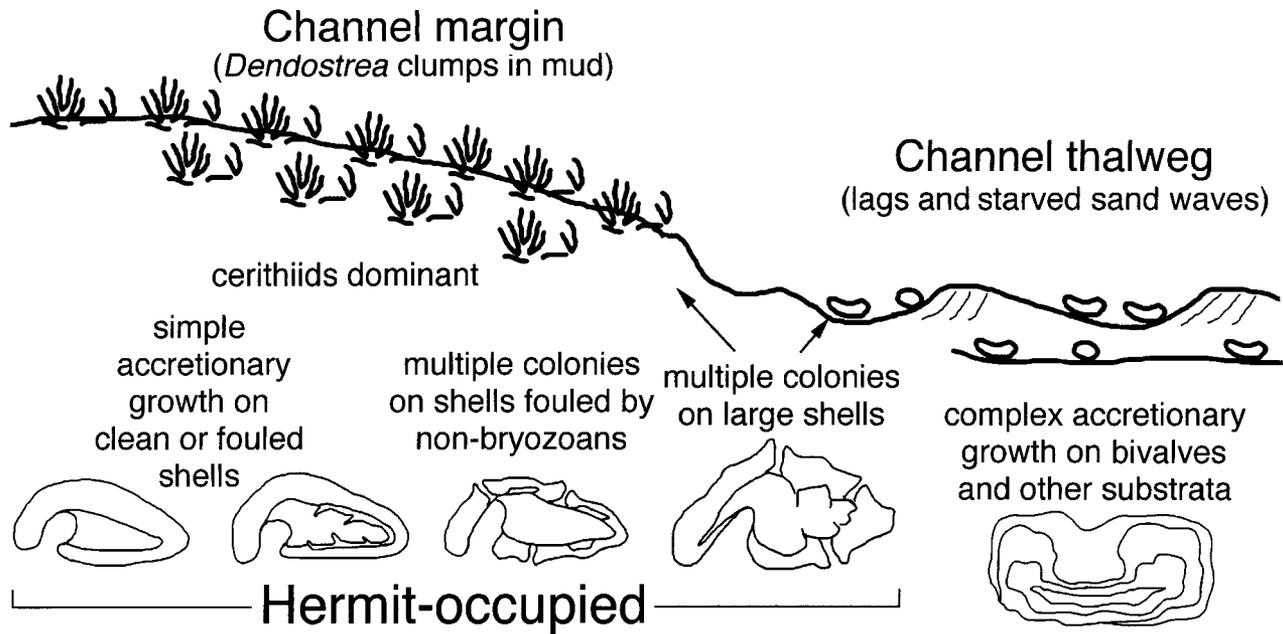
Fig. 10. Dominant pathways of bryolith genesis in Pliocene tidal flats of the Imperial Formation. □A. On hermit-occupied gastropod shells, which may have been fouled by *B. commensale* and other epibionts during the life of the gastropod. One or more cycles of hermit abandonment and re-occupation are possible, as inferred from erosional unconformities and epibiont infestations. □B. On bivalves and other shell debris; usually transformed from disc, to bowl-shaped atoll, to oblate spheroid.

est (still mobile) bryoliths, analogous to the effect of cobble size on epibiont diversity in modern marine communities (the intermediate-size hypothesis of Sousa 1979; Petraitis *et al.* 1989; Wilson 1987), and (3) bryozoan colonies show greatest tolerance of non-bryozoan epibiont competitors away from the aperture of hermit-occupied shells, a pattern that is most clear on the largest gastropod-nucleated bryoliths; this is consistent with colony condition depending upon proximity to the hermit (cf. Taylor 1991, 1994).

