POLYPIDE MORPHOLOGY AND FEEDING BEHAVIOR IN MARINE ECTOPROCTS

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ABSTRACT

Observations on living colonies of 56 species of marine bryozoans from Florida and Panama have shown that these organisms possess a variety of morphological and behavioral adaptations related to feeding activities. In the species studied mean lophophore diameter varies from 187 to 1,012 μm, mouth size from 15 to 91 μm, and tentacle number from 8 to 31. Polypide morphology, particularly introvert length and lophophore symmetry, also varies from species to species, and this variation is linked to behavioral strategy. With respect to individual polypide behavior species can range from passive filterers (e.g. *Crisia elongata*), to tentacle feeders (e.g. *Pasythea tulipifera*), to cage-captors (e.g. *Bugula neritina*), to particle jugglers (e.g. *Sundanella sibogae*). Colony-wide patterns of morphology and behavior also reflect various methods of dealing with water currents. These range from weakly integrated patterns characterized by separation and a high degree of functional independence of individual polypides to highly integrated patterns in which both skeletal morphology and polypide orientation serve to enhance and/or channel feeding currents. Similar strategies have evolved in all three orders of marine bryozoans, apparently in response to the common problem of changing the characteristics of water flow in the immediate vicinity of the colony so that food particles may be extracted.

Behavior is not a word one commonly associates with colonial marine organisms, particularly those as sessile and apparently inactive as ectoprocts. Seeing the calcified crusts or seaweed-like festoons of their colonies among the rocks of breakwaters or on the undersurfaces of platy corals, it is hard to imagine writing of any of them as, "remarkable among an active tribe for the vivacity of its movements," or, "A colony in full health and vigor affords a rare display of delicate structure, vivacious movement and graceful form" (Hincks, 1880). Yet to 19th century naturalists, enchanted by the newly discovered miniature world of the tide-pool, the ectoprocts were indeed active creatures.

In most species feeding activities of individual zooids are limited to movements of the polypide: protrusion, retraction, expansion and bending of the lophophore, and associated actions of the ciliated tentacles. The basic features of the anatomy of the ectoproct polypide were understood by the early 19th century. Farre (1837) was able to make detailed and accurate observations on the structure of the polypide in several species, noting size and activity of the tentacles, distribution of cilia and "bristles," the form of various portions of the gut, the fate of food particles and the action of swallowing. Hincks (1880) included in his survey of the British marine Polyzoa much information indicating his understanding of individual morphology and behavior, including the presence of sensory cells on the tentacles, though most of this information is buried in species descriptions. Yet the comparative aspects of polypide morphology have not received attention, and, indeed, examination of later 19th and 20th century literature shows a gradual loss of information on polypide structure and function.

Although the 19th century knowledge of individual (polypide) behavior was never codified, it is apparent from species descriptions and illustrations (Grant, 1827; Lister, 1834; Farre, 1837; Hincks, 1880, and

others) that individual behavior has been observed. Even the process of feeding was studied (Grant, 1827; Farre, 1837; Hincks, 1880), and, while the language in which it was described is overly metaphorical for present-day scientific tastes, the observations themselves are generally correct. These authors noted both that the current generated by the cilia of the tentacles acts to "create a very maelstrom in the water, which sweeps the passing animalcule or the floating food particle toward the central mouth" (Hincks, 1880, p. xiv), and that the tentacles themselves might play an important role in feeding: "The tentacula are exquisitely sensible, and we frequently observe them either singly or all at once, striking in their extremities to the centre of the bell-shaped cavity, when any minute floating body comes in contact with them" (Grant, 1827, p. 114).

While individual polypide behavior was understood by those early workers, the phenomena of colony-wide patterns in feeding behavior do not seem to have been discovered until much more recently. Banta, McKinney, and Zimmer (1974) showed the presence of excurrent chimneys, based on polypide morphology and orientation in *Membranipora membranacea* and speculated on the possible function of monticules and other skeletal modifications in fossil and living ectoprocts in providing effective water circulation throughout colonies.

In reviewing the feeding biology of marine ectoprocts (Winston, in press) I became aware of the limited knowledge, the controversies, and the possibilities, regarding polypide morphology and feeding behavior in these animals. The research reported here was started in order to learn (1) the range and variation of morphology possible in the gymnolaemate polypide, with specific reference to variation in lophophore shape, and in the positioning of possible sensory structures, (2) what different types of behavior patterns were possible for individual polypides and for colonies, and (3) in what ways these behavior patterns could be related to parameters of morphology, ecology and taxonomy. This paper covers qualitative observations on morphology and behavior. The quantitative relationships between them will be explored in a future publication (Winston, in prep.).

Materials and Methods

Ectoprocts were collected in various subtropical and tropical habitats: in Florida, from estuarine grassbeds, fouling panels, breakwaters, and intertidal beachrock ledges, in Panama, from coral reef and intertidal and subtidal rocky areas. No attempt was made to collect all the ectoprocts from any one habitat, rather the emphasis was on collecting as many different kinds of colonies and as many representatives of the different groups, cheilostomes, cyclostomes, and ctenostomes, as possible.

Animals were taken to the laboratory where they were observed and measured in seawater under the dissecting microscope. Most observations were made as soon as possible after collection, as the behavior of many species changes markedly within a few hours after being collected. Some species could be kept in aquaria without harm, and these were maintained and fed with *Dunaliella* or *Isochrysis*.

Because there was so little information available on the ways in which polypides behave, the first few weeks of the project were spent in making detailed observations on a variety of species in order to learn what behavioral characters occurred and how they could be combined in a data sheet that could be used with other species. Table 1 summarizes the characteristics for each of 56 species of marine ectoprocts from Florida and Panama studied. The analysis for each species included characters of polypide morphology: shape of the lophophore, shape of the mouth, length of the introvert; individual behavior: tentacle flicking activity, other types of individual actions, particle rejection mechanisms; and colony level behavior: relative amount of time polypides remained expanded, level of behavioral integration,

Table 1. Parameters of polypide morphology and feeding behavior of 56 species of marine ectoprocts

SPECIES	POLYPIDE MORPHOLOGY							BEHAVIOR				
	Mean Lophophore Diam μm	Mean Tentacle Length μm	Mean Tentacle Number	Lophophore Shape	Mean Mouth Diam μm	Mouth Shape	Introvert Length	Tentacle Flicking Activity	Other Individual Actions	Scanning Behavior	Type of Colony Behavior	Colony Currents
1. *Acverrillia armata* (1)	264	344	8	BT	29	R	M	M	—	MS	1	W
2. *Alcyonidium polyoum* (1)	331	262	14	ET	25	ET	L	A	F,MC,AvR	MS	3	M
3. *Alcyonidium polypylum* (1)	523	545	15	ASc	41	ET	L	M	F,AvR	LS	3	S
4. *Amathia alternata* (1)	302	300	8	ET	26	R	M	M	AvR	MS	1,2	W
5. *Anguinella palmata* (1)	205	124	10	ET	18	R	S	M	—	MS	2	W
6. *Beania hirtissima* (1)	520	551	18	ET	32	ET	L	H	—	MS	3	M
7. *Beania intermedia* (1)	657	630	26	ET	65	ET	L	H	MC,AvR	MS	1	W
8. *Bowerbankia gracilis* (1)	382	315	8	ET	19	R	L	A	MC	MS	1	W
9. *Bowerbankia* (Indian River species) (1)	751	686	8	ET	42	ET	L	A	—	MS	1	W
10. *Bowerbankia imbricata* (1)	246	211	10	ET	22	R	L	A	—	MS	1	W
11. *Bugula neritina* (1)	764	616	23	ET	74	ET	M	H	F,MC,CC,AvR	VS	2	S
12. *Bugula stolonifera* (1)	441	447	14	AOT	49	ET	M	M	AvR,W	VS	2	S
13. *Bugula turrita* (1)	393	322	14	AOT	38	ET	M	H	MC,CC,AvR	VS	2	S
14. *Canda simplex* (2)	451	420	16	AOT	30	R	M	H	F,MC	VS	2	S
15. *Caulibugula dendrograpta* (2)	407	428	12	AOT	47	ET	S	M	AvR	VS	2	S
16. *Caulibugula pearsei* (1)	277	271	12	AOT	48	ET	M	M	MC,AvR	VS	2	M
17. *Celleporaria albirostris* (2)	631	578	18	AOT	46	ET	L	H	AvR,W,FLD	LS	3,6,7	S
18. *Celleporina hassalli* (1)	373	459	13	SSc	35	R	M	A	F,MC,FLD	LS	5	M
19. *Chlidonia pyriformis* (2)	187	169	9	ET	16	R	S	H	MC	O	2	W
20. *Conopeum seurati* (1)	621	444	15	SSc	31	OR	L	A	—	MS	3	S

Table 1. (Continued)

SPECIES	POLYPIDE MORPHOLOGY							BEHAVIOR				
	Mean Lophophore Diam μm	Mean Tentacle Length μm	Mean Tentacle Number	Lophophore Shape	Mean Mouth Diam μm	Mouth Shape	Introvert Length	Tentacle Flicking Activity	Other Individual Actions	Scanning Behavior	Type of Colony Behavior	Colony Currents
21. Conopeum tenuissimum (1)	475	339	12	ET	26	OR	L	A	—	MS	3	S
22. Crassimarginatella tincta (1)	326	268	12	SSc	28	R	L	A	F	MS	3,5	S
23. Crisia elongata (1)	266	191	8	ET	18	R	N	M	—	O	2	W
24. Crisia (Pacific sp.) (3)	207	166	8	ET	15	R	S	M	—	O	2	W
25. Discoporella umbellata depressa (1)	453	351	13	ET	36	R	L	H	F,MC,FLD	LS	3,6,7	S
26. Electra bellula (2)	255	203	10	ET	17	R	M	H	F	MS	3	M
27. Gemelliporidra multilamellosa (2)	850	780	24	ET	69	ET(L)	M	H	F,MC	O	6	S
28. Hippoporina verrilli (1)	428	308	12	SOT	29	OR	M	M	F,MC	O	4	S
29. Hippothoa hyalina (1)	253	194	11	ET	23	R	M	—	—	O	—	—
30. Lichenopora buskiana (2)	345	349	8	BT	20	R	N	H	—	O	6	S
31. Lichenopora intricata (3)	319	262	8	BT	20	R	N	M	—	O	6	S
32. Margaretta buski (2)	712	666	23	ET	47	R	S	M	F	VS	2,3	M
33. Membranipora arborescens (3)	295	211	10	ET	29	OR	M	A	MC	MS	3	S
34. Membranipora tenuis (1)	275	237	10	ET	26	R	M	M	MC	MS	3	S
35. Membranipora tuberculata (1)	478	385	15	SOT	28	OR	M	A	F	O	4	S
36. Nolella stipata (1)	616	575	17	ET	36	R	S	A	F,MC	MS	1,3	W
37. Parasmittina nitida (1)	419	293	13	SOT	27	R	M	M	AvR	LS	4	S
38. Pasythea tulipifera (1)	217	167	10	ET	16	R	S	H	—	VS	2	M
39. "Plagioecia" sp. (3)	253	206	10	OT	25	R	N	M	MC	O	6	S
40. Reteporellina evelinae (2)	419	418	12	BT	25	R	S	A	AvR,W	LS	2,7	S

Table 1. (Continued)

