Palaeoecology of free-lying domal bryozoan colonies from the Upper Eocene of southeastern USA

FRANK K. MCKINNEY and PAUL D. TAYLOR

Dome-shaped cheilostome bryozoan colonies, most commonly about 2 cm in diameter, are common in Upper Eocene off-shore deposits of southeastern North Carolina, USA. This colony-form is anachronistic in the Eocene, being more typical of Palaeozoic bryozoans. There are three types of domes: individual colonies of *Parasmittina collum* (Canu and Bassler), individual colonies of *Osthimosia glomerata* (Gabb and Horn) and multispecies intergrowths. The bryozoans grew laterally beyond initial shell substrata to become free-lying. *P. collum* colonies grew by local eruptive budding, forming subcolonies that extended radially over the underlying layer of zooids. Undersides of subcolonies that extended beyond the original substratum have basal exterior walls that are more commonly fouled by encrusters than is the upper side of the colony. By contrast, lateral growth of *O. glomerata* colonies was limited by size of the original substratum, subcolonies were not developed, and colony growth occurred by prolific frontal budding over the entire upper surface of the colony. Undersides of colonies beyond the substratum consist of the lateral interior walls of marginal zooids and are much less commonly fouled than are undersurfaces of *P. collum*. The upper surfaces of multispecies domes by definition are always fouled, and their undersurfaces are also commonly fouled.

Key words: Bryozoa, colony morphology, fouling, Eocene, Castle Hayne Formation.

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Introduction

Free-lying, dome-shaped bryozoan colonies are common in many Palaeozoic marine sedimentary rocks but are much rarer in the post-Palaeozoic. These bryozoans typically began growth on upwardly-convex skeletal debris littering the sea floor, eventually growing laterally beyond the original skeletal substratum so that the periphery of the colony rested directly on finer-grained surrounding sediments. Although diverse organic materials served as substrata for Palaeozoic dome-shaped colonies (Männil 1961), brachiopod valves were the prevalent substrata (Ross 1970; McKinney 1971a), whereas individual valves of bivalves have been the most common substrata for the relatively few post-Palaeozoic examples of this colony-form (e.g., Cook 1965).

The oldest free-lying domal bryozoans occurred in the Early–Middle Ordovician and include diverse species assigned to the trepostomes *Dianulites*, *Diplotrypa*, *Esthoniopora*, *Hemiphragma*, *Mesotrypa*, *Monotrypa*, *"Nicholsonella"*, *Orbipora*, *Prasopora*, and *Stigmatella*, and the cystoporates *Anolotichia*, *Ceramopora*, and *Favositella*, (Bassler 1911; McKinney 1971a; Larwood and Taylor 1979; Spjeldnaes 1996; Wyse Jackson et al. 2002). Domal colony shapes continued to be common for both trepostomes and

cystoporates into the Carboniferous (e.g., Ulrich 1890; Nekhoroshev 1956; McKinney 1971b, 1972). Although similar colonies from Permian rocks are occasionally noted (e.g., Morozova 1970), they are apparently much rarer. Species with consistently dome-shaped, free-lying colonies may be absent altogether in the Mesozoic. Free-lying domes do, however, make a reappearance among Cenozoic cheilostomes but are essentially an anachronistic bryozoan colony-form in the post-Palaeozoic (cf. irregular mound-shaped colonies which are distributed among both cheilostomes and cyclostomes).

Unusually for the post-Palaeozoic, domal bryozoan colonies are very common in the late Eocene Castle Hayne Formation of eastern North Carolina, USA. They are among the most conspicuous and frequently collected bryozoans in this bryozoan-rich carbonate. In this paper, we describe Castle Hayne bryozoan domes built by two different species, plus domal masses constructed of intergrowths involving multiple species. Both of the dome-building species seem only to occur with this colony-form, i.e. they appear to be obligate dome building bryozoans, at least in the Castle Hayne Formation. We examine substratum preferences, morphology of the domal constructions, types and distribution of fouling encrusters on the domes, and consider some of the ecological implications of the domal constructions.

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Occurrence

Specimens for this study were collected over a period of 32 years (1968–2000) from the surface of extensive spoil piles in the Martin Marietta Ideal Quarry. This quarry is located approximately 3.2 km east of the intersection of U.S. Highway 117 and N.C. 1002, on the north side of N.C. 1002, near Castle Hayne, Hanover County, North Carolina.

Material was collected from two additional sites in November 2000. Numerous specimens were collected from extensive spoil piles in the Martin Marietta Rocky Point Quarry, located immediately east of Interstate Highway 40, approximately 2 km southeast of Rocky Point, Hanover County, North Carolina. A smaller surface collection was made from spoil material surrounding the abandoned Lanier Pit, on N.C. Rural Route 1532, 0.6 km southwest of its junction with N.C. 50, near Maple Hill, Pender County, North Carolina. In addition, all domal bryozoans and typical skeletal substrates on which they develop were picked from a 3.2 kg bulk sample of spoil material from the Lanier Pit.

Spoil piles in the Ideal Quarry contain material derived from the entire Castle Hayne Formation and the upper portion of the underlying Upper Cretaceous Peedee Formation (Harris et al. 1986). Exposed portions of the Peedee Formation in the quarry consist of dark gray quartz arenite and arenaceous pelecypod-mold lime packstone. The basal New Hanover Member of the Castle Hayne Formation consists of various bryozoan-rich carbonate lithologies, all of which are well indurated, and much of which contains abundant phosphate pebbles (Baum et al. 1978). The overlying Comfort Member of the Castle Hayne Formation consists of poorly indurated bryozoan-rich lithologies. The Castle Hayne Formation varies slightly in thickness across the large Martin Marietta Ideal Quarry but is on average about 16 m thick (Harris et al. 1986), and the Comfort Member constitutes 85–90% of the total thickness.

Zullo and Harris (1986) recognized four depositional sequences within the Castle Hayne Formation, all of which are exposed in the Ideal Quarry. Sequences 3 and 4 correspond with the Comfort Member and are separated by a ravinement surface 9–10 m above the base of the approximately 14 m thick Member. Calcareous plankton indicate that sequence 3 ranges from upper Bartonian to lower Priabonian and that sequence 4 is Priabonian (Worsley and Laws 1986), and Zullo and Harris (1987) correlated these sequences respectively with Global Coastal Onlap Cycles TA4.1 and TA4.2 of Haq et al. (1987). The *Periarchus lyelli* Assemblage Zone characterizes all but a relatively thin basal portion of sequence 3 (Zullo and Harris, 1986).

Although collected only from spoil piles, the domal bryozoans from the Ideal Quarry appear to be exclusively or largely derived from sequence 3 of the Castle Hayne Formation. They come from the extensive areas of disaggregated spoil derived from the poorly indurated Comfort Member, where they are associated with the irregular echinoid

Periarchus lyelli and species of the bivalve *Chlamys*, i.e., the components of the *Periarchus lyelli* Assemblage Zone.

Spoil piles in the Rocky Point Quarry contain material derived from the upper portion of the Upper Cretaceous Peedee Formation and sequences 1 through 3 of the Castle Hayne Formation (Harris et al. 1986). In this quarry, the exposed portions of the Peedee Formation consist of a thin zone of dark gray clayey sand overlain by quartz arenite and arenaceous pelecypod-mold lime packstone. The basal New Hanover Member (sequences 1 and 2) of the Castle Hayne Formation consists of various bryozoan- and mollusc-rich carbonate lithologies, all of which are well indurated, and much of which contains abundant phosphate pebbles (Baum et al. 1978). The overlying Comfort Member consists of poorly indurated bryozoan-rich lithologies within sequence 3 of the Castle Hayne Formation. The Comfort Member is only about 3 m thick in the Rocky Point Quarry and is the only unit from which the domal bryozoans were collected.

Only Castle Hayne sequences 1 and 3 occur at the Lanier Pit (Zullo and Harris 1987). All domal bryozoans at the Lanier Pit were collected from spoil of disaggregated, originally poorly indurated, bryozoan-rich lime mudstone to packstone, in association with the fauna that characterizes the *Periarchus lyelli* Assemblage Zone. Therefore, the domal bryozoans from the Lanier Pit appear to be derived entirely from the upper portion of sequence 3.

In summary, the domal bryozoans all appear to have been collected from spoil material derived from sequence 3 of the Castle Hayne Formation. They are therefore late Bartonian to early Priabonian in age.

Material and methods

All domal bryozoans were collected by searching the surfaces of spoil piles, except specimens from the single supplementary bulk sample. There was no conscious selectivity for particular sizes or shapes. Differences among the three types of domes were not taken into account in the field. They were sorted later, using a binocular microscope to discriminate taxa. Figured specimens have been registered into the collections of The Natural History Museum, London (NHM).