Other observations were unexpected, for example: (4) that the immediately adjacent channel-margin and thalweg environments exhibit such strong differences in the types of gastropods available for hermits and thus in bryolith growth histories; (5) that hermit-occupied bryoliths nucleated on larger gastropods suffer more abandonment cycles than those nucleated on small gastropods within the oyster bank facies, and that those nucleated on globose buccinids would suffer more complex growth histories than those on elongate fascioliid gastropods in the channel thalweg; (6) that competitive standoffs are less stable in position, not only on non-occupied bryoliths compared to hermit-occupied bryoliths but also on hermit-occupied large gastropods compared to hermit-occupied small gastropods (together with point 6 indicating multiple effects of shell size on the bryozoan-

hermit relationship); (7) that unconformities within hermit-occupied bryoliths (and their exteriors) are commonly encrusted by other epibionts, whereas those of non-occupied bryoliths are rarely encrusted (an unexplained correlate of hermit occupancy); (8) that the epibionts show strong facies preferences, being primarily oysters in the oyster banks and primarily serpulids and solitary corals in the channel thalwegs (this spatial heterogeneity is one of several lines of evidence strongly suggesting that bryoliths were buried in their life environments); and (9) that there is a strong gradient in acrothoracican boring, which is most pervasive in bryoliths not inhabited by hermits, reasonably common but limited to unconformities within large-gastropod bryoliths in the channel thalweg, less common among large-gastropod bryoliths in channel margin oyster banks, and extremely rare among cerithiid gastropod bryoliths in channel margin oyster banks (Fig. 11).

The acuity with which growth dynamics are preserved within bryoliths provides a valuable paleontological window for reconstructing physical environmental conditions in past shallow-water facies: Recent and late Cenozoic examples are known from a range of continuously and episodically high-energy settings and thus offer opportunities for dynamical study analogous to previous work on other macroids (cf. Hottinger 1983). The preser-



Substratum type	Clean cerithiid shell	Cerithiid shell fouled by bryozoans	Cerithiid shell fouled by non-bryozoans	Larger gastropod shells	Other shells & shell fragments
Competitive stand-offs among colonies of <i>B. commensale</i>	rare, stable in position	rare, stable	common, stable	common, tend to be stable in specimens from channel margin, unstable in thalweg	variable in number, unstable in position
Borings	<i>Helicotaphrichnus</i> in columella	<i>Helicotaphrichnus</i> in columella	<i>Helicotaphrichnus</i> in columella, <i>Trypanites</i> in standoffs	<i>Helicotaphrichnus</i> in columella, <i>Trypanites</i> in standoffs and, in thalweg, on some unconformities	<i>Trypanites</i> and others common, especially on unconformities
Encrusters of bryolith	rare	rare	common oysters & agglutinated tubes	very common oysters in channel margin; serpulids, agglutinated tubes, corals common in channel thalweg	rare
Erosional unconformities	rarely global	some global	commonly global	commonly global	variable, can be multiple & complex
Sediment inclusions, other than at standoffs	rare	rare	rare	present on specimens from channel thalweg	variable, can be abundant
Overall histories	simple accretionary growth	simple accretionary growth	hermit abandonment and reoccupation common	hermit abandonment and reoccupation common, very common in thalweg	complex accretionary growth

Fig. 11. Summary of environmental distribution of bryolith types in the Camel Head Member, and their ecological dynamics.

vational acuity afforded by bryoliths also provides a window on evolutionary changes in epibiont interactions, as the ecological communities containing these substrate islands have changed substantially over geologic time. Class and ordinal changes in the composition of bryozoan faunas through the Phanerozoic were probably accompanied by changes in physiologic and ecological capabilities and preferences of the pool of potential encrusters (e.g.,

McKinney 1993, 1995b). Further, evolution in the identity and ecology of hermits (with pagurids known back to the Jurassic, and sipunculid worms suspected as hermits in the Paleozoic; Palmer & Hancock 1973; Brett & Cottrell 1982) and possible changes in the disturbance imposed by bioturbators could have changed the patterns of availability or persistence of the substrata. These long-term shifts provide ripe opportunities for substantial change in bry-

olith dynamics over time, including strategies of intra- and inter-specific and inter-phyletic competition and symbiosis.

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