SPECIES	POLYPIDE MORPHOLOGY							BEHAVIOR				
	Mean Lophophore Diam μm	Mean Tentacle Length μm	Mean Tentacle Number	Lophophore Shape	Mean Mouth Diam μm	Mouth Shape	Introvert Length	Tentacle Flicking Activity	Other Individual Actions	Scanning Behavior	Type of Colony Behavior	Colony Currents
41. "Rhynchozoon" sp. (2)	763	688	17	OT	35	R	M	L	—	O	4,5	—
42. Schizoporella floridana (1)	507	395	17	OT	44	ET	M	—	F,W	O	4	S
43. Scrupocellaria regularis (1)	464	357	13	OT	38	—	S	M	AvR	O	2	S
44. Steganoporella magnilabris (2)	1,012	814	25	SOT	89	ET	L	H	F	MS	3,4	M
45. Sundanella sibogae (1)	820	859	31	ET	82	ET	L	H	MC,AvR	MS	1	W
46. Synnotum aegyptiacum (1)	231	164	10	ET	18	R	S	M	MC,W	VS	2	W
47. Terebripora sp. (3)	209	173	8	ET	16	R	M	M	—	MS	1,3	W
48. Tetraplaria dichotoma (2)	495	484	17	ET	37	R	L	A	—	MS	2	M
49. Thalamoporella falcifera (1)	460	385	16	ET	40	OR	M	H	MC	MS	3	W
50. Trematooecia aviculifera (2)	757	821	18	OT	50	ET	M	H	MC	O	5,7	S
51. Trematooecia turrita (2)	767	866	19	SSc	48	ET	L	H	F,MC	LS	4,5	S
52. "Tubulipora" sp. (3)	618	538	16	OT	42	OR	N	M	AvR,W	O	6	M
53. Victorella pavida (1)	369	280	8	BT	19	R	L	M	—	MS	1,3	W
54. Vittaticella contei (1)	253	202	12	ET	18	R	S	M	MC	O	2	W
55. Watersipora subovoidea (1)	662	589	21	ET	63	ET	L	A	—	O	3	M
56. Zoobotryon verticillatum (1)	320	278	8	ET	29	R	M	A	F,AvR	MS	1,2	M

KEY TO TABLE 1. *Lophophore Shape*: ET = equi-tentacled, SOT = some polypides with obliquely truncate lophophores, AOT = all polypides with obliquely truncate lophophores, SSc = some polypides with scalloped lophophores, ASc = all polypides with scalloped lophophores. BT = bent-tentacled (campylonemidan). *Mouth Shape*: R = round, OR = round to ovoid, ET = elongate to triangular. *Introvert Length*: N = none, S = short, M = medium, L = long. *Tentacle Flicking Activity*: L = little activity, M = moderate degree of activity, A = high degree of activity. H = high degree of activity and range of activity greater. *Other Individual Actions*: F = fanning, MC = makes cage, no prey observed, CC = cage capture, AvR = avoidance retraction, W = writhing, FLD = flattens lophophore to disk. *Scanning Behavior*: O = not present, MS = multi-directional scanning, VS = chiefly vertical scanning, LS = chiefly lateral scanning. *Type of Colony Behavior*: 1 = behavior individualized; 2 = colony skeleton separates polypides; 3 = polypides form temporary clusters, not reflected in skeletal morphology; 4 = polypides form fixed clusters, not reflected in skeletal morphology; 5 = polypides form fixed clusters, reflected in skeletal morphology, skeletal patterning irregular; 6 = polypides form fixed clusters, skeletal patterning regular; 7 = polypides show trend toward unified behavior. *Colony Currents*: W = weak, M = moderate, S = strong.
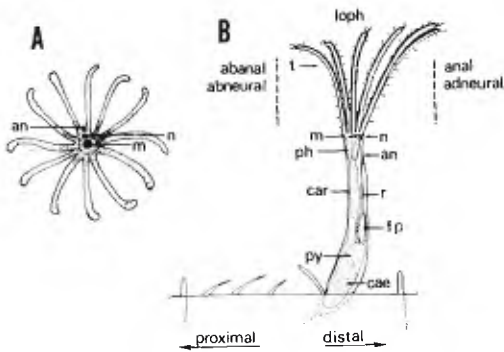
Figure 1. Diagram of a gymnolaemate polypide —showing orientation and main features (Refer to text for explanation of abbreviations).

and strength of colony currents. Measurements were also made of several skeletal characters: length and width of zooecium, length and width of orifice, as well as the most important polypide characters: number of tentacles, lophophore diameter, tentacle length, mouth diameter (greatest length), and tentacle width so that a quantitative analysis of the possible relationships between skeletal, morphological, and behavioral characters could be carried out (Winston, in prep.). The observations on morphology and behavior were documented with slides of polypide morphology and 16-mm microcinematography of polypide activity.

POLYPIDE MORPHOLOGY

The most important parameters describing polypide morphology are illustrated by Figure 1. Figure 1A shows the arrangement of the lophophore as viewed from above. The tentacles are arranged in a circle around the mouth (m), with the anus (an) outside and below the funnel formed by the tentacles. In side view (Fig. 1B) the complete polypide (lophophore, tentacles, sheath-introvert, digestive tract, and muscular and nervous tissue, including the nerve ganglion (n) associated with it) can be seen.

The tentacles comprising the lophophore are hollow tubes, each with an epidermis separated from the peritoneum by a layer of connective tissue containing collagen fibers, and with a lumen filled with coelomic fluid (Lutaud, 1955; Smith, 1973; Gordon, 1974). By various means, in ctenostomes, cheilostomes and cyclostomes, muscle action upon flexible portions of the zooid wall yields a change in hydrostatic pressure resulting in protrusion or retraction of the lophophore. When the lophophore is retracted it is enclosed in a tentacle sheath, which when expanded functions as an introvert.

The gut in bryozoans (reviewed by Winston, in press) is U-shaped, beginning with a ciliated pharynx (ph), an esophageal or cardial region (car), in some ctenostomes modified into a gizzard. The stomach consists of a sac-like caecum (cae) and a ciliated pyloric region (py) where food is processed in a whirling mass. This is divided by a constriction from the rectal region (r) where digested food remains are formed into fecal pellets (fp) to be excreted through the anus (an). The shape of the gut also varies from species to species and group to group (Silén, 1944), and seems primarily a function of the shape of the zooid, though little comparative study has been made.

Lophophore Shape and
Tentacle Orientation

The gymnolaemate and stenolaemate lophophore is generally thought of as circular (in cross-section or oral view) in contrast with the horse-shoe or spiral shaped lophophores of phylactolaemate ectoprocts, phoronids, and brachiopods. Yet, while a simple circular lophophore is common in these groups within the restrictions imposed by their small size, the morphology of the lophophore has undergone modifications and elaborations with respect to size, number of tentacles, lophophore shape and tentacle positioning.

Equi-tentacled Lophophores

Lophophores in the form of circular funnels with all tentacles of equal length are

common in all three groups of marine ecto-procts: ctenostomes, cheilostomes, and cyclostomes. Most species with small lophophores are of this simplest type, though even these can be quite different in appearance, depending on whether the tentacles are held moderately close together (Fig. 2A), or spread far apart (Fig. 2B). Species with large lophophores may also be of this type. In some large species the numerous long tentacles, held very straight, give the lophophore a crowded narrow appearance (Fig. 2C). In other species the tentacles appear more flexible and bend outward at the free ends giving the lophophore a bell-like shape (Fig. 2D).

Obliquely Truncate Lophophores

It was noted by Farre (1837) that some polypides of *Alcyonidium gelatinosum* have tentacles much shorter on one side of the lophophore than on the other. Hincks (1880) also noted a dissimilarity of tentacle length in *Electra pilosa*: "Very commonly those on one side are inferior in height to those on the other, and the tentacular bell is obliquely truncate above." Recently Gordon (1974) has pointed out this same phenomenon in *Cryptosula pallasiana*, but no one has attempted to explore its functional or taxonomic significance. As can be seen from Figure 3 the anal (distal) tentacles are the longest and the abanal (proximal) tentacles are the shortest, with the intermediate tentacles showing a smooth gradation in height. Because of the flexibility of the introvert, however, the polypide may be twisted on expansion so that the longest tentacles may appear to be oriented in various other directions.

The present study has shown that obliquely truncate lophophores occur in two patterns (Table 1). Species with erect branching colonies such as *Bugula stolonifera* or *Caulibugula armata*, commonly have all polypides of the colony with obliquely truncate lophophores (Fig. 3A). In such species, in which the individual polypide has little flexibility, but all polypides act in
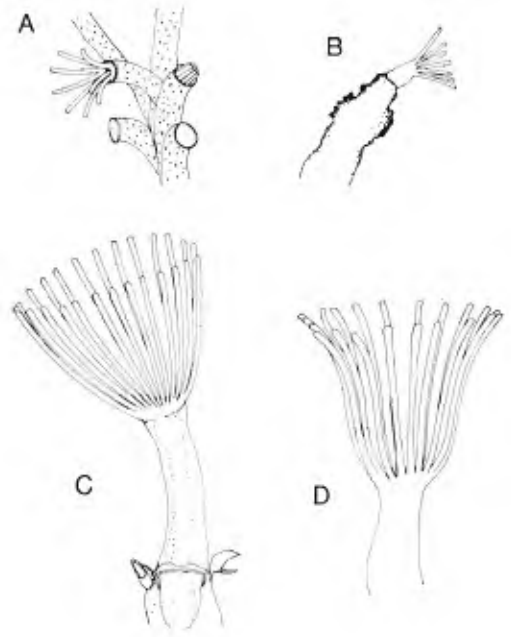

Figure 2. Examples of equi-tentacled lophophores: A. *Crisia* sp., B. *Anguinella palmata*, C. *Beania intermedia*, D. *Watersipora subovoidea*.

unison to produce a very strong current flow through the colony, the shape of the lophopore appears suited to increasing current production.

In other colonies, polypides may have lophophores equi-tentacled or obliquely truncate depending on their position with respect to incurrent cells. In colonies in which the polypides form fixed clusters, either of the skeletally or non-skeletally reflected type (see behavior section), the polypides in the center of the incurrent cell are equi-tentacled while those toward the outside of the cell have obliquely truncate lophophores with the longer (anal) tentacles being toward the outer margin of the incurrent cell, while the excurrent chimneys (Banta, McKinney, and Zimmer, 1974) are fringed with polypides having extremely long anal tentacles (Fig. 3B). In many of these species the longest tentacles may be bent in at the tips, while the abanal tentacles bend out, giving the lophophore a decided scoop
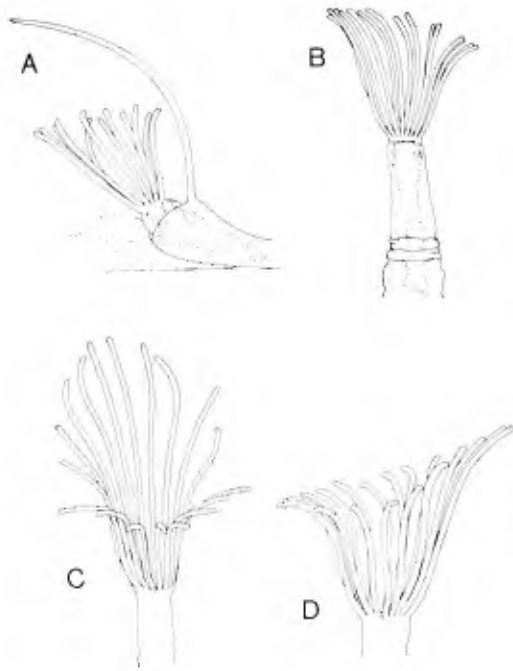
Figure 3. Examples of obliquely truncate and scalloped lophophores: A. *Bugula stolonifera* or *Caulibugula pearsei*, B. *Alyconidium polypylum*, C. *Celleporaria albirostris*, D. *Trematooecia turrita*.

shape (Fig. 3C). In such species, viewed from above, the tentacle tips form an oval or triangle (apex anal, base abanal), rather than a circle, so that the lophophore approaches a bilateral symmetry.