Specimens were sorted into three categories: *Parasmittina collum* (Canu and Bassler, 1920), *Osthimosia glomerata* (Gabb and Horn, 1862), and multispecies domes (Fig. 1). In order for a domal specimen to be recognized as *P. collum* or *O. glomerata*, it had to be constructed from encrusting base to upper surface by essentially a single colony of the species. Where the substratum was preserved, it was impossible to discern the presence of other small colonies that might have been established on the substratum but that were eventually overgrown by the dome-building colony. Diverse organisms, including other bryozoan colonies, commonly grew on undersurfaces where the dome-building colonies extended beyond the original substratum. Small encrusting organisms also commonly occurred on the upper
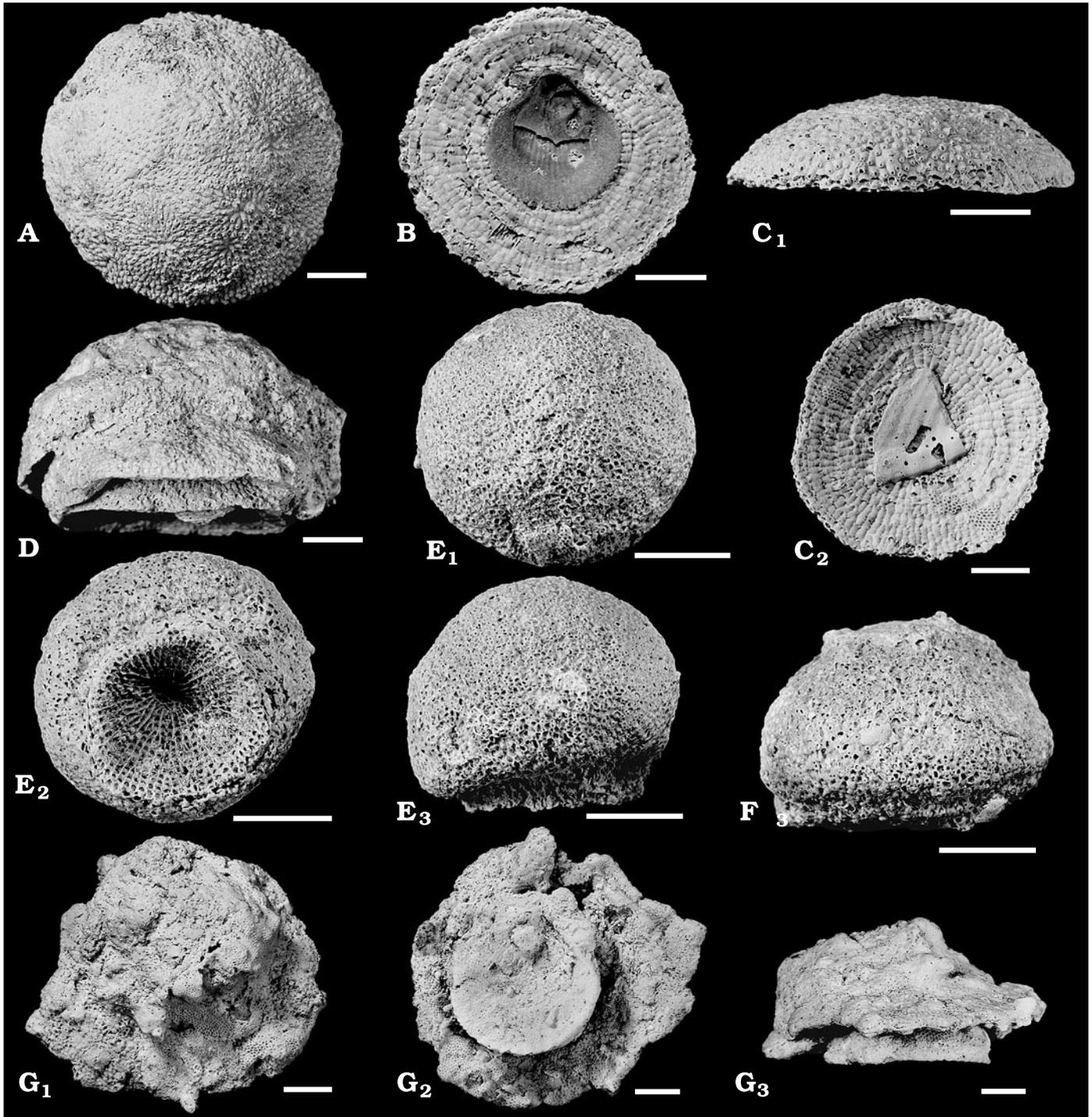
Fig. 1. Domal bryozoans from the Castle Hayne Formation. **A–D**. *Parasmittina collum* (Canu and Bassler). **A**. Upper surface with multiple subcolonies visible; NHM BZ4963. **B**. Undersurface of colony established on *Chlamys*; NHM BZ4964. **C**. NHM BZ4965. C_1. Lateral view. C_2. Undersurface, established on bivalve fragment. **D**. Lateral view of colony with renewed growth indicated by second lateral flange; NHM BZ4966. **E**, **F**. *Osthimosia glomerata* (Gabb and Horn). **E**. NHM BZ4967. E_1. Upper surface. E_2. Undersurface, established on *Lunulites* sp. E_3. Lateral view. **F**. Lateral view of colony with renewed growth indicated by broader flange developed above short basal portion with a curved surface consisting of frontal surfaces of zooids; NHM BZ4968. **G**. Multispecies dome; NHM BZ4969. G_1. Upper surface. G_2. Undersurface showing *Chlamys* substratum. G_3. Lateral view. Scale bars 1 cm.

surface of the dome constructors. Domal specimens were still assigned to *P. collum* or *O. glomerata* if encrusting organisms constituted a proportionally small volume of the specimen, were confined entirely or largely to the outer-most surfaces, and did not entirely cover the upper surface of the dome-constructing colony.

Domal specimens that were obviously generated by the intergrowth of multiple colonies of various species were

grouped as multispecies domes. These include domes built in part by *Parasmittina collum* or *Osthimosia glomerata* but with the upper surfaces completely covered by other taxa, commonly constituting several layers of encrusting colonies.

All specimens of *Parasmittina collum* and *Osthimosia glomerata* that grew beyond the original substratum consisted of frontally convex colonies with essentially circular outlines, i.e. radially symmetrical domes. Although many multispecies domes were radially symmetrical, others did not have such well developed symmetry. A boundary between multispecies domes and more irregular multispecies masses had to be established, although it needed to be invoked only rarely. Geometric characteristics of multispecies domes are 1) lateral growth beyond the original substratum, 2) a distinctly convex-upward profile when viewed laterally from all orientations, and 3) either a single basal colony or several colonies collectively projecting laterally beyond the original substratum, without having developed attachment to other objects lying on the adjacent sedimentary substratum.

Measurements included diameter and height of domes, and, where visible, maximum diameter and height of substratum. Type of substratum was recorded where visible. For many specimens, the type, number, and distribution (upper surface vs underside) of encrusters were recorded. On the undersurfaces, encrusting organisms attached directly to the bryozoan dome-builder were counted, but not those attached solely to the substratum on which the domal growth was established as these may have antedated the dome builder.

Surface areas were calculated for domes for which number and distribution of encrusting organisms were determined. The area of the lower surface (A_L) of a given colony was calculated as

$$A_L = \pi r_C^2 - \pi r_S^2,$$

where r_C is radius of the colony and r_S is radius of the substratum. The formula was used as given for *Parasmittina collum* and multispecies domes. However, the transition from upper to lower surfaces of *Osthimosia glomerata* is rounded, and the undersurface of the colony actually begins about 1 mm inward from the colony perimeter. Consequently r_C used for calculation of the undersurface of *Osthimosia glomerata* colonies is half the measured colony diameter minus 1 mm. Area of the upper surface (A_U) of a *P. collum* colony, each of which constituted a hemisphere or usually less than a complete hemisphere, was calculated as

$$A_U = \pi r_{SPH} (2h_C + r_C) - \pi r_C^2 ,$$

where r_{SPH} is radius of the sphere of which the upper surface of the colony is a partial sector, and h_C is height of the colony. Area of the upper surface of a *Osthimosia glomerata* colony, each of which constituted a hemisphere or slightly more of a sphere than half, was calculated as

$$A_U = 2\pi r_C^2 + \pi r_C (h_C - r_C).$$

For calculation of upper surfaces of *Osthimosia glomerata* colonies, r_C equals half the measured colony diameter. Area of the upper surface of multispecies domes was not calculated.

Results

Parasmittina collum **(Canu and Bassler, 1920)**.—*Parasmittina collum* is an ascophoran cheilostome with a slightly convex cryptocystal frontal shield pierced at the outer edges of the zooid by areolar pores and with a few additional non-marginal pores in the proximal part of the zooid (Fig. $2A_1$–B_2). The orifice has a low peristome which often obscures the lyrula, a tooth-like structure characteristic of smittinids, that projects into the orifice from its proximal edge. Some zooids have ovicells (Fig. $2B_2$), usually broken, and an adventitious avicularium is occasionally present proximolaterally of the orifice. Local frontal budding from which laterally budding subcolonies are established generates a moderately well defined layering within colonies (Fig. 2D).

The species was comprehensively described and illustrated by Canu and Bassler (1920) as *Smittina collum*, but *Smittina* is characterized by a pseudoporous frontal shield and a median suboral avicularium (e.g., Soule and Soule 1973), neither of which is present in this species. We consider the species to belong to the related genus *Parasmittina* because of the marginal areolar pores, the lyrula and cardelles, perforated ovicells, and the non-suboral avicularium present on many zooids.

Colonies have a circular outline and a characteristically uniformly curved upper surface (Fig. 1A–C) so that the domal colony profile typically subtends approximately 170° of arc. Colonies average slightly over 20 mm in diameter (Fig. 3A; $\overline{X}$ = 21.5±8.4 mm, median = 20.0 mm, range = 9.6–87.0 mm). Height of the *P. collum* colonies was approximately 40% of the diameter (Fig. 3B), and high correlation between diameter and height (r = 0.845) is due to the smooth constant curvature maintained across colony surfaces. One of the three conspicuous outliers of the diameter:height trend in Fig. 3B is an anomalously broad colony (bottom center of figure), and the other two have approximately equal diameter and height (left center) due to stacking that resulted from colony regeneration. Height of colonies averages slightly under 10 mm ($\overline{X}$ = 9.5±4.3 mm, median = 8.6 mm, range = 3.7–37.6 mm, N = 356).

Diverse skeletal fragments served as substrata on which colonies were founded (Figs. $1C_1$, C_2, 3D), but all tended to be about 10 mm in maximum diameter (Fig. 3C; $\overline{X}$ = 9.3±3.7 mm, median = 8.7 mm, range = 2.4–25.7 mm, N = 262; original substrata were obscured by sediment in about 25% of the specimens). *Chlamys*, the cap-shaped bryozoan *Lunulites*, *Cardium*, and other bivalves were the most common substrata, but selectivity for particular substrata cannot be determined because the ratio of various potentially available substrata is unknown. However, no concave-up substrata were seen; most were gently convex and were about 2 mm in maximum height ($\overline{X}$ = 1.8±1.2 mm, median = 1.8 mm, range = 0–5.9 mm; N = 252). Correlation of substratum height with maximum diameter is poor (r = 0.501), reflecting the diversity of substrata on which colonies were established, ranging
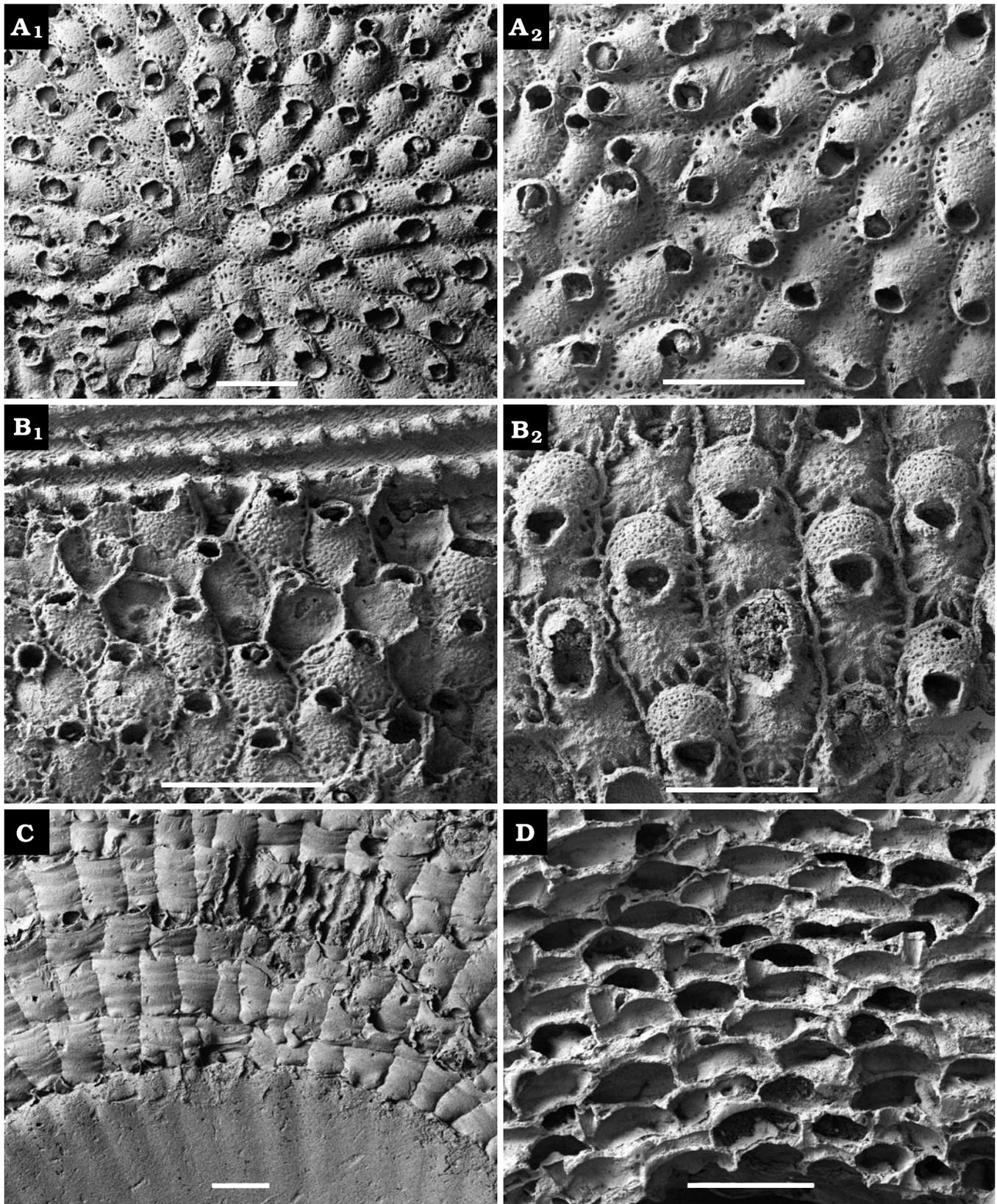
Fig. 2. *Parasmittina collum*. **A**. NHM BZ4963. A_1. Autozooids radiating from center of subcolony. A_2. Junction between two subcolonies, indicated by line of convergence of zooids that extends from top left to right end of scale bar. **B**. NHM BZ4970. B_1. Edge of colony growing across *Chlamys* sp. B_2. Fertile zooids, each with inflated ovicell distal to zooidal orifice. **C**. Underside of colony extending free beyond *Chlamys* substratum, with wrinkles suggestive of growth lines and larger-scale arc-shaped overlapped edges of successive subcolonies; NHM BZ4964. **D**. Fractured surface through colony showing moderately well defined layers of zooids that develop from a combination of local eruptive budding and lateral budding; NHM BZ4971. Scale bar in B_2 500 μm; all others 1000 μm.
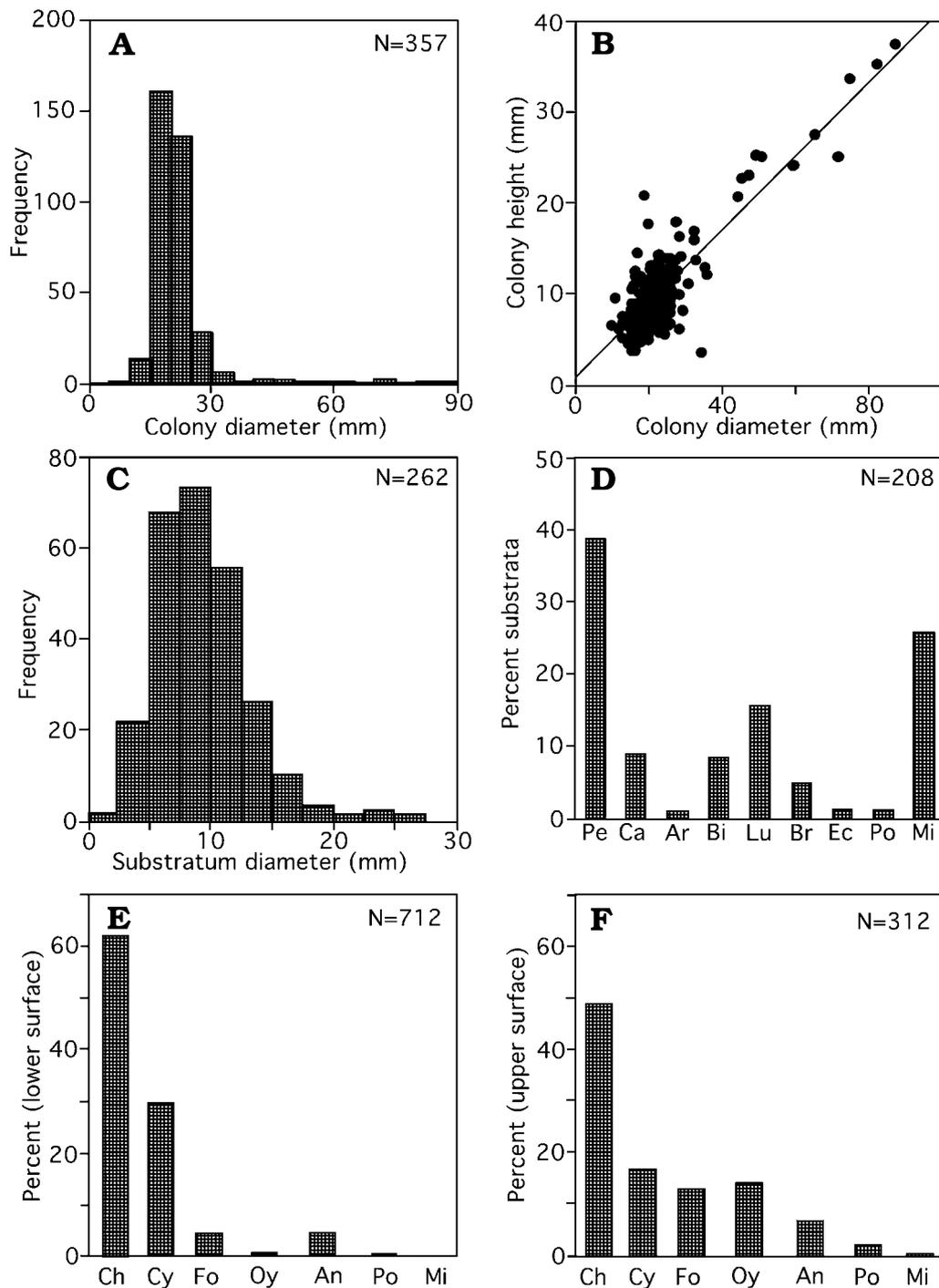
Fig. 3. *Parasmittina collum*. **A**. Distribution of colony diameters. **B**. Regression of colony height on colony diameter; Y = 0.408X + 0.632 mm. **C**. Distribution of substratum diameters. **D**. Proportion of types of substrata on which colonies were established. **E**. Frequency distribution of encrusting organisms on lower surface. **F**. Frequency distribution of encrusting organisms on upper surface, with same identifying. Abbreviations: An, annelids (serpulids); Ar, *Arca* sp.; Bi, other bivalves; Br, bryozoan fragments; Ca, *Cardium* sp.; Ch, cheilostomes; Cy, cyclostomes; Ec, echinoid fragments; Fo, foraminiferans; Lu, *Lunulites* sp.; Mi, miscellaneous; Oy, oysters; Pe, pectinid bivalves, probably all *Chlamys* spp.; Po, poriferans.