Scalloped Lophophores

Other elaborations of lophophore shape are possible. Several species have been observed (e.g. *Celleporaria albirostris*) in which the tentacles of the obliquely truncate lophophore do not grade evenly toward the ventral side, but by variation in length and amount of bending of the tips, form a scalloped margin to the lophophore (Fig. 3D). The functional significance of this shape is unknown, but as it occurred in a species which appeared to have reached a high level of behavioral integration, it probably plays

some role in increasing the efficiency of current channelling. It also indicates that there may be even more elaborate patterns that have not yet been observed.

Bent-tentacled Lophophores

One of the most important observations made by Hincks (1880) was that in the lophophores of several species of ctenostome ectoprocts two tentacles were consistently bent away from each other (campylonemidan). Unfortunately, Hincks used the campylonemidan lophophore structure as the basis for his classification of the ctenostomes, and when this classification was discarded on various grounds, his observations on campylonemidan symmetry were also discarded. Later authors (Kraepelin, 1887; Loppens, 1908) questioned its existence and Hyman (1959) did not even include the term.

But, although possession of a campylonemidan lophophore did not provide a good basis for ctenostome classification, Hincks' observations of the peculiar lophophore structure of some members of this group, *Valkeria uva*, *Valkeria tremula*, and *Victorella pavida* are valid, although he believed that the two everted tentacles were anal while in all the specimens I have examined they are abanal. Like the other lophophore shapes, the significance of the campylonemidan lophophore appears more functional than taxonomic. In the ctenostomes it occurs at least in *Victorella* (suborder Carnosa), *Valkeria* and *Aeverrillia* (Fig. 4A) (Suborder Stolenifera), all delicate creeping forms. In the cheilostomes, it is well developed in at least one species of the Sertellidae (Fig. 4C), *Reteporellina evelinae*, a group characterized by a rigid branching or fenestrate colony form in which both zooid skeletons and polypides seem aligned to produce the most effective current flow through the colony (Fig. 13B). The campylonemidan trend has also occurred in the lunulitiform cheilostome, *Discoporella umbellata depressa*, whose highly

integrated colonies are free-living on sandy bottoms. This type of lophophore is found in cyclostomes, too, being particularly pronounced in species of *Lichenopora* (e.g. *L. buskiana*, *L. intricata*) in which the zooids are arranged one above the other in a column, with a channel between and a hollow center to the colony or sub-colony, so that truly colony-wide current flow obtains. Thus, similar lophophore conformations have evolved in all three orders of marine bryozoans, apparently in response to the need to more efficiently channel feeding currents.

Figure 4. Examples of bent-tentacled (campylonemidan) lophophores: A. *Aeverrillia armata*, B. *Lichenopora buskiana*, C. *Reteporellina evelinae*.

Introvert Length

The length and flexibility of the introvert region supporting the expanded lophophore crown is an important determinant of the type of behavior possible to the polypide. The amount of introvert protruded from the zooid can range from none (Fig. 2A) in cyclostomes, to short (Fig. 2B), to moderate (Fig. 3A), to long (Fig. 1, Fig. 3C, D), in which case most of the gut can be seen within the introvert. In general, a very short introvert means a greater restriction in the degree of rotation afforded to the lophophore crown, but this depends also on the structure of the colony and other aspects of behavior (see behavior section).

Lophophore Dimensions
Tentacle Number

The number of tentacles in marine bryozoans varies from a minimum of eight to a maximum of 30 or more. Tentacle number is related both to taxonomic position (Winston, *in press*, for review) and to polypide size. Of the species examined, 20 (eight ctenostomes, six cheilostomes and six cyclostomes) had mean tentacle numbers between eight and ten. In two ctenostomes and 16 cheilostomes mean tentacle number was between 11 and 15, while in one cyclostome, one ctenostome and nine cheilostomes it was between 16 and 20. Six species (all cheilostomes) had mean tentacle number
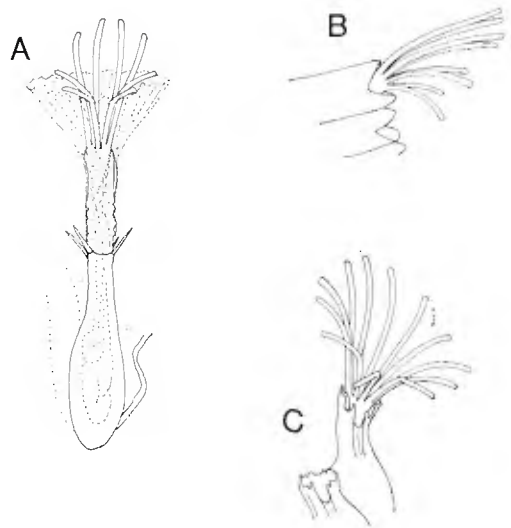
counts between 21 and 30, but the species with the highest tentacle number was a ctenostome *Sundanella sibogae* (mean tentacle number 31).

Variation in tentacle number may occur within a species, and between polypides of the same colony of a species. Jebram (1973) pointed out that external factors (chiefly nutrition) can influence the tentacle number. My own work (Dudley, 1973) on the growth of *Conopeum tenuissimum* has shown that this variability follows an orderly pattern. Polypide size, tentacle number and variability in tentacle number increase in the distal direction as zooid size increases, and variability is therefore a function of genetic as well as environmental control of the colony. This pattern appears to apply to other species as well. In those species in which zooid size increases toward the younger outer edges of the colony, polypide size, tentacle number and variation in tentacle number also increase.

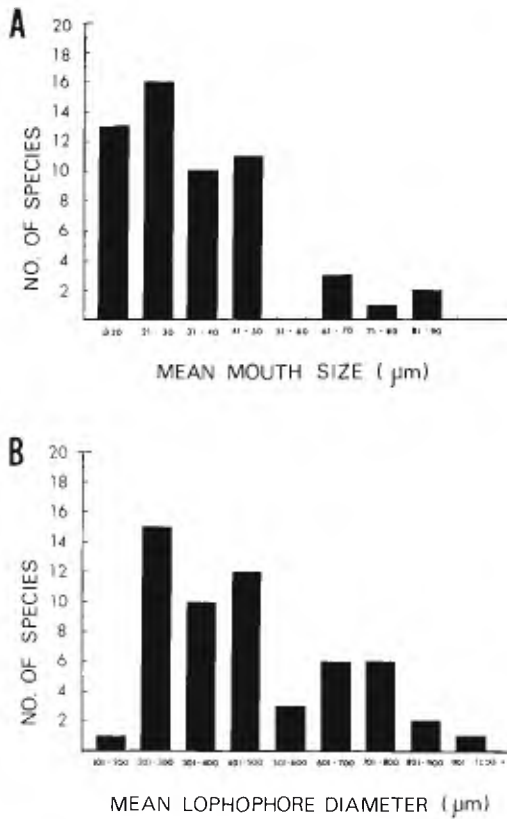It is possible that variation in tentacle

Figure 5. A. Distribution of mouth size in bryozoan species from Florida and Panama; B. Distribution of lophophore size in bryozoan species from Florida and Panama.
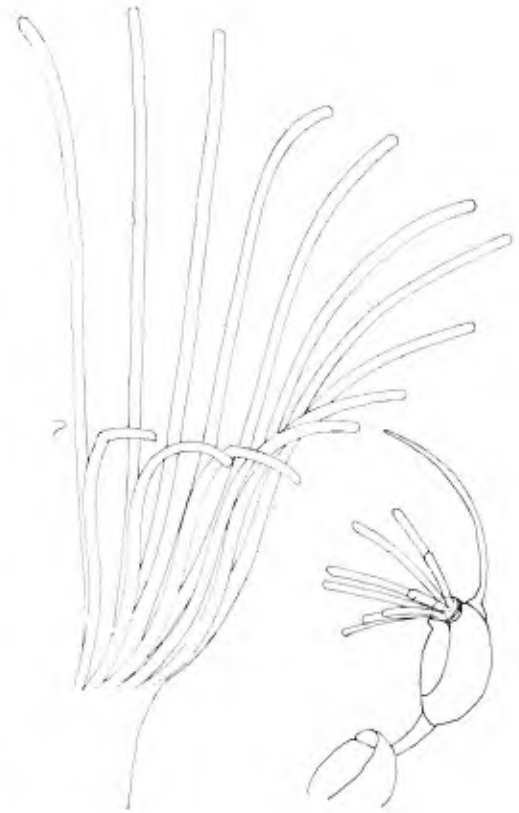
Figure 6. *Steganoporella magnilabris* and *Chlidonia pyriformis*—contrasting lophophore size in the largest and smallest species studied.

number within a colony is due to increase in number of tentacles with aging of the polypide. Tentacle length can increase as the polypide ages. For example, in many species, the young recently developed or regenerated polypides (distinguishable by their greater transparency and the lack of food in their guts) has short, equi-tentacled lophophores, while older polypides in adjacent zooids have longer or obliquely truncate lophophores. An increase in anal tentacle length occurs especially wherever polypides are positioned so that these tentacles must elongate to produce an effective incurrent cell.

Lophophore Size

In the species I have studied from Florida and Panama mean lophophore diameter varied from 187 μm to 1012 μm (Fig. 5B), and as tropical species in most groups of invertebrates are generally smaller than cold-water forms, the actual possible range in size is probably even greater. The largest species is 5 times the size of the smallest, and this size differential produces even more important differences with respects to feeding and behavior. Figure 6 shows the lophophore of the smallest species studied (*Chlidonia pyriformis*) in comparison with that of the largest (*Steganoporella magnilabris*).

Mouth Size and Shape

The size and shape of the lophophore and the length of the tentacles may set physical limits on the type and size of particles that can be collected (Strathmann, 1973), but the most important physical limiting factor is, of course, imposed by the size of the mouth. In the 53 species measured mouth size ranged from 15 to 91 μm (Fig. 5A). Even without allowing for behavioral differences between species, the food available to the first species is surely much more restricted than that available to the second.

The mouth in marine bryozoans is usually described as round (Hyman, 1959), but this is not the case in all species observed. Species with small mouths (less than 30 μm in diam) all had round mouths. Species with mouths of intermediate size (30 to 40 μm in diam) had mouths of shapes varying from round to ovoid. In the larger species (mouths greater than 41 μm in diameter) mouths were always elongated either into key-hole or triangular shapes. In all but one species (*Gemelliporidra multilamellosa*) this elongation was parallel to the elongation of the lophophore, in the dorsal-ventral direction, in contrast to the lateral elongation of mouth and lophophore that occurs in phylactolaemates, phoronids and brachiopods.

Comparative Tentacle Structure

The fine structure of the gymnolaemate tentacle has recently been examined in detail by several workers (Smith, 1973; Lutuad, 1973; Gordon, 1974), and it seems a reasonably safe assumption that this general structure is common to all members of the group. The position and structure of the frontal and lateral cilia seem to be fairly universal, as would be expected considering that they are basic to the food collection mechanism (Strathmann, 1973). It is with the occurrence and distribution of possible sensory structures that most of the potential for variation lies, and this, too, is expected on the basis of differences in ecology and behavior.

There are four kinds of structures which may be presumed to have a sensory function (Fig. 7): latero-frontal cilia, tentacle-tip cilia tufts, and abfrontal structures, either bunches of stiff cilia, or single ciliary structures which may be immovable or may show a whip-like activity.

Latero-frontal cilia

The latero-frontal cilia were not noticed by early workers and were first reported by Lutaud (1955) for the cheilostome *Electra pilosa*. Since then they have been observed on a ctenostome, *Zoobotryon verticillatum* (Bullivant, 1968), other cheilostomes, *Membranipora villosa* (Strathmann, 1973), *Cryptosula pallasiana* (Gordon, 1974), and the cyclostome, *Crisia elongata* (my observations). These cilia, at least in *Cryptosula* and *Electra*, have two-branched rootlets, like the frontal cilia, but in living animals they appear thicker than the frontal and lateral cilia (fused cilia?) (Fig. 7A). According to Gordon (1974) these structures in *Cryptosula* are not always immotile but may make occasional flicking movements. However, in other species (pers. obs.) they do not show any motility (at least under the microscope). Strathmann (1973) has suggested that the latero-frontal cilia may serve as upstream particle sensors, governing the ciliary reversals which play a large role in the process of particle transport down the tentacles. If this is the case, these structures could (1) detect a wider range of food particles than the lateral cilia alone, and (2) if longer than the lateral cilia themselves, allow the animals to detect particles that would pass outside the range of the lateral cilia, making it possible for them to utilize a faster moving feeding current. Strathmann found species of *Bugula* to have some latero-frontal cilia 1.5 times as long as the lateral cilia. In the species of *Bugula* I have observed latero-frontal cilia are also longer than lateral cilia in keeping with the ability of these species to create more rapid feeding currents than species with other colony types (see behavior section).
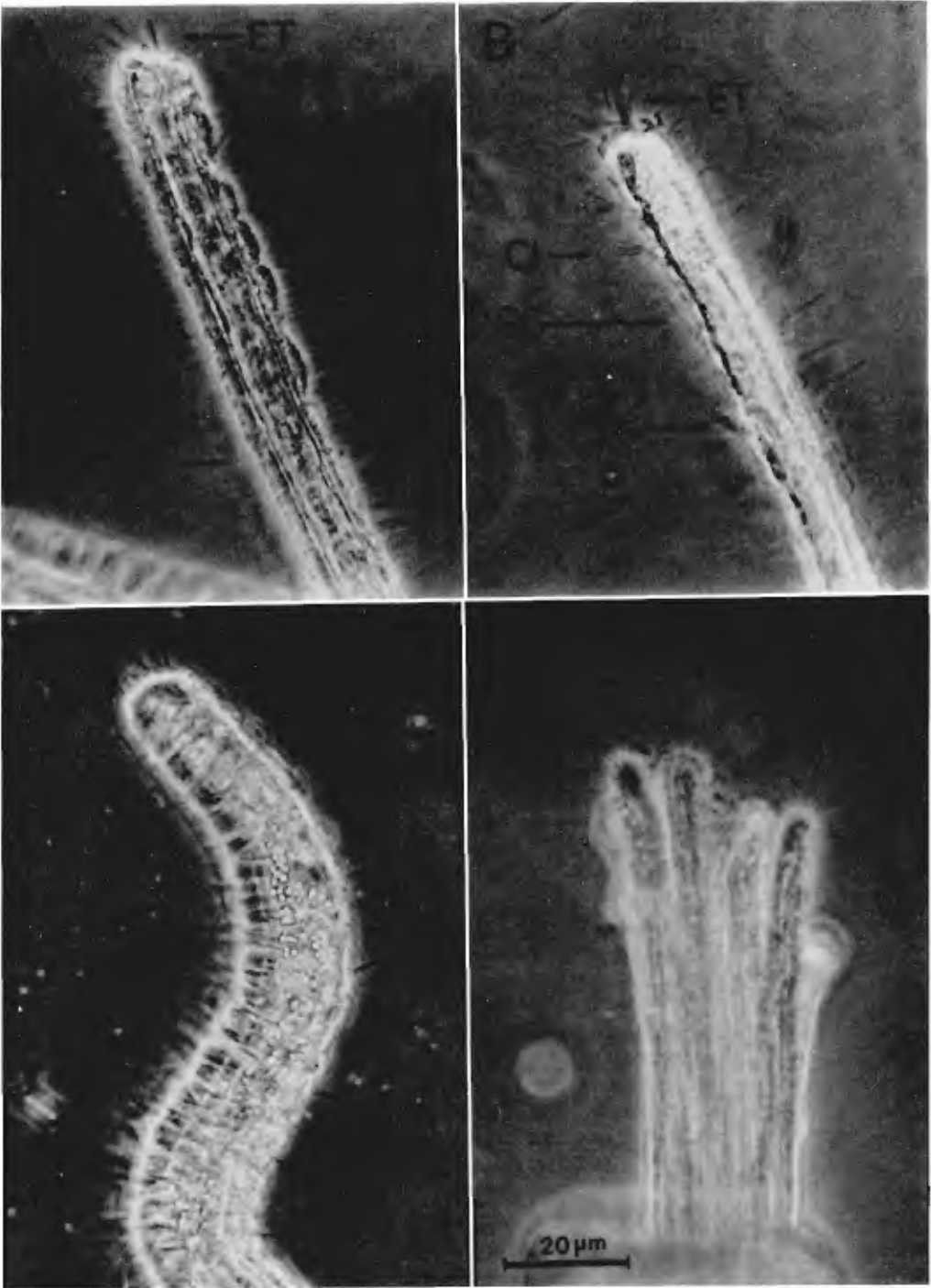
End Tufts

Clumps of cilia can be seen at the tips of the tentacles in the illustration of *Electra pilosa* given by Lister (1834, plate XII, Fig. 2), although he did not mention them in the text. Gordon (1974) mentioned a clump of cilia on the tips of *Cryptosula* tentacles, but they are not mentioned by other recent authors, although they are present in all species I have observed. In *Crisia elongata* these end tufts are particularly long (Fig. 7B), three or four times the length of the lateral cilia. If these are truly touch-sensory cilia (or palpocils, to use Hincks' (1880) term) it is not hard to imagine why they are concentrated on the tentacle tips. Most species of marine bryozoans utilize a testing position before the lophophore is expanded (see Fig. 10E), during which time only the tips of the tentacles protrude from the orifice. Very likely it is these bunches of cilia which enable the animal to monitor the movement and particle content of the surrounding water.

Abfrontal Structures

Abfrontal structures are of several types: clusters of immotile cilia (Fig. 7C) similar to those found at the tentacle tips and solitary structures, either immotile cilia, or whip-like structures which display a flicking activity (Fig. 7D). These abfrontal structures were known to the 19th century biologists (Lister, 1834; Farre, 1837; Hincks, 1880), and their presence or absence in various species was noted. Lister (1834) was apparently the first to detect the presence of abfrontal "hairs" or cilia which he suggested might "give notice of anything coming within their touch." Farre (1837) called these structures "spines," and described them in *Bowerbankia densa* (= *Bowerbankia imbricata*) as follows:

"armed at the back with about a dozen fine hairline processes, which project at nearly right angles from the tentacula, remaining motionless, while the cilia are in constant and active vibration." Farre did not discuss the possible sensory nature of these structures, but by the time of Hincks (1880) it seemed to be accepted that the tentacles "must also be regarded as tactile organs, and in many species are furnished with special appendages, by which their sensitiveness and power of detecting the presence of minute particles are greatly increased."

The most comprehensive description of these cilia is given by Gordon (1974) who found the abfrontal tentacle surface of *Cryptosula* to be adorned with short tufts of about ten immotile cilia, alternating with solitary motile cilia. Bullivant (1967) described pairs of bristles on the abfrontal tentacle surface of *Zoobotryon*. In my observations I have found that all species possess some abfrontal sensory structures. These are most commonly tufts of various sizes with solitary bristles in between. Whip-like structures similar to those of *Cryptosula* occurred in *Watersipora*.

It seems probable that the latero-frontal cilia could be functioning in controlling ciliary feeding, while the end bristles are also in a position to act as particle sensors, both in the testing and expanded positions, but the possible role of the abfrontal structures is not so clear. Possibly, if they sense water movement or particles, they could have some role in controlling polypide orientation relative to other polypides and so functioning in the formation of temporary clusters, and permanent current cells. Thus, it would be interesting to examine their comparative structure and position in species that are known to have differing kinds of feeding behavior.

Figure 7. Tentacle sensory structures: A. Tentacle of *Watersipora subovoidea*, B. Tentacle of *Bugula neritina*. C. Tentacle of *Bowerbankia* (Indian River sp.), D. Tentacles of *Crisia elongata*. B = abfrontal "bristle"; ET = end tuft of cilia; Cl = abfrontal clumps of cilia; SC = non-motile abfrontal single cilia; W = abfrontal motile "whip" cilia; LC = band of lateral cilia; LFC = lateral-frontal cilia.
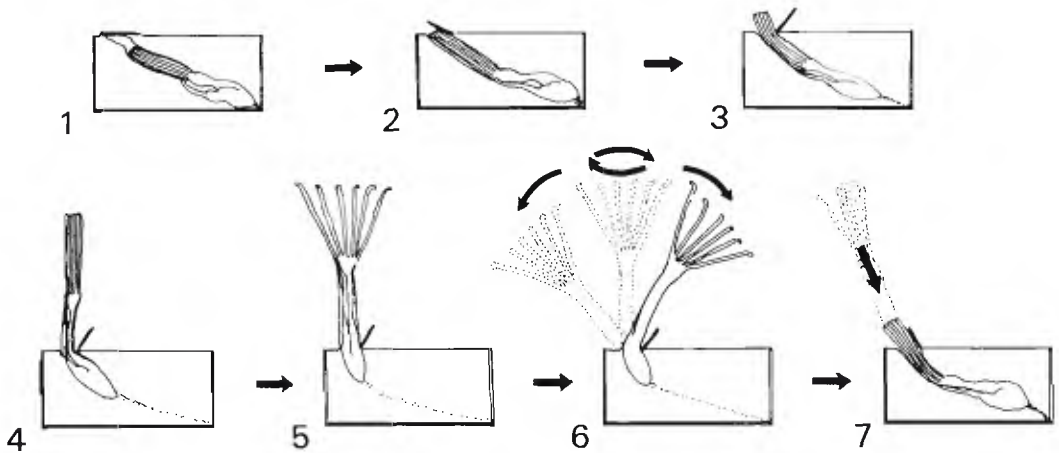
Figure 8.   Basic components of polypide behavior.   (1) Fully retracted, orifice closed; (2) opening of operculum or lip; (3) extrusion of tentacles through orifice in "testing" position; (4) extrusion of polypide; (5) expansion of lophophore; (6) bending of polypide in scanning activity; (7) retraction of lophophore.