from flat, planar shell fragments (Fig. 1C₂) to *Lunulites* colonies for which height averages about one-third the diameter. Substratum diameter is also poorly correlated with colony diameter (r = 0.256).

Of the 357 *Parasmittina collum* colonies studied, 11 had their upper surfaces and 95 their undersurfaces obscured by

adhering sediment. On average, 19% of the undersurface area of *P. collum* domes was occupied by the substratum on which the colony initially grew before spreading laterally with a free epitheca. The presence of the original substratum occupying part of the undersurface, in combination with greater original surface area of the sphere-sector upper sur-
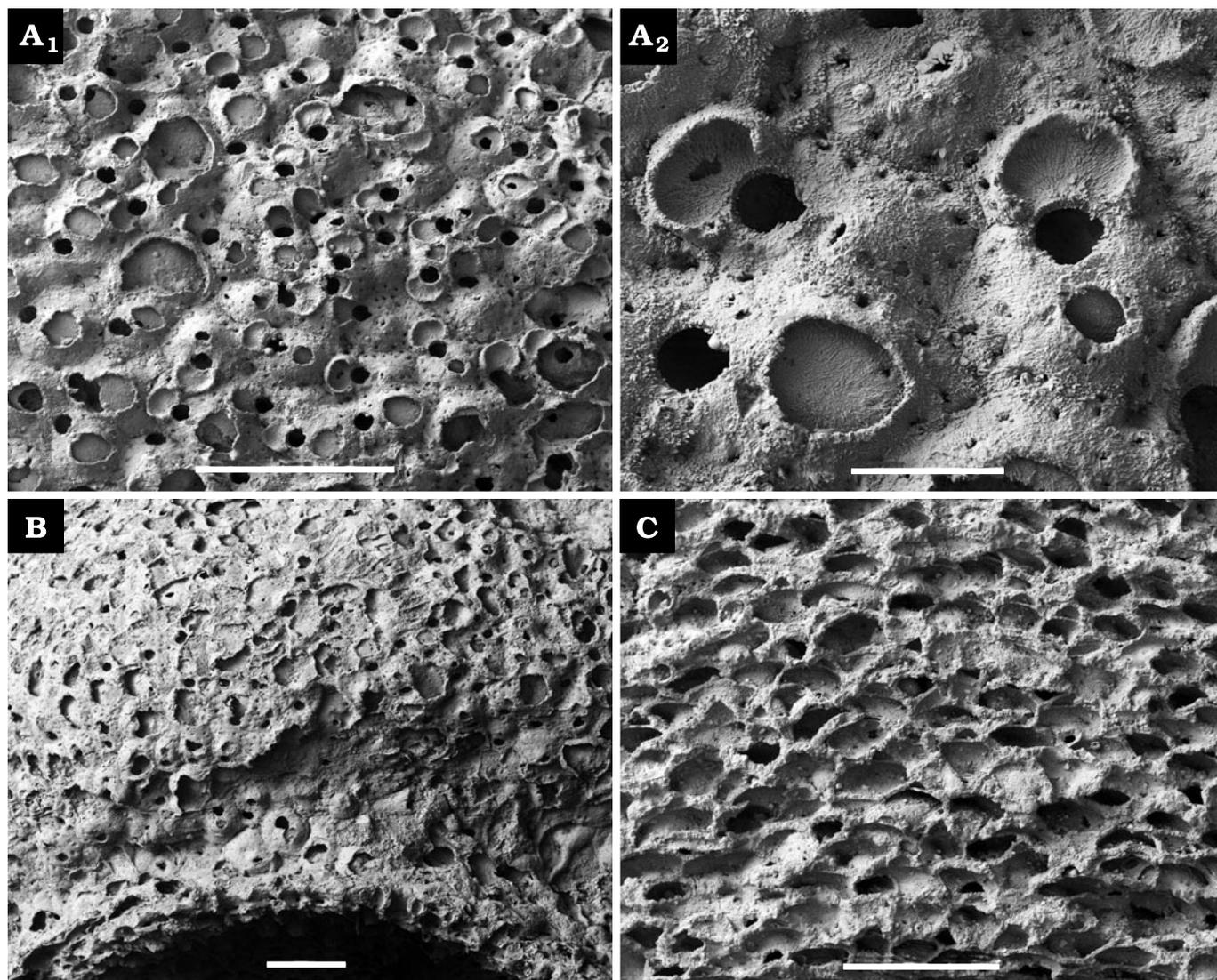
Fig. 4. *Osthimosia glomerata*. **A**. NHM BZ4972. A$_1$. Surface of colony showing frontally budded autozooids in various stages of development. A$_2$. Detail of surface with complete suboral avicularium in left central zooid, incomplete chamber of suboral avicularium in right central and lower zooids, and incomplete brood chambers distal to left central and right central zooids. **B**. Lateral view of lower edge of colony, with frontally budded zooids extending to base of colony, which is visible at lower edge of photograph; NHM BZ4967. **C**. Fractured surface through colony showing chaotic stacking of frontally budded zooids; NHM BZ4973. Scale bar in A$_2$ 200 μm; all others 1000 μm.

face, resulted in approximately 2.75 times as much area of upper surface of colonies that was visible and examined for encrusting organisms as there was of undersurfaces.

Only 69% (240/346) of upper surfaces, whereas 99% (260/262) of undersurfaces, were fouled by skeletalized encrusters. For 82 specimens examined in detail, fouling organisms recruited more densely on undersurfaces than on upper surfaces. Undersurfaces were fouled by 712 encrusters, giving an average of one per 41 mm^2, while upper surfaces were fouled by 312 encrusters, for an average of one per 291 mm^2.

The same taxonomic groups of organisms encrusted upper and lower surfaces of *Parasmittina collum* domes (Fig. 3F, E). Cheilostome bryozoans, followed by cyclostome bryozoans, were the most abundant organisms attached to both surfaces. However, they constituted a higher proportion of the total on the undersurfaces than on upper surfaces, and oysters and foraminiferans especially were less well represented on undersurfaces.

***Osthimosia glomerata* (Gabb and Horn, 1862)**.—*Osthimosia glomerata* is another ascophoran cheilostome and belongs to a group, often referred to as "celleporids", in which colonies are built of piles of chaotically-arranged zooids with a cyst-like structure in vertical section (Fig. 4C). Zooids have convex cryptocystal frontal shields bordered by areolar pores (Fig. 4A$_1$, A$_2$). The orifice has a broad sinus. An adventitious avicularium placed proximally of the orifice is generally abraded to reveal the avicularian chamber which occupies a large part of the frontal surface (Fig. 4A$_2$). Many zooids are ovicellate but in all of those we have observed the delicate

roof of the ovicell is missing (Fig. 4A$_1$, A$_2$). The absence of this feature places a question mark over the generic assignment of the species as the presence and distribution of pores in the ovicell roof cannot be ascertained. It is also worth remarking that our identification of this species is based on Canu and Bassler's (1920) interpretation of Gabb and Horn's (1862) species described originally from Vicksburg, Mississippi but inadequately illustrated.

Castle Hayne *Osthimosia glomerata* colonies have a height that is approximately 60% their colony width (Fig. 5B), so that colonies are slightly in excess of hemispherical, subtending approximately 210° of arc. Colonies average slightly under 20 mm in diameter (Fig. 5A; $\overline{X}$ = 18.3±5.2 mm, median = 17.2 mm, range = 9.3–42.8 mm). Height of colonies averages slightly over 10 mm ($\overline{X}$ = 11.5±4.6 mm, median = 10.6 mm, range = 5.5–39.3 mm, N = 130). High correlation between diameter and height (r = 0.669) is due to the smooth constant curvature maintained across colony surfaces.