INDIVIDUAL AND COLONIAL BEHAVIOR

Parameters of Individual Behavior

Before species-specific differences in behavior can be explained it is necessary to understand the basic components of polypide behavior. Figure 8 illustrates these processes beginning with the protrusion of the polypide from the zooid.

Extrusion of the Polypide and Expansion of the Lophophore

(1) When the polypide is fully retracted within the zooid, the orifice (governed by operculum, lips, or terminal membrane) is completely closed. The first hint of emergence of the polypide is (2) the opening of the operculum or lip or widening of the terminal membrane; this is generally accompanied by a shifting of the polypide forward or upward from the fully retracted position. The extrusion of the tentacles through the orifice (3) is usually a fairly slow movement. The polypide may pause here in a "testing" position, as if it is sensing water movement or particles present—e.g. when food particles (*Dunaliella*) are added to the water zooids of many species rapidly emerge

to the testing position and then expand (Fig. 10E, F). Extrusion of the polypide (4) consists of extending the compressed tentacles of the lophophore and a varying amount of the introvert and upper region of the gut from the zooecium. This also usually occurs rather slowly, though the rate differs between species and also depends on how well the animals are adapted to the conditions in the experimental situation. At this stage the tentacles are still held tightly together; if the tenacles are long they may be bunched or twisted together. Once the polypide extends as far as possible from the zooecium the lophophore unfurls (5). In those species with long tentacles it usually takes a little more time for the ends of the tentacles to untwist and straighten out. Animals may not expand the lophophore fully immediately, but instead may keep withdrawing or contracting the bell for a period of time until they become accustomed to laboratory (or natural?) conditions. When the lophophore is expanded (in cheilostomes and ctenostomes) the introvert may bend (6) in order to orient the opening of the lophophore in various directions (Fig. 10A also). As noted earlier the de-

gree of flexibility depends partly on how much the polypide can be protruded from the zooecium (introvert length), but it also seems to be a species-specific component of behavior. (7) Retraction of the lophophore is a very rapid motion. The tentacles are compressed and snapped back in (mucous surfaces and interior collagen rod giving protection from the stress of this action). Polypides may retract all the way back into the zooecium or may retract only partially to the testing position, depending on the degree of disturbance.

Tentacle Flicking Activity

Flicking of the tentacles has been noted by many authors (Borg, 1926; Mangum and Schopf, 1967; Strathmann, 1973) to be one of the most important components of polypide behavior, and this character was analyzed in several ways. Tentacle flicking varies from species to species both in quantity: the amount of flicking, how often it occurs, and in quality: the intensity and the length of tentacle involved. Speed may be fast or slow, or a species may be capable of both fast and slow flicking. The intensity varies from gentle to strong. Fast flicking is usually a sharp, hard action almost too rapid to follow with the eye. Often the tentacle appears to "bat" a particle in toward the mouth. In slow flicking it is possible to follow the action of the tentacle as it curves around the particle and whips it down toward the mouth. Usually tentacles flick in toward the mouth, but they may also flick outward (shaking off unwanted particles). The tentacles of a few species seem to twitch the free ends from time to time (e.g. *Celleporina hassalli*) or constantly (e.g. *Zoobotryon verticillatum*). In most species observed some kind of flicking activity occurred. In only a very few species (e.g. *Rhynchozoon* sp.) was tentacle flicking rare.

The length of tentacle invloved in flicking action can vary from just the outer tip, to the outer third (the most common type, occurring in almost all species) to one half or even the full length of the tentacle (usually

associated with tentacle feeding or more complex tentacle action than the first type).

Other Individual Actions

Other actions shown by polypides of one or more of the species observed include integrated activity of several tentacles or of the whole lophophore. These include widening or contracting the lophophore bell (especially in *Beania* spp.), bending the free ends of all the tentacles in, a movement which could occur either in rejecting heavy particle concentrations or in making a cage of the lophophore around particles. Several species, particularly *Bugula neritina* (Fig. 11), were observed actually using this cage to capture larger particles or protistans. "Waving" or "fanning" tentacles—the movement of several tentacles in and out in unison, "avoidance" retractions, a motion in which the lophophore is rapidly pulled partway back into the zooid leaving the bunched together ends of the tentacles extruded, and "writhing," a continuation of this activity in which the partially withdrawn tentacles writhe about like snakes on the zooid surface also occurred in several species. A few species could flatten all the tentacles outward so that the lophophore assumed a saucer or disk shape (*Celleporaria albirostris, Celleporina hassalli*).

Bending of the polypide occurs in many species so that the lophophore can scan in various directions (see Table 1). Some species (Fig. 10A, *Bowerbankia*) are capable of multidirectional scanning, by bending and rotating the introvert region they can scan in a wide circle around the perimeter of the space occupied by the erect lophophore. Many species which have a long introvert (e.g. *Beania intermedia, Sundanella sibogae, Conopeum* spp.) practice multidirectional scanning. In a few species bending is not limited to the introvert, for example *Victorella pavida* can bend both at the mouth and the orifice level and the flexible zooid can bend, too. Other species (usually those described below under Type II colony behavior) are very limited in scanning activity, but the loph-

Figure 9. Rejection mechanisms. (A) Polypide of *Membranipora tenuis* rejecting *Dunaliella* particles between the tentacle bases. (B) and (C) Polypide of *Membranipora tenuis* rejecting a large mass of debris by contraction and retraction of the lophophore.

ophore is capable of a slight degree of up and down motion (vertical scanning). In those type II species in which the introvert is very short (e.g. *Synnotum aegyptiacum, Vittaticella contei*) the lophophore can scan only very slightly. In other species, although the introvert may range from moderate to long the presence of colonial patterns involving incurrent and excurrent water pathways may mean that very little scanning is done by the polypides. When scanning activity does occur in these species it is chiefly lateral scanning or bending of the lophophore.

Particle Rejection Mechanisms

The force and persistence with which polypides of most species can reject unwanted particles is astonishing. The mechanisms used are varied, a particular species may reject particles by one or several methods. Rejection mechanisms might be expected to be most highly developed in those organisms found in the most particle-laden waters (e.g. *Conopeum* spp.), but to most species observed the ability to reject unwanted particles was clearly of great importance. Only two species, *Alcyondium polyoum* and *Alcyondium polypylum* behave completely indiscriminantly in swallowing *Dunaliella* particles. Only when their guts were crammed completely full did they begin to reject particles between the bases of the tentacles. One species, *Parasmittina nitida*, was observed to swallow not only the *Dunaliella* particles, but also rough-edged detrital fragments also present in the water obtained from its natural habitat on the undersides of rocks in a sand-bottom intertidal area. Rejection of small particles commonly occurred in streams (usually indicating species with a pharyngeal rejection tract), or more or less individually between the bases of all of the tentacles (Fig. 9A). Large particles or masses of debris were commonly rejected by retraction of the lophophore (Fig. 9B, C). Some species could reject both small and large particles in "puffs," an action which seemed to involve ciliary reversals, plus muscular action

of the pharynx and tentacles, forcing water and the particle or particles to be ejected very forcibly from the vicinity of the lophophore. In at least one species (see *Sundanella sibogae*) this form of rejection has apparently evolved into a method for concentrating small particles for consumption. A few ctenostome species (*Aeverrillia armata, Amathia alternata, Zoobotryon verticillatum*) utilized a "rejection action," widening the bell, bending distal ends of tentacles out and then contracting the bell all in extremely rapid succession. Like puffing, this action seemed to clear the lophophore of large, or too many small particles.

Movements of the Mouth and Pharynx Region

Though the mouth is always open it is capable of some constriction or dilation. Particles may be rejected after being engulfed by the mouth via a ventral ciliated rejection tract in the pharynx, or motile organisms, like *Dunaliella*, may manage to swim out of the pharynx and away between the tentacles during the interval between swallowings to the caecum. In all species studied, a pharynxful of particles would be collected before the muscular gulping action of the pharynx caused them to be swallowed into the caecum (or gizzard in certain ctenostomes). In a tiny species like *Anguinella palmata*, 3–4 *Dunaliella* particles (each 6–10 μm diameter) would fill the pharynx, while in large species like *Bugula neritina* a large bolus of particles would collect before swallowing took place.

Examples of Individual Feeding Behaviors

Crisia elongata "filterer"
Figure 10F

The bushy erect colonies of this cyclostome species occurred intertidally in Florida on rock surfaces, among the roots of large hydroids like *Thyroscyphus ramosus*, and seemed to be especially well-developed among masses of sponges and colonial tunicates. The zooecia are arranged alternately on the jointed branches and polypides are well separated from each other even with the lophophores expanded. The lophophore is small (mean diam = 266 μm) and equi-tentacled, and the eight tentacles are usually widely-spread. The mouth is round and tiny, averaging only 18 μm in diam. Observations under the dissecting microscope and by microcinematography showed that *Crisia* feeds by almost passively filtering particles, only occasionally directing them by a slight flicking of the outer ends of the tentacles. Examination of the polypides with the compound microscope showed that the species is admirably equipped to be a filterer, as it possesses long evenly spaced latero-frontal cilia, which, when the lophophore is expanded, almost fill the space between adjacent tentacles. These latero-frontal cilia are graded in length from the tip to the mouth, and are spaced about 2 μm apart, forming a lattice work which prevents most particles from escaping. The tiny lophophore creates only a slow-moving current, but apparently suitably-sized particles which do come within reach of the filter can be efficiently trapped. The abundance of *Crisia* among sponge and tunicate colonies indicates that it takes advantage also of the currents produced by other organisms in obtaining particles to filter.

Pasythea tulipifera "tentacle feeder"
Figure 10D

Other species, though of similar size and found in the same hydroid-stem microhabitat as *Crisia elongata*, feed in a very different manner. Such species, for example, *Pasythea tulipifera* (Fig. 10D), *Chlidonia pyriformis*, *Synnotum aegyptiacum* and *Vittaticella contei*, actively "grab" for particles, using the tentacles to roll or toss them into the mouth, and can hardly be classified as filter feeders.