Diverse skeletal fragments served as substrata on which colonies were founded (Fig. 5D), but all tended to be about 10 mm in maximum diameter (Fig. 5C; $\overline{X}$ = 9.6±3.0 mm, median = 9.5 mm, range = 3.4–17.6 mm, N = 103; original substrata were obscured by sediment in about 20% of the specimens). All substrata were gently convex and averaged over 2 mm in maximum height ($\overline{X}$ = 2.6±1.4 mm, median = 2.6 mm, range = 0.4–11.0 mm; N = 95). Various bivalve shells, especially *Chlamys*, were the most common substrata, followed by the cap-shaped bryozoan *Lunulites*. As for *Parasmittina collum*, selectivity for particular substrata cannot be determined because the ratio of various potentially available substrata is unknown. However, *Osthimosia glomerata* recruited on average onto more highly convex substrata than did *P. collum*. Ratio of height to diameter for *P. collum* substrata was 1:5.2, whereas for *O. glomerata* substrata the ratio was 1:3.7. The more highly convex substrata utilised by *O. glomerata* are reflected in part by the greater prevalence (30%) of *Lunulites* as substrata than seen for *P. collum* (15% *Lunulites* substrata), so some selectivity by one or the other species is probable. Correlation of substratum height with maximum diameter is even poorer (r = 0.103) than for substrata of *P. collum*, and substratum diameter is also poorly correlated with colony diameter (r = 0.263).

Of the 130 *O. glomerata* colonies studied, two had their upper surfaces obscured and 66 had their undersurfaces obscured by adherent sediment. On average, 44% of the undersurface area of *O. glomerata* domes was occupied by the substratum on which the colony initially grew before spreading laterally beyond it. The presence of the original substratum occupying part of the undersurface, in combination with greater original surface area of the sphere-sector upper surface, resulted in approximately 3.9 times as much area of upper surface of colonies that was visible and examined for encrusting organisms as there was of undersurfaces.

Skeletalized organisms encrusted 73% (93/128) of upper surfaces and 84% (54/64) of visible undersurfaces. Fouling was denser on undersurfaces than on upper surfaces: under-

surfaces were fouled by 236 encrusters, giving an average of one per 52 mm^2, while upper surfaces were fouled by 531 encrusters, for an average of one per 165 mm^2.

The same groups of organisms encrusted upper and lower surfaces of *Osthimosia glomerata* domes (Fig. 5F, E) as was seen on *P. collum*. Cheilostome bryozoans were the most abundant organisms attached to both surfaces. Foraminifera were the second most abundant on upper surfaces, whereas cyclostome bryozoans were the second most abundant on undersurfaces. Oysters were relatively more frequent on upper than lower surfaces.

Multispecies domes.—Multispecies domes were constructed by a large variety of cyclostome and cheilostome bryozoans. Cheilostomes were both more diverse and constituted a larger volume of multispecies domes than did cyclostomes (e.g., Fig. 6A$_1$). These domes have less regularly circular outlines than do those constructed by single species (compare Fig. 1G$_1$ with Fig. 1A, E$_1$); they range from circular to irregularly oval. However, like the single-species domes, they average slightly over 20 mm in diameter (Fig. 7A; $\overline{X}$ = 22.1±5.5 mm, median = 21.3 mm, range = 12.2–41.1 mm). Height of the multispecies domes is approximately 55% of their diameter (Fig. 7B), and correlation between diameter and height (r = 0.637) is slightly less than that for the more regularly constructed single-species domes. Average height is slightly over 12 mm ($\overline{X}$ = 12.3±4.4 mm, median = 12.0 mm, range = 3.9–27.3 mm, N = 75).

As for single-species domes, diverse skeletal fragments served as substrata on which the multispecies complexes were founded (Fig. 7D), though they tended to be slightly larger (Fig. 7C; $\overline{X}$ = 12.2±4.6 mm, median = 8.7 mm, range = 2.4–25.7 mm, N = 45; original substrata were obscured by sediment in 40% of the specimens). The cap-shaped bryozoan *Lunulites* was the single most numerous substratum on which multispecies domes were founded, but pectinids and other bivalves collectively were the most common substrata. As is true for single-species domes, selectivity for particular substrata cannot be determined because the ratio of various potentially available substrata is unknown. However, multispecies domes were established on average onto more highly convex substrata than either of the single-species domes. Ratio of height to diameter for substrata on which multispecies complexes were established was 1:3.1, possibly reflecting the small proportion of pectinid shells and the absence of flat mollusc-derived plates as substrata among the multispecies domes studied. In contrast with single-species domes, correlation of substratum height with maximum diameter is fairly good (r = 0.719) whereas that between substratum diameter and colony diameter remains poor (r = 0.192).

Of the 75 multispecies domes studied, three had their upper surfaces and 26 their undersurfaces obscured by adherent sediment. On average, 44% of the undersurface area of multispecies domes was occupied by the substratum on which the colony initially grew before spreading laterally with a free epitheca.
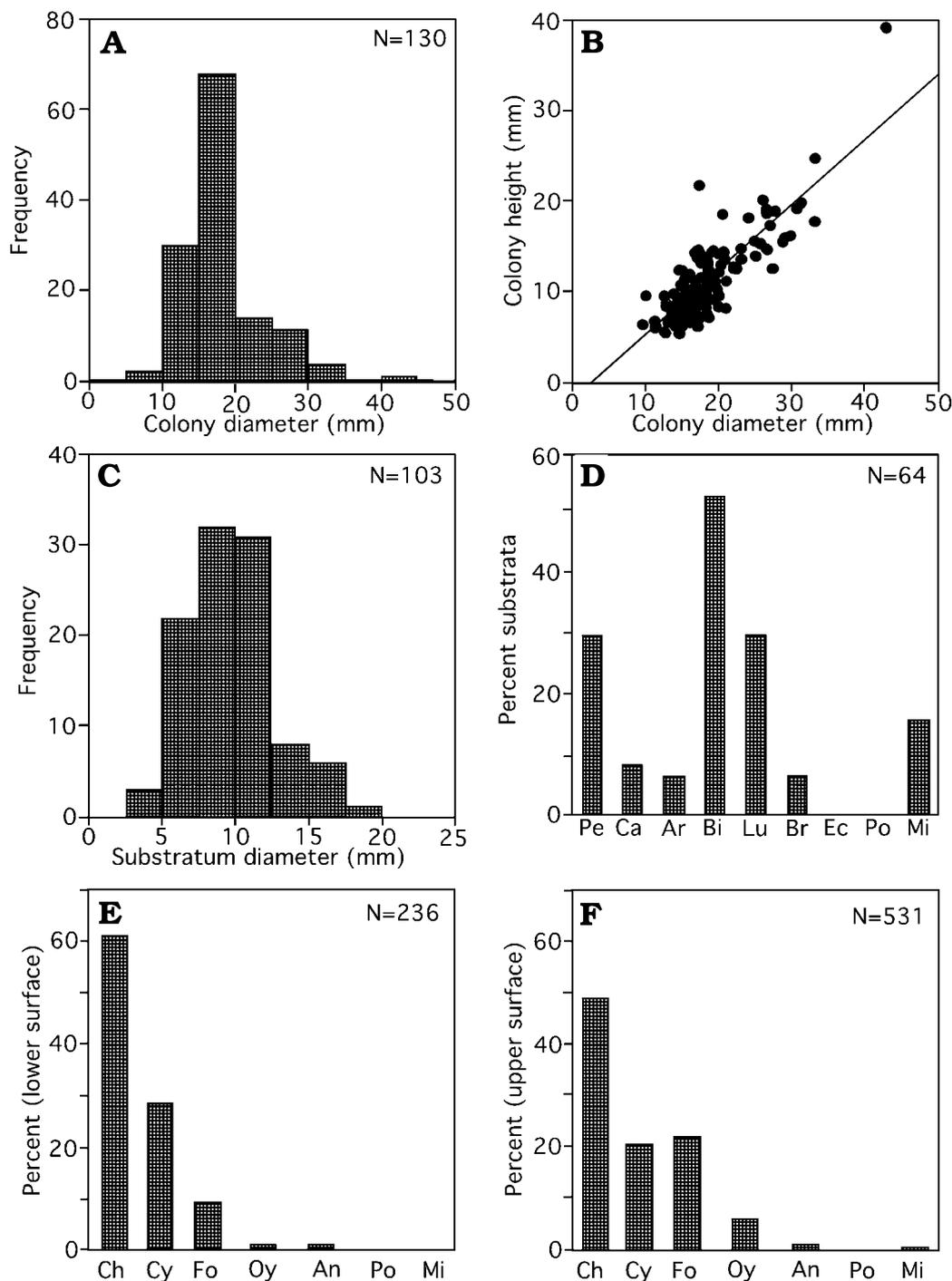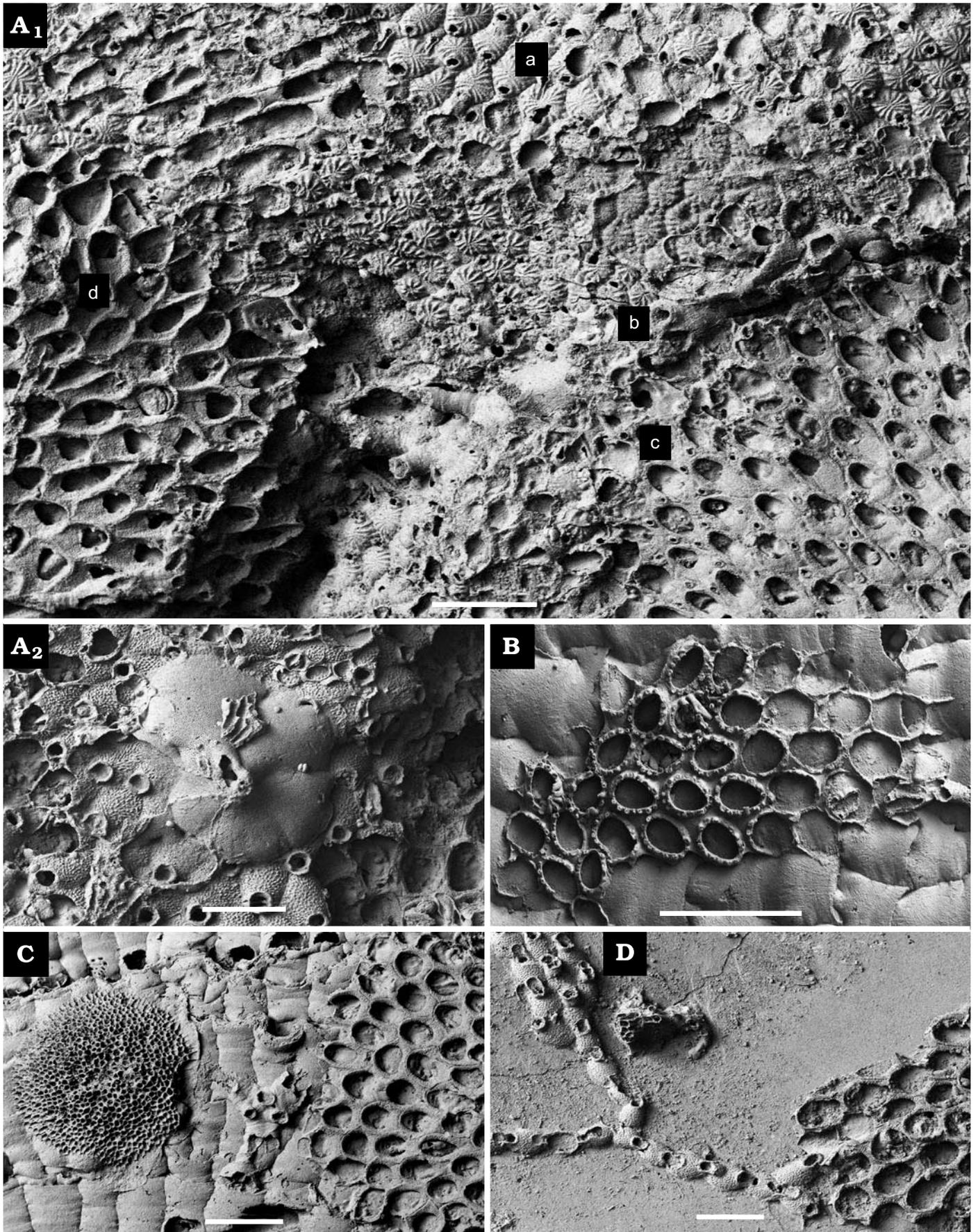
Fig. 5. *Osthimosia glomerata*. **A**. Distribution of colony diameters. **B**. Regression of colony height on colony diameter; $Y = 0.715\overline{X} - 1.579$ mm. **C**. Distribution of substratum diameters. **D**. Proportion of types of substrata on which colonies were established. **E**. Frequency distribution of encrusting organisms on lower surface. **F**. Frequency distribution of encrusting organisms on upper surface. Abbreviations: An, annelids (serpulids); Ar, *Arca* sp.; Bi, other bivalves; Br, bryozoan fragments; Ca, *Cardium* sp.; Ch, cheilostomes; Cy, cyclostomes; Ec, echinoid fragments; Fo, foraminiferans; Lu, *Lunulites* sp.; Mi, miscellaneous; Oy, oysters; Pe, pectinid bivalves, probably all *Chlamys* spp.; Po, poriferans.

By definition, multispecies domes are constructed by recruitment of bryozoan colonies onto the upper surface. Therefore, bryozoans were not counted among the upper-surface encrusters. Non-bryozoan encrusters were found on 65% (47/72) of upper surfaces but only 12% (6/49) of under-surfaces. Including bryozoans, 81% (40/49) of undersurfaces

were fouled by 122 encrusters, for an average of one per 75 mm².

The same groups of organisms encrusted multispecies domes as grew on domes constructed by single bryozoan colonies (Fig. 7F, E). Cheilostome bryozoans, followed by cyclostome bryozoans, were the most abundant organisms attached
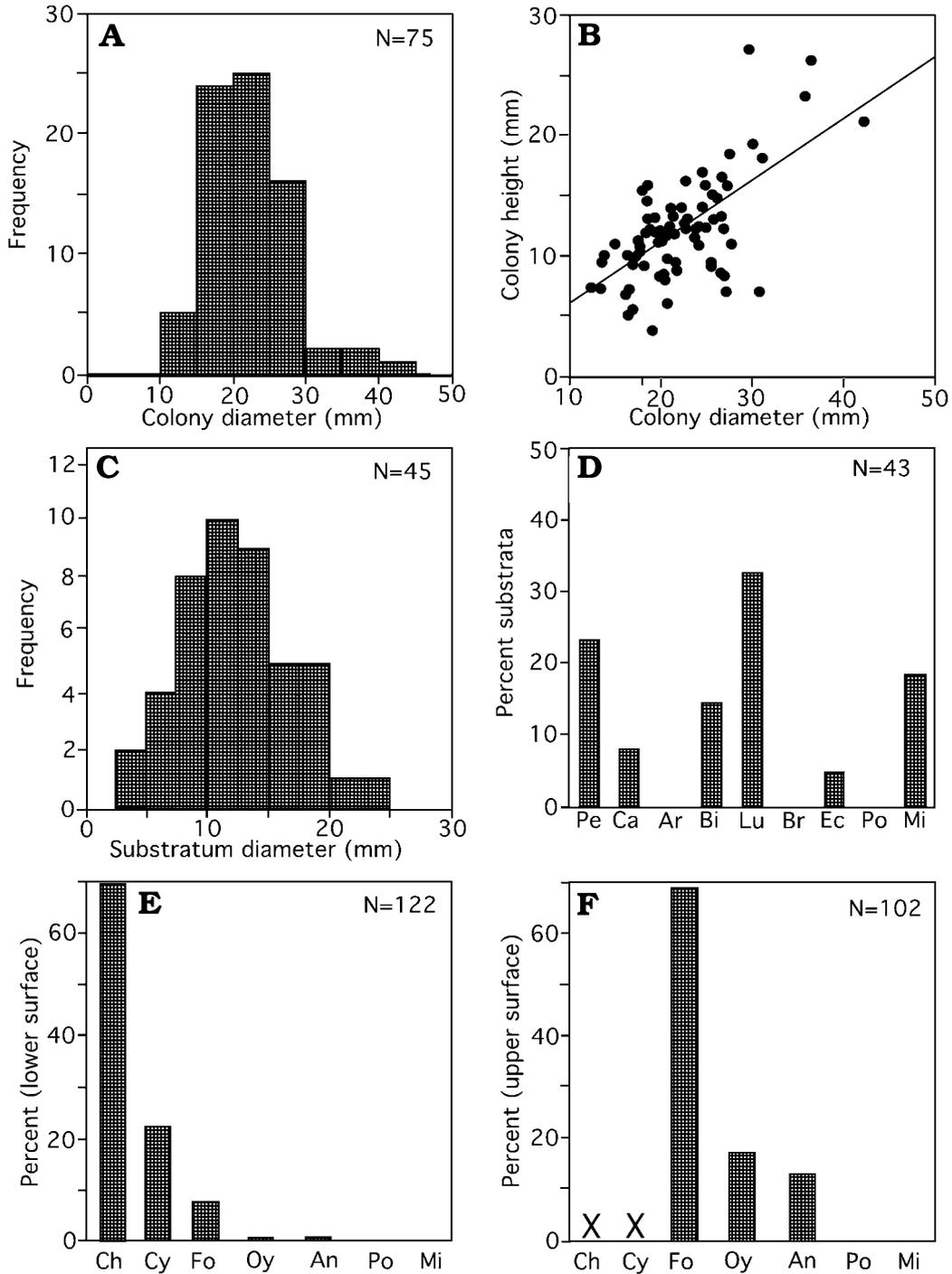
Fig. 7. Multispecies domes. **A**. Distribution of dome diameters. **B**. Regression of colony height on colony diameter; $Y = 0.512\overline{X} + 0.927$ mm. **C**. Distribution of substratum diameters. **D**. Proportion of types of substrata on which colonies were established; see Fig. 3D for identifying abbreviations. **E**. Frequency distribution of encrusting organisms on lower surface. **F**. Frequency distribution of non-bryozoan encrusting organisms on upper surface. Abbreviations: An, annelids (serpulids); Ar, *Arca* sp.; Bi, other bivalves; Br, bryozoan fragments; Ca, *Cardium* sp.; Ch, cheilostomes; Cy, cyclostomes; Ec, echinoid fragments; Fo, foraminiferans; Lu, *Lunulites* sp.; Mi, miscellaneous; Oy, oysters; Pe, pectinid bivalves, probably all *Chlamys* spp.; Po, poriferans.