Pasythea tulipifera also possesses a colony with erect jointed branches, but in this species, the autozooids are arranged in triads, so that the middle polypide of the triad faces
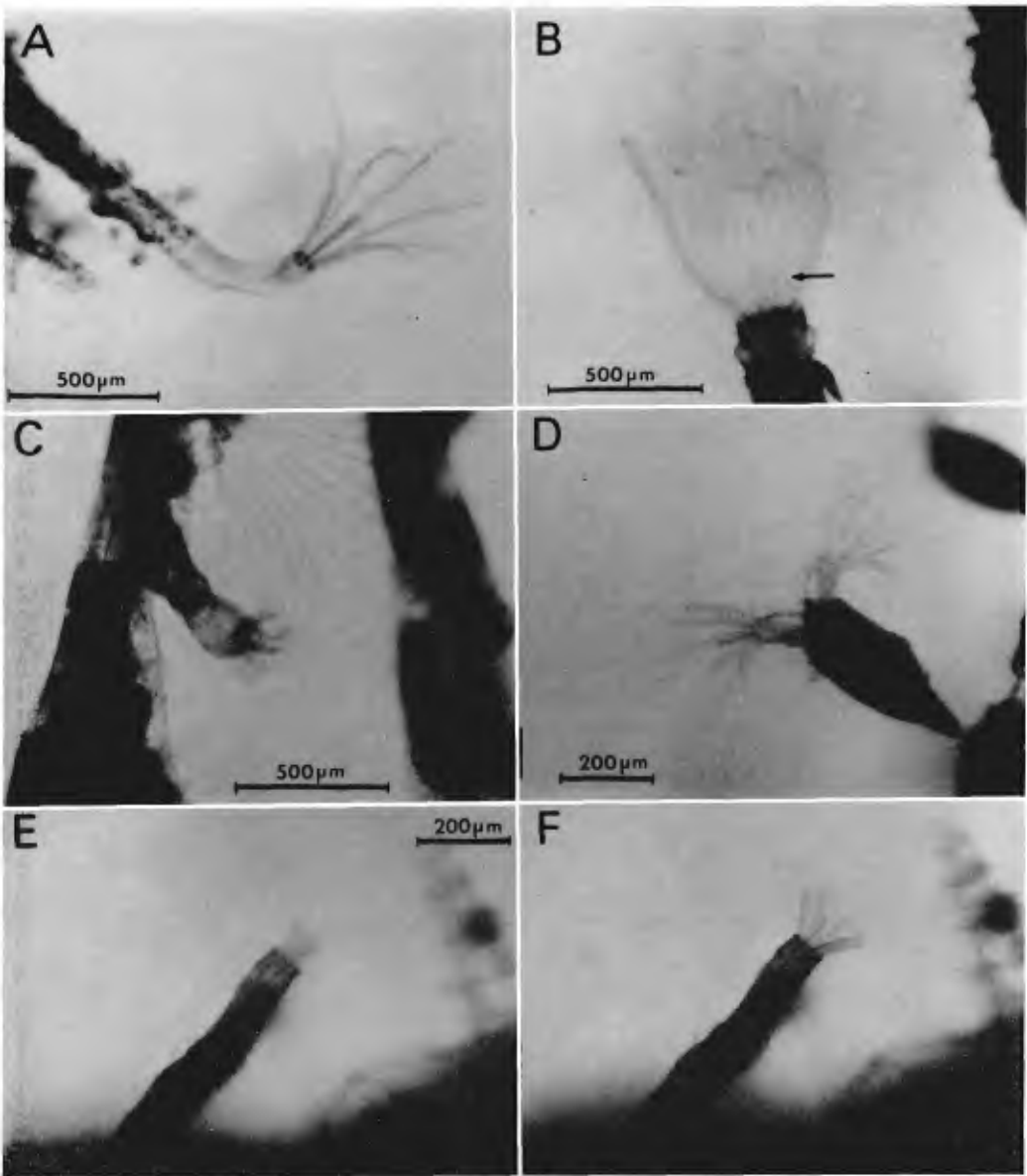
Figure 10.   Examples of individual behavior. A. Scanning activity by a polypide of *Bowerbankia* (Indian River sp.); B. *Sundanella sibogae* using tentacles to concentrate a ball of *Dunaliella* particles at the base of the lophophore (arrow); C. *Bugula neritina* making lophophore into a cage for the capture of active protists. Ends of tentacles are twisted together to prevent prey from escaping; D. *Pasythea tulipifera* using tentacles to roll particles down into the mouth. E. *Crisia elongata* polypide in testing position; F. *Crisia elongata polypide* in expanded position.

in one direction and the outer two in the opposite direction (Fig. 10D). The lophophore is equi-tentacled, averaging 217 μm in diam, and the ten tentacles, usually rather widely spread, may be held straight, bent in at the tips, or most commonly the upper (anal) tentacles curve in while the lower two curve out. Unlike *Crisia*, in which only the ends of the tentacles flick, tentacle action in *Pasythea* ranges from a fast flicking of the outer tips to a slower bending in of the whole outer half of the tentacle. Observations of feeding showed that while ciliary currents alone resulted in some particles reaching the mouth, the action of the tentacles is also important in rolling or pushing particles in. Often the anal tentacles were seen to be curved in just slightly while two to four abanal tentacles were being used to stuff *Dunaliella* into the mouth. Because there is a short introvert region protruded when the polypide is expanded, each polypide is capable also of a certain amount of vertical scanning, extending the area in which it can capture particles.

Bowerbankia spp. "scanners"
Figure 10A

Species in which the zooids are uniserial or very well separated from each other along stolons are often characterized by an individualized pattern chiefly composed of scanning activity. In ctenostomes of the genus *Bowerbankia* both body wall and polypide show a great deal of flexibility. When the polypide is retracted the zooid is contracted and often flattened against the substrate. When the polypide is expanded the zooid elongates and rises into a vertical or diagonal position relative to the substrate. In the species of *Bowerbankia* studied the lophophore is equi-tentacled. The small species *Bowerbankia gracilis* and *Bowerbankia imbricata* hold the tentacles straight, while on the larger (mean lophophore diam = 751 μm) polypide of *Bowerbankia* (Indian River species) the tentacles are bent outward at the tips. All three species studied were quite similar in feeding behavior. The

polypides scan the water in a circle for particles, bending the flexible introvert. This movement is quite slow (it may take a minute or more for the lophophore to complete the circle) but scanning goes on more or less continuously. In these species adjacent lophophores are quite well separated; they may touch each other in scanning, but when this happens they quickly retract. Occasionally two or three adjacent polypides bend toward each other to form a cluster which produces a stronger current. In *Bowerbankia* scanning is a smooth action, but in some other species characterized by scanning (e.g. *Victorella, Zoobotryon*) rotation of the lophophore is accompanied by a dancing, jerky motion of the tentacles.

Bugula neritina "cage-captor"
Figures 10C, 11

At least one species, the cheilostome *Bugula neritina*, appears to have developed an adaptation for zooplankton feeding, forming the tentacles of its lophophore into a cage with the tops of the tentacles twisted tightly together, and using this cage to trap active ciliates and other protistans, which are then ingested. Bullivant (1967) saw *Bugula neritina* capture a tintinnid in this manner, but did not believe it could be the normal mode of feeding. However, in my observations, this activity occurred constantly. In any situation where large particles and protistans were present, there were always some polypides of the colony making cages with their tentacles and feeding in this manner. While such carnivorous behavior has not been reported for bryozoans, it has been found for copepod crustaceans for example, that very small species are completely herbivorous, but larger ones capture zooplankton or other large particles as well as filtering nannoplankton (Marshall, 1973). In fact, it has even been suggested (Parsons and LeBrasseur, 1970) that the larger species of copepods require large food in addition to nannoplankton or must have some method of concentrating small food particles in order to maintain themselves.
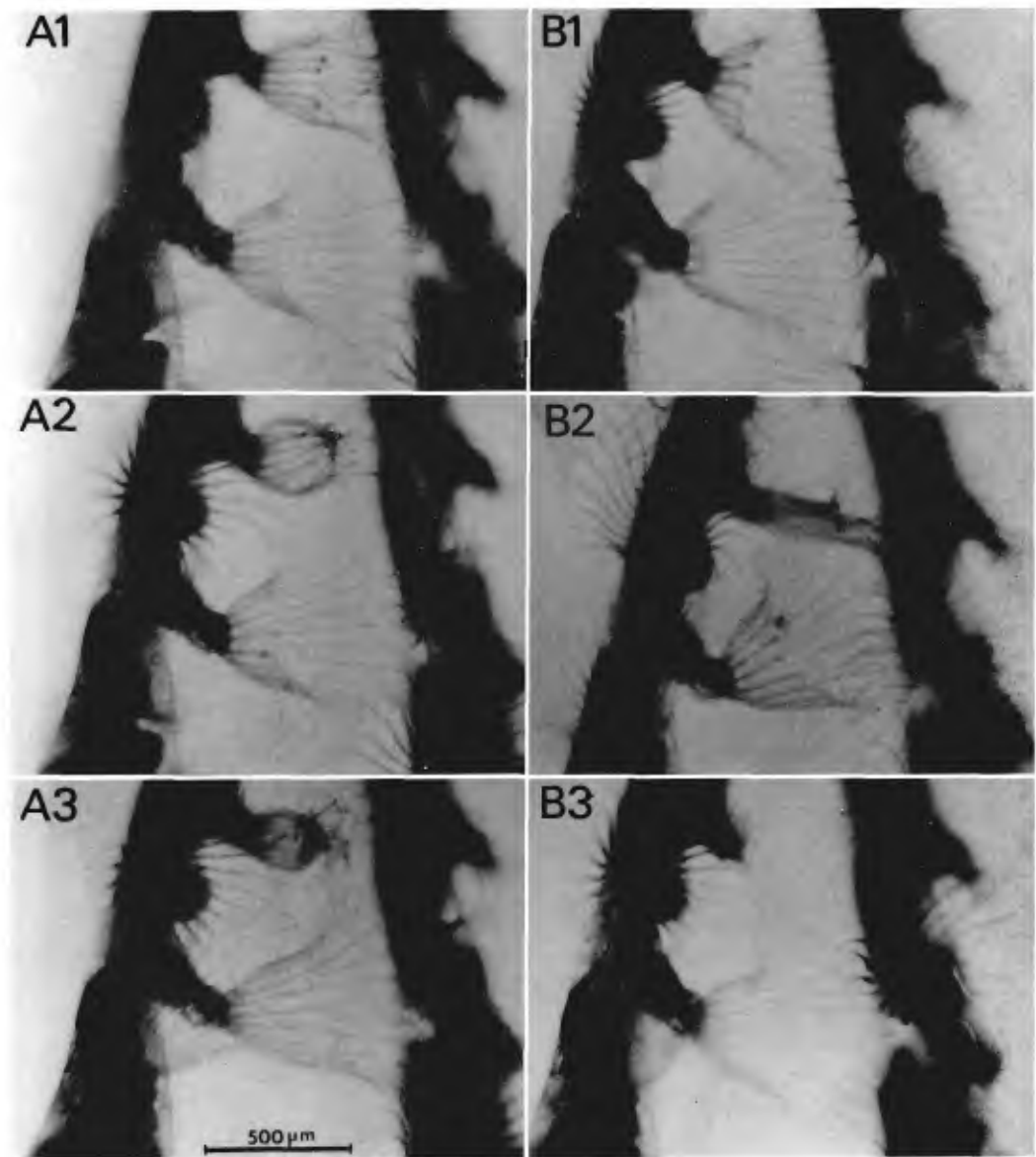
Figure 11. *Bugula neritina* behavior sequences: A1–A3 One lophophore (top center) forms a cage; B1–B3 One lophophore (top center) goes from expanded, to contracted, to retracted position.

Sundanella sibogae "particle juggler"
Figure 10B

One of the largest species studied, the ctenostome *Sundanella sibogae*, showed an unusual behavioral adaptation that might reflect a need to concentrate small food par-

ticles. In this species the zooids are arranged uniserially and each polypide appears to function individualistically. The equi-tentacled lophophore averages 820 μm in diam, with 31 long slender tentacles, and a mouth averaging 82 μm in size. The poly-

pide constantly scans back and forth, bending and moving the whole introvert and the upper half of the flexible zooecium to complete its rotations. It is characterized by a very slow flicking of the tentacles which bend in to about half their length, then slowly bend back out. When fed high concentrations of *Dunaliella*, polypides of *Sundanella* used this tentacle flicking combined with ciliary action to concentrate the particles into a large ball which tumbled about in the region just above the mouth. This ball of particles was rapidly ejected above the lophophore, then sucked back down above the mouth, the juggling action being repeated several times until the polypide finally withdrew back into the zooid, taking the food bolus with it.

Patterns of Colony Behavior

Even more striking than these individual behaviors are the colony-wide adaptations which marine ectoprocts have evolved in order to separate, increase and channel feeding currents. Species can be grouped in various levels of integration based on the extent to which the individual has become subordinated to the colony and the extent to which individuals of the colony act together to produce an effect beneficial to all. These categories are not mutually exclusive and are meant to describe functional differences in behavior, although there are taxonomic and phylogenetic implications as well. Table 2 shows 55 species of marine ectoprocts grouped according to type of colony behavior pattern.

Colonies in Which the Individual is Dominant
Figure 12

Eleven of the species for which the colony behavior pattern was studied fell into a group in which the individual zooid appeared dominant and multidirectional scanning behavior predominated. Polypides in this type of colony were completely or partially separated from each other and there was little or no interaction of feeding

Table 2. Species grouped according to type of colonial behavior pattern

Type I Individual Dominant	Colonial Behavior Pattern/Colony Currents	
Aeverrillia armata	1	W
Beania intermedia	1	W
Bowerbankia gracilis	1	W
Bowerbankia (Indian River species)	1	W
Bowerbankia imbricata	1	W
Sundanella sibogae	1	W
Zoobotryon verticillatum	1,2	M
Amathia alternata	1,2	W
Nolella stipata	1,3	W
Terebripora sp.	1,3	W
Victorella pavida	1,3	W

Type II Separated by Colony Structure		
Anguinella palmata	2	W
Bugula neritina	2	S
Bugula stolonifera	2	S
Bugula turrita	2	S
Canda simplex	2	S
Caulibugula dendrograpta	2	S
Caulibugula pearsei	2	M
Chlidonia pyriformis	2	W
Crisia elongata	2	W
Crisia (Pacific sp.)	2	W
Pasythea tulipifera	2	M
Scrupocellaria regularis	2	S
Synnotum aegyptiacum	2	W
Tetraplaria dichotoma	2	M
Vittaticella contei	2	W
Margaretta buski	2,3	M
Reteporellina evelinae	2,7	S

Type III Temporary Clustering Dominant		
Alcyonidium polyoum	3	M
Alcyonidium polypylum	3	S
Beania hirtissima	3	M
Conopeum seurati	3	S
Conopeum tenuissimum	3	S
Electra bellula	3	M
Membranipora arborescens	3	S
Membranipora tenuis	3	S
Thalamoporella falcifera	3	W
Watersipora subovoidea	3	M
Steganoporella magnilabris	3,4	M
Crassimarginatella tincta	3,5	S

Type IV Permanent Cluster, Non-Skeletal		
Hippoporina verrilli	4	S
Membranipora tuberculata	4	S
Parasmittina nitida	4	S
Schizoporella floridana	4	S

Table 2.   (Continued)

Type V. Permanent Cluster, Irregular-Skeletal	Colonial Behavior Pattern/Colony	Currents
"Rhynchozoon" sp.	4,5	—
Trematooecia turrita	4,5	S
Celleporina hassalli	5	M
Trematooecia aviculifera	5,7	S
Type VI. Permanent Cluster, Regular-Skeletal		
Gemelliporidra multilamellosa	6	S
Lichenopora buskiana	6	S
Lichenopora intricata	6	S
"Plagioecia" sp.	6	S
"Tubulipora" sp.	6	M
Celloporaria albirostris	3,6,7	S
Discoporella umbellata depressa	3,6,7	S

currents among individuals in the same colony. Ten of the species in which this type of behavior occurred were ctenostomes, but this type of pattern can also occur in cheilostomes (e.g. Beania intermedia). The currents produced by such colonies are generally weak, although the currents produced by individual polypides may be quite strong, depending on the size of the polypide. In polypides of this type of colony the introvert is usually medium to long as figure 10A shows.

Colonies in Which Polypides are Separated and Their Orientation is Controlled by the Skeletal Structure of the Colony
Figures 11, 13

In the second group (12 species) the colony appeared to dominate the individual. Individual polypides were separated to a greater or lesser degree. Polypide orientation was controlled by colony structure and only a limited range of polypide motion was possible. Within this framework polypide size ranged from small to large, individual behavior from simple to complex, and colony current production from weak to strong. These colonies occurred in all three orders of marine ectoprocts and the type of behavior appeared to be a functional consequence of erect branching colony form. Though this group contained tentacle feeders like Pasythea and Vittaticella which pro-

duced only weak colony currents, it is probably better characterized by Bugula- or Reteporellina-type colonies in which the lophophore-covered branches draw a strong current of water through the meshwork of the branches. Microcinematographic and dye studies of Bugula turrita colonies showed clearly the current being drawn down through the spiral of the colony, impinging with great force on the sides of the branches where the lophophores protruded and drifting gently around the non-polypide bearing outer surface of the branches. Aside from flicking of the tentacles the polypides in this species change their orientation very little. The lophophores are all obliquely truncate, curving out slightly at the tips, and are moderate in size (mean lophophore diam = 393 μm, 14 tentacles). Their most characteristic actions are forming a cage by putting the tips of the tentacles together around a bolus of particles, and rejection of particles by avoidance retractions (clearing the meshwork of large particles) and the puffing away of large concentrations of small particles which have accumulated in the mouth area but cannot be swallowed because of a full pharynx.

Colonies Characterized by the Formation of Temporary Clusters of Polypides
Figure 14A

In the third category (12 species) zooids are arranged in contiguous sheets and polypides are capable of forming temporary clusters of lophophores which may serve to increase and direct feeding currents. This type of behavior is found in both encrusting ctenostomes and cheilostomes. The two species of Conopeum studied (Conopeum tenuissimum and Conopeum seurati) serve as excellent examples of this type of behavior pattern. In Conopeum the polypides show a constant twitching activity, rapidly flicking the outer third of the tentacles in and out, while at the same time slightly expanding and contracting the lophophore bell. The polypides do a lot of popping in and out of the zooids and when expanded
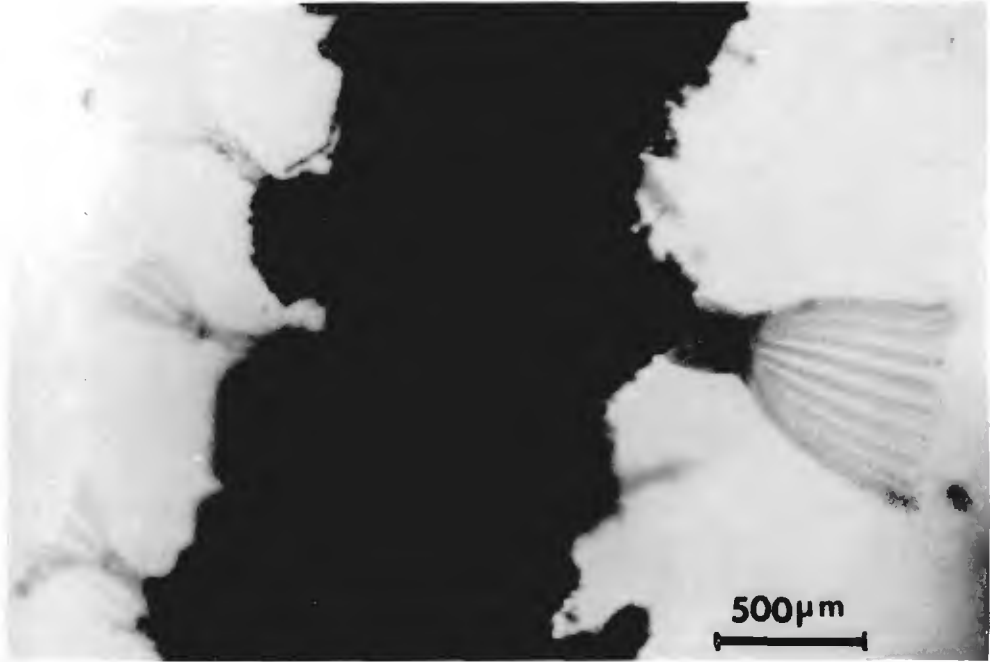
Figure 12. Example of a Type I colony: *Bowerbankia* sp. (left) growing along branch of the erect colony of *Margaretta buski* (large polypide on right).

they form clusters in which three or four lophophores are oriented toward each other (Fig. 14A). In doing so they may lie with the long introvert stretched out parallel to the colony surface, and the outer tips of the tentacles of some polypides may even be touching the surface of the colony. When the polypides first emerge from the zooid they scan in all directions and orient toward the nearest polypides which are also expanded in order to make the clusters, but the associations change as one polypide retracts and is replaced by another in a slightly different position. The currents produced by the clusters of polypides are stronger than those that could be produced by individual polypides alone, and flow of water and turbulent reworking of water over the colony surface is enhanced. Even in colonies like those of *Conopeum tenuissimum* in which individual lophophore size is only moderate (mean lophophore diam = 475 μm, 12 tentacles) the colony currents produced are

strong, apparently an advantage of this type of behavior.

Colonies in Which Polypides Form Fixed Clusters, but Without Reflection by Skeletal Morphology
Figure 14B–E