← Fig. 6. **A**. Upper surface of multispecies dome; NHM BZ4969. A_1. Taxa are a) *Puellina* cf. *P. carolinensis* (Gabb and Horn, 1862); b) *Proboscina* cf. *P. clavatula* Canu and Bassler, 1920; c) *Dacryonella octonaria* Canu and Bassler, 1920; d) *Rectonychocella* sp. A_2. Foraminiferan *Carpenteria* sp. (identified by Dr J.E.P. Whittaker). **B–D**. Bryozoans encrusting undersides of domes. **B**. *Membraniporella* sp. on undersurface of *P. collum*; NHM BZ4965. **C**. Cyclostomes "*Lichenopora verrucosa* Phillippi" of Canu and Bassler (1920) (left) and *Proboscina* sp. (center) and the cheilostome *Ogivalina eximipora* Canu and Bassler, 1917 (right) on the undersurface of *P. collum*; NHM BZ4974. **D**. Unidentified cyclostome (center), uniserial to pluriserial runner-like cheilostome (left), and sheet cheilostome (right) on undersurface of mollusc shell fragment on which a colony of *P. collum* grew; NHM BZ4975. Scale bar in B 500 μm; all others 1000 μm.

to lower surfaces. Foraminifera, oysters and serpulids recruited in about the same proportions relative to one another on both upper and lower surfaces.

Discussion

Occurrence.—Facies distribution of the three types of domal bryozoans in the Castle Hayne Formation is unknown, because all were collected from quarry spoil material. This spoil apparently derived entirely from sequence 3 of the Castle Hayne Formation, and the predominant facies within the quarries from which collections were made are bryozoan, mollusc, and sponge biomicrites and biomicrudites (Harris et al., 1986). Where sediment adhered to specimens, it was in all cases a mixture of sand–sized skeletal grains between which mud had infiltrated ("biomicrudite"), suggesting an environment of fluctuating low to moderate kinetic energy.

Patchiness of occurrence is suggested by unequal representation of taxa and dome sizes in collections made at different times and places. Older collections from the Ideal Quarry have a high proportion of *Osthimosia glomerata*, which is relatively less common in more recent collections and is almost absent in collections from the Rocky Point Quarry. The anomalously large colonies—those that have diameters greater than 1.5X the median—were derived from a relatively small area in the Ideal Quarry during the earlier years of collection. Absence of very large domes from more recent collections may reflect localized occurrence in facies infrequently encountered in recent years during the mining operations or may be due entirely or partially to progressively more intense scouring by an increasing number of fossil collectors.

Growth of the domes.—*Parasmittina collum* colonies became established on shell or skeletal fragment substrata as encrusting sheets that were initially one zooid thick, spread radially by zooidal budding at the outer colony edge, and were firmly cemented to the substratum. In addition, local eruptive budding of zooids (pseudoancestrulae) established new points of growth on the pre-existing surface of the colony, from which single-zooid-thick subcolonies spread laterally by zooidal budding, each firmly cemented to the underlying surface and reaching 8.5±2.1 mm diameter (N = 25). Where growing margins of subcolonies met, the converging margins coalesced, generating a boundary of variably shaped autozooids and some kenozooids (Fig. 2A$_2$). Subcolonies that began close to the colony perimeter extended laterally beyond the underlying former edge of the colony, expanding the diameter of the colony either by further encrusting the initial substratum (Fig. 2B) or, where the edge of the substratum was reached, by growing beyond it as a single layer of zooids bounded on the underside by an epitheca, which is an unattached basal exterior wall (Figs. 1B, C$_2$, 2C). As a result, the undersurface of colonies has, in addition to the fine-scale growth banding typical of exterior walls that were free-grow-

ing rather than attached to a substratum, broadly arcuate growth checks that mark the cessation of growth of individual subcolonies followed by expansion beyond by younger subcolonies.

The early ontogeny of *Osthimosia glomerata* colonies is unknown. However, at some stage relatively early in their growth, colonies began to grow largely by frontal budding. Once they extended beyond the original substratum growth was exclusively by frontal budding. Increase in colony diameter and colony height are closely correlated, and are related by the formula

$$Y = 0.715X - 1.579,$$

where Y represents colony height and X represents colony diameter. However, the point of origin is near the center of the basal diameter in hemispherical domal colonies, so comparison of directional growth rates should be based on rate of increase in colony height and rate of increase of the colony's basal radius. Therefore, comparison of the directional growth rates is

$$Y = 0.715(X/0.5) - 1.579, \text{ or}$$
$$Y = 1.430X - 1.579$$

In colonies of *Osthimosia glomerata*, colony height increased by 140% relative to colony radius on average, indicating that frontal budding was more active centrally in colonies than along the perimeter. Similar analysis of the upward and lateral increase in colonies of *Parasmittina collum* shows an increase in height of only 80% the increase in radius, as would be expected from colonies that increase primarily by lateral budding and secondarily by localized frontal eruptive budding.

Where colonies of *Osthimosia glomerata* grew laterally beyond the initial substrata, the undersurface of the colony was occupied by lateral and frontal surfaces of obliquely and downwardly orientated frontally-budded zooids rather than by a basal epitheca. Such a highly textured surface of potentially functioning zooids from which normal or modified lophophores might protrude was quite different from the smoothly textured, static underside of *Parasmittina collum* colonies.

A small percentage of both *Parasmittina collum* and *Osthimosia glomerata* colonies have a shelf generated by abrupt lateral expansion from an area near the centre of the colony upper surface. In the *P. collum* colonies the undersurface of the abruptly expanded region is characterized by a basal epitheca with the same growth pattern as the initial undersurface of the colony. In colonies of *Osthimosia glomerata* the abruptly expanded region is marked by a hip (Fig. 1F) composed of obliquely and downwardly oriented zooids that is similar in lateral profile to the basal perimeter of the colony. Colonies of the two species characterized by such shelves commonly are much thicker than normal colonies and appear as outliers in Figs. 3B and 5B. They are interpreted as colonies in which the original basal perimeter died, possibly by burial in sediment, after which the central surviving portion continued both upward and lateral growth.

Growth of multispecies domes was much more chaotic than was growth of the domes constructed by a single species. Diverse taxa were involved (Fig. 6A$_1$), including species in which the colonies grew as sheets expanding around the entire perimeter by lateral budding, as three-dimensional masses that increased by both lateral budding around the perimeter and by frontal budding across portions of or the entire frontal surface, and also as runners and ribbons that extended laterally by localized lateral budding. Species within multispecies mounds include various anascan and ascophoran cheilostomes as well as cyclostomes. Whereas the domes produced by both *Parasmittina collum* and *Osthimosia glomerata* probably grew either continuously or in some regularly episodic pattern, the multispecies domes may have grown at highly irregular rates, including periods during which nothing was alive, followed by renewed recruitment and lateral growth.

Comparison with growth of other domal bryozoans.— Männil (1961) noted contrasting growth habits of free-lying domal Ordovician trepostome bryozoans that make an interesting comparison with the two contrasting growth habits of *Parasmittina collum*, which involves a spreading basal epitheca, and *Osthimosia glomerata*, which lacks a basal epitheca. Several of the domal Ordovician trepostomes studied by Männil had a basal epitheca, in some of which almost all new zooids were budded basally, along the spreading epitheca, while in others budding occurred across the colony surface, and the most basal zooids were oriented parallel with the base and had one lateral side consisting of the epitheca. These two types of development of free-lying domes have aspects comparable with *P. collum*, which increased its diameter by lateral budding of new zooids but also developed new zooids locally across the colony surface (although by frontal budding rather than by interpolative budding as occurred in trepostomes and many other stenolaemate bryozoans).

In contrast with the taxa which had basal epithecae spreading beyond the original substratum, other domal trepostomes studied by Männil (1961) lacked a basal epitheca but had a peripheral zone of budding from which autozooids curved toward the upper surface and short heterozooids curved down toward the substratum. This is roughly comparable with the growth of *Osthimosia glomerata*, which also lacked a basal epitheca and increased the basal surface by adding frontally budded zooids oriented obliquely or directly down toward the substratum.

However, in contrast with *Osthimosia glomerata* and the generally comparable Ordovician domal colonies with basal heterozooids, most domal bryozoan colonies, from Paleozoic to Recent, have spread by basal epithecae and lateral budding.