In other encrusting forms (four species) zooids were contiguous, and polypide orientation was fixed, but was not reflected in zooecial (skeletal) morphology. In these species, like the *Membranipora membranacea* described by Banta, McKinney and Zimmer (1974), polypides are organized onto fixed clusters or incurrent cells, with excurrent chimneys between them. In small circular colonies of *Hippoporina verrilli*, for example, one or two incurrent cells were observed (Fig. 14B). Although the polypides in this species have an introvert of medium length there is no scanning activity (though flicking of tentacles and cagemaking do occur). The polypides in the center of an in-
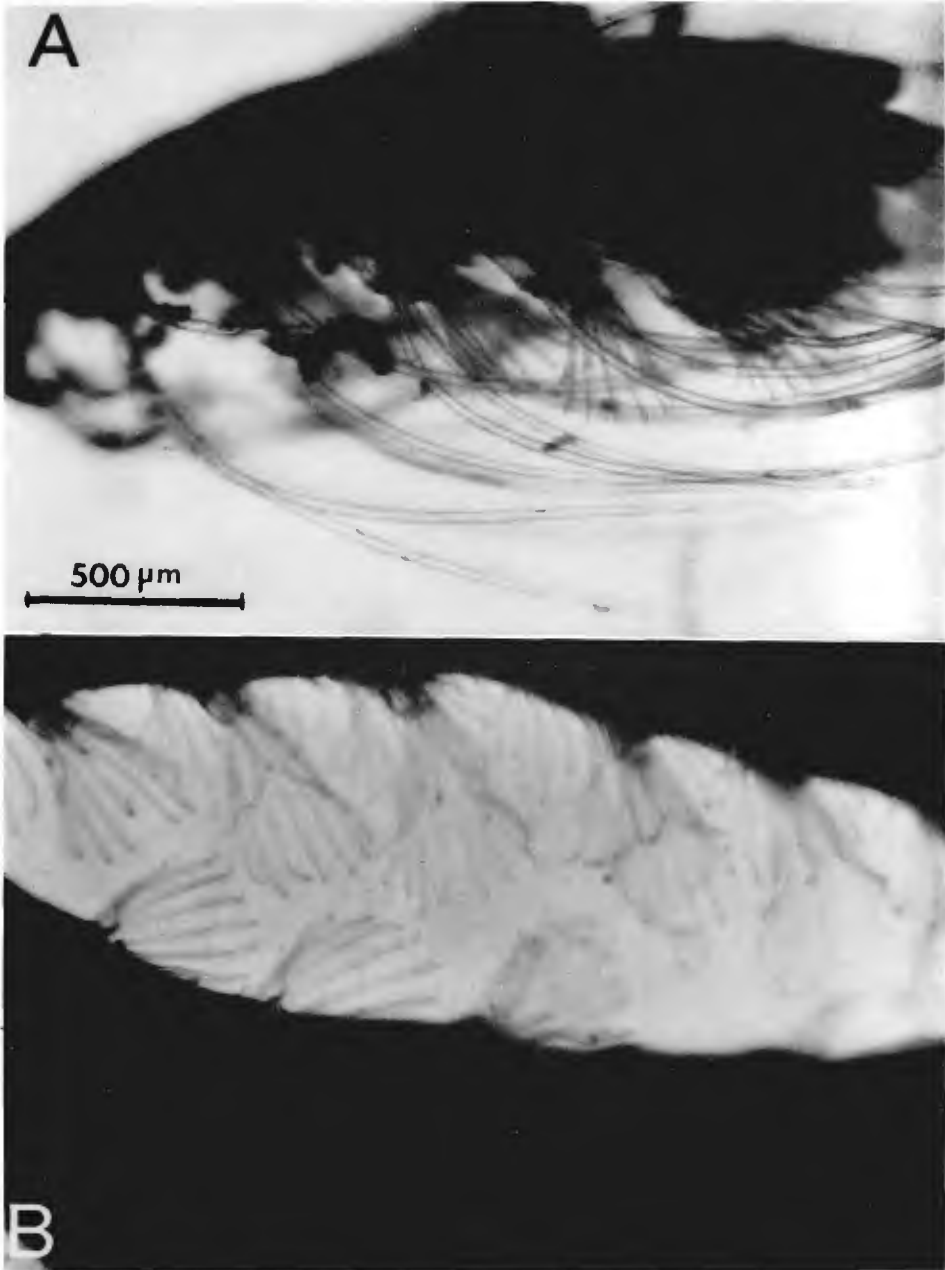
Figure 13.   Examples of Type II colonies: A. *Caulibugula dendrograpta* branch, showing obliquely truncate lophophores; B. *Reteporellina evelinae*, showing orientation of campylonemidan lophophores into the space between two branches.
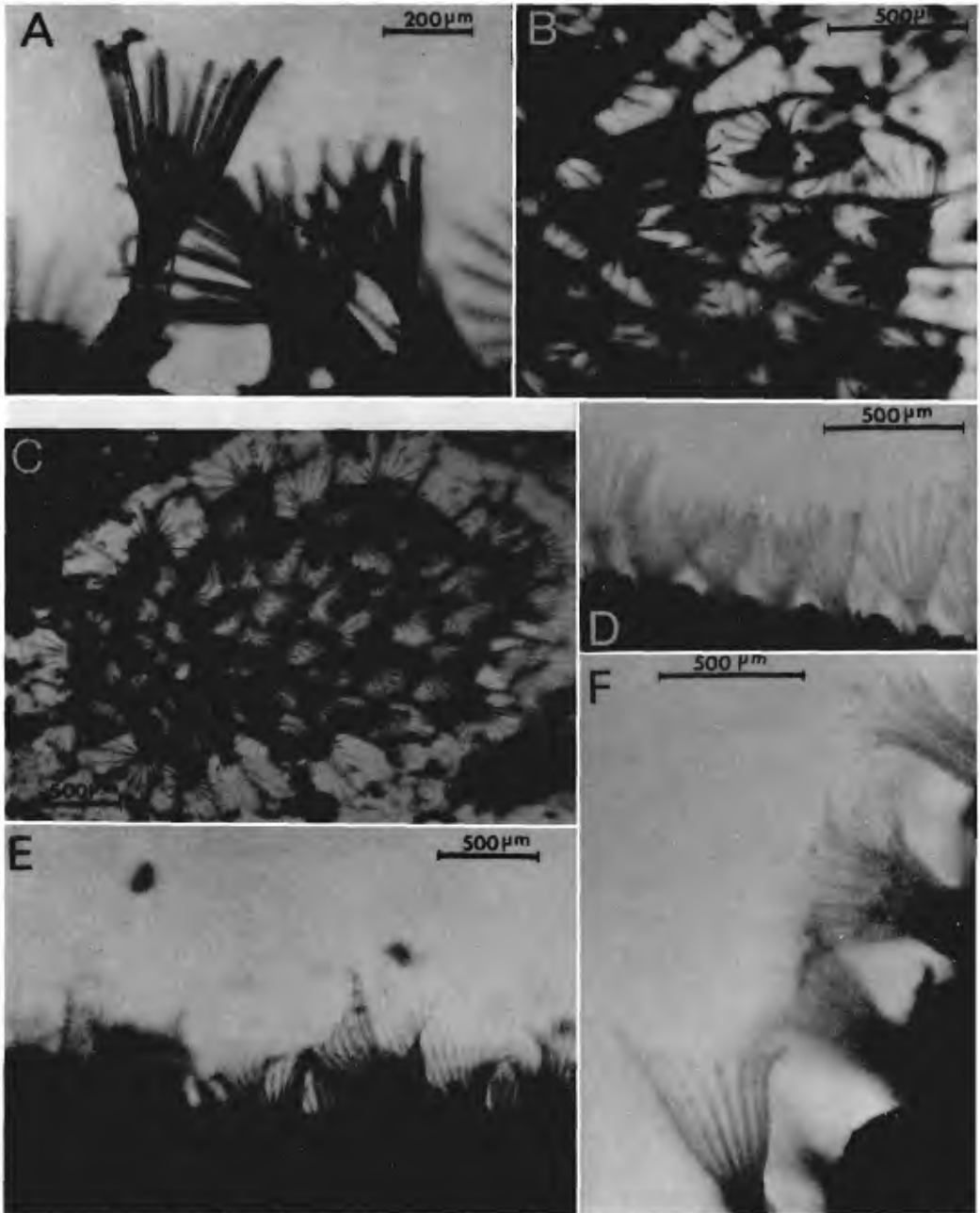
Figure 14. Examples of Type III, IV and V colonies: A. Type III. Polypides of *Membranipora tenuis* forming temporary clusters; B. Type IV. Incurrent cell of *Hippoporina verrilli* colony; C. Type IV. Small colony of *Schizoporella floridana* forming one incurrent cell; D. Incurrent cell (side view) of *Membranipora tuberculata*; E. Incurrent cell and excurrent chimney in *Steganoporella magnilabris* (Type IV); F. Incurrent cell in *Trematooecia aviculifera* (Type V).

current cell are equi-tentacled and the loph-ophore is held straight up, in outer rows the introverts bend toward the center of the cell, and the lophophores become more and more obliquely truncate, so that in side view the cup-shaped incurrent unit is clearly defined. The most obliquely truncate lophophores are found on polypides bordering on and bent away from the excurrent chimneys.

Small unilaminate colonies of *Schizo-porella floridana* (Fig. 14C) showed a simi-lar behavior pattern, though polypides of this species are more active, showing a slight amount of lateral scanning, and cage making activity, using the cages to capture balls of *Dunaliella* ejected by puffing rejections from adjacent lophophores. Polypides of *Schizoporella* also are capable of "writhing"— pulling back part-way into the zooid, then lashing the tentacles around.

Membranipora tuberculata, commonly found on floating sargasso weed, also shows a type IV behavior pattern, though the poly-pides in this species seem much more active, popping in and out of the zooids, and flick-ing one or more tentacles to give the effect of constant flickering motion. In places where a group of polypides has degenerated or the sargasso leaf is irregular, polypides may be influenced in their orientation; but except for these irregularities, unless some-thing disturbs a large portion of the colony, all polypides are usually expanded so the colony surface shows a mass of lophophores all with tentacles just about touching. In side view (Fig. 14D) it can be seen that those at the edges of incurrent cells (bor-dering excurrent chimneys) may have slightly longer anal tentacles and the scal-loped profiles of the incurrent cells are ob-vious.

Colonies in Which the Polypides Form Fixed Clusters, and the Clusters are Enhanced by an Irregular Patterning of the Colony Skeleton
Figure 14E & F

In the fifth kind of colony (five species studied) polypide orientation is fixed to form

current cells as in IV, but the formation of these cells is enhanced by the skeletal form of the colony itself, with raised and sunken areas which also channel the current flow.

One species found in Florida, *Celleporina hassalli*, forms nodular colonies around the bases of *Thyroscyphus* stems. In these col-onies frontal budding of zooids and the curvature of the colony around the hydroid stem gives a bumpy irregular surface to the colonies. The skeleton and the orientation of the polypides (with both equi-tentacled and obliquely truncate lophophores) to-gether form well-defined current cells.

Another species, *Trematooecia aviculifera* (Fig. 14F) occurring on dead coral rubble in shallow water at Galeta Reef, Panama, has colonies which form thick masses with raised and hollow areas, often concentrically arranged in circular colonies, but not always regular in nature. Due to the frontal bud-ding of zooids, the zooecia may be oriented in various directions, but the polypides al-ways form functional clusters. Figure 15A shows the arrangement observed in one col-ony: in the very center of the colony no lophophores are expanded and an exhalent current occurs; in the slope of the adjacent furrow the lophophores tilt out, those at the bottom of the furrow are held straight up, those on the side of the next ridge tilt to-ward the center again so that current chan-nels are created in the furrows. The lopho-phores in this species are large (mean lophophore diam = 757 μm, 18 tentacles) and obliquely truncate, and while they show some range of tentacle activity and were ca-pable of cage-making behavior, they do not seem to scan at all.

Colonies in Which Polypides Form Permanent Clusters Enhanced by a Regular Patterning of the Zoarium

This type of pattern was observed in both cyclostomes and cheilostomes. Among the cyclostomes *Lichenopora buskiana* offered one of the simplest examples of beautifully functional behavior based on skeletal pat-terning. The tiny colonies occurred on red

algae and the undersurfaces of corals at Galeta Reef. Each colony consisted of several radiating rows of zooids with channels formed by alveoli (non-zooidal areas of small coelomic spaces surrounded by calcareous walls) between them and a large hollow area in the center of the colony formed by the roof of the brood chamber. Dye studies showed that water currents entered at the base of the colony and exited in little puffs from the excurrent chimney formed by the hollow colony center. The presence of a lighter green color in the colony center also seemed to indicate that some reworking of the water was taking place.

Another striking example of regular skeletal patterning was observed in *Lichenopora intricata*. In this species, obtained both intertidally and subtidally in Panama Harbor, the complex colony consists of subcolonies with zooecia arranged in rows. In each row the zooids were progressively higher toward the center of the colony. Between the radiating lobes filled with zooid tube rows are channels floored by alveoli, and each subcolony has a hollow center. The polypides are densely packed, one above the other, each has the two bottom tentacles spread apart and curved away, and the rest curving around in a scoop shape. The lophophores of the raised zooid rows orient toward each other to form "food grooves" which move the particles along. No polypides orient on the channels that lead into the colony or toward the excurrent siphon formed by the depression in the subcolony center. A particle caught between the rows of zooecia in a channel gets carried out to the excurrent siphon. It might be expected that the chimney would be efficiently puffing water away, but in