Free-living domal bryozoans belonging to four cheilostome species from the Holothurian Bank, N.W. Australia, and the Tsu Sima, Korea Strait, Japan, differed from those described here in having much thinner colonies with more deeply concave under-surfaces (Cook 1965). The convex surfaces of small bivalve shells were the most common substrata (6/10 specimens with visible substrata) followed by lunulitiform bryozoans (4/10 specimens), i.e., substrata similar to those of the domal bryozoans from the Castle Hayne Formation. Growth in the Australian and Japanese specimens was largely by radial budding around the colony edge, although frontal budding was at least locally present in all species. Growth of these species was more similar to that of *Parasmittina collum* than to the almost exclusively frontal budding of *Osthimosia glomerata*.

Distribution of fouling organisms.—Upper surfaces of *Parasmittina collum* domes were less heavily fouled by encrusting organisms than were those of *Osthimosia glomerata* or multispecies domes, having only about half as many encrusters per unit area (Table 1). This difference is not due to the proportion of colonies that were fouled, because about 70% of upper surfaces were encrusted in both species. Two potentially important attributes for development of encrustation on the two species are that they have very different surface textures (*P. collum* is smoother than *O. glomerata*), and *Osthimosia glomerata* produces more spherical colonies, which may have more easily overturned and transported than colonies of *P. collum*. Unfortunately, the lack of precise information on environmental and stratigraphic distribution of the two species hampers determination of the cause of the different density of encrustation of their upper surfaces.

Lower surfaces of Castle Hayne domal bryozoans are fouled on average almost 5 times as densely as upper surfaces (Table 1). The difference may be due partially to burial of live specimens which may have had their undersurfaces fouled by cryptic organisms during life of the colony whereas skeletalized encrusters would have been essentially absent from the upper, feeding surface. Frontal surfaces of living bryozoans usually become fouled only when the colony is senescent and lacks actively feeding zooids (e.g. Palumbi and Jackson 1983). *Parasmittina collum* and *Osthimosia glomerata* both grew by types of budding that continually cover the surface with young zooids, and the smoothly curved frontal surfaces suggest that there were seldom if ever any local senescent regions before death of the entire colony.

However, recruitment restricted to or primarily on the lower surface during life of the colonies is unlikely to be the most important cause of the great difference in density of encrusting organisms on upper and lower surfaces, because about 70% of colonies in both *Parasmittina collum* and *Osthimosia glomerata* were encrusted on the upper surface. This suggests that they spent some time lying on the sea floor after death and before burial, when both surfaces were available for settlement. Many of the encrusters probably settled preferentially in cryptic environments, such as the lower surfaces of the domal bryozoans.

Different distributions of the groups of encrusting organisms suggest different recruitment patterns, with some recruiting preferentially on exposed (upper) surfaces, some recruiting preferentially on cryptic (lower) surfaces, and some showing no clear pattern (Table 1). Oysters recruited preferentially by a factor of four onto the upper surfaces across all

Table 1. Distribution and relative abundance of encrusting organisms attached to dome-shaped bryozoan growths from the Castle Hayne Formation. Area given is in cm^2, and density is given as average number per cm^2. Cheilostome and cyclostome bryozoans on the upper surfaces of multispecies mounds were not counted, and numbers relevant to cheilostomes and cyclostomes are included in parentheses for the combined upper surface data and are based only on records from the surfaces of *Parasmittina collum* and *Osthimosia glomerata* colonies.

	Surface	*Parasmittina collum*	*Osthimosia glomerata*	Multispecies domes	Combined
Number of examined surfaces	upper	73	117	52	242
	lower	67	64	63	194
Area of examined surfaces	upper	919	881	489	2289
	lower	296	125	73	490
Number of fouling cheilostomes	upper	152	262	–	(414)
	lower	440	143	85	668
Density of fouling cheilostomes	upper	0.17	0.30	–	(0.23)
	lower	1.49	1.19	1.16	1.61
Number of fouling cyclostomes	upper	52	111	–	(163)
	lower	210	66	26	302
Density of fouling cyclostomes	upper	0.06	0.13	–	(0.09)
	lower	0.71	0.53	0.36	0.62
Number of fouling forams	upper	39	118	70	227
	lower	28	23	9	60
Density of fouling forams	upper	0.04	0.13	0.14	0.10
	lower	0.09	0.18	0.12	0.12
Number of fouling oysters	upper	43	35	18	96
	lower	4	2	1	7
Density of fouling oysters	upper	0.05	0.04	0.04	0.04
	lower	0.01	0.02	0.01	0.01
Number of fouling serpulids	upper	19	4	14	37
	lower	29	2	1	32
Density of fouling serpulids	upper	0.02	<0.01	0.03	0.02
	lower	0.10	0.02	0.01	0.07
Number of fouling sponges	upper	6	0	0	6
	lower	1	0	0	1
Density of fouling sponges	upper	0.01	0	0	<0.01
	lower	<0.01	0	0	<0.01
Number of other foulers	upper	1	1	0	2
	lower	0	0	0	0
Density of other foulers	upper	<0.01	<0.01	0	<0.01
	lower	0	0	0	0
Total no. of foulers	upper	312	531	–	(843)
	lower	712	236	122	1070
Total density of foulers	upper	0.34	0.60	–	(0.46)
	lower	2.38	1.89	1.64	2.17

three types of bryozoan domes, foraminifera (Fig. 6A$_2$) recruited almost uniformly onto both upper and lower surfaces, serpulids recruited erratically, and both cheilostome and cyclostome bryozoans (Fig. 6B–D) recruited seven times more frequently onto lower than upper surfaces.

Undersurfaces of the domal bryozoans described by Cook (1965) from the Pacific were fouled by 27 invertebrate species. The range and relative abundance of the attached groups is very similar to those on the undersurfaces of domal bryozoans collected from the Castle Hayne Formation and includes cheilostome bryozoans (48%), cyclostome bryozoans (14.5%), bivalves (14.5%), sponges (11%), foraminiferans (4%), hydroids (4%), and serpulid annelids (4%). The most conspicuous differences between the organisms epizoic on the undersides of domes in the Castle Hayne Formation and those from the Pacific reported by Cook (1965) is that several of the bryozoans fouling the underside of the Pacific specimens are erect, whereas very few of those on the undersides of Castle Hayne specimens are erect. This difference probably is related to the greater height available under the Pacific specimens, which commonly had larger diameters than Castle Hayne specimens and thinner, more arched colonies.

The contrast in density of preserved encrusting organisms on the upper surface versus the lower surface of domal bryo-

zoans from the Castle Hayne Formation compares with patterns noted in some previous studies. On shell-substratum islands, bivalves and commonly serpulid annelids tend to grow preferentially on exposed surfaces (e.g. Lescinsky 1993; McKinney 1996), whereas bryozoans in general are more abundant on cryptic surfaces (Harmelin 1977; Schäfer 1991; Ward and Thorpe 1991; Lescinsky 1993; Reguant and Mayoral 1994; McKinney 1996). However, some bryozoans seem to prefer certain surface textures of skeletal substrata (Eggleston 1972; Ward and Thorpe 1989), which may play a role in the greater abundance of some bryozoan species on exposed surfaces.

Encrusting bryozoans that occur more commonly on exposed surfaces generally are cheilostomes that grow to larger colony sizes than the more cryptic encrusting cyclostome and cheilostome species that reach smaller colony sizes (Harmelin 1977; Bishop 1988, 1989; McKinney 2000; McKinney and McKinney 2002). In addition, erect bryozoans tend to grow preferentially on exposed surfaces (Ward and Thorpe 1989; McKinney and McKinney 1993), which reduces the possibility of the colony encountering an obstruction as it grows. This pattern of more robust species occurring on exposed surfaces and more diminutive taxa on cryptic surfaces holds in general for bryozoan species distributions on the Castle Hayne domes, demonstrated in part by cyclostomes being seven times more abundant on undersurfaces of domes in comparison with upper surfaces. Among the cheilostomes, delicate colonies such as those illustrated in Fig. 6B and 6D are prevailingly abundant on undersurfaces of domes, whereas more extensive encrusting sheets and bases of erect colonies predominate on upper surfaces (Fig. 6A$_1$).

Conclusions

Free-lying bryozoan domes in the Castle Hayne Formation were constructed by single colonies of *Parasmittina collum* and *Osthimosia glomerata* or by intergrowths of numerous species. All the bryozoan-constructed domes have a generally similar size and shape, although each type has its own subtly different size and shape characteristics. In addition, each type of dome was constructed differently. Dome-shaped colonies of *P. collum* grew by lateral budding to produce a colony-wide basal epitheca, followed by localized frontal budding that generated centers from which laterally budding subcolonies developed, overlapping the outer colony margin and increasing the dome diameter. Colonies of *O. glomerata* grew exclusively by frontal budding once they reached the margin of the original substratum, so that both the colony thickness and freely-extended diameter were increased only by this single type of budding. Multispecies domes increased largely by recruitment of new bryozoan colonies onto the upper, exposed surface.

Organisms that fouled the domes occurred preferentially on the undersides, probably reflecting larval settlement behaviors, inhibition of settlement by upper live surface of domal bryozoans, or by a combination of these factors. Distributional patterns of fouling encrusters generally resemble patterns described from Recent dome-shaped bryozoans and other substrata that have clearly differentiated exposed and cryptic surfaces. This is particularly well seen in the pattern of encrusting, diminutive bryozoan species preferentially occurring on the cryptic undersurfaces of the domes, with more robust encrusting and erect taxa surviving preferentially on the exposed surfaces.

Acknowledgements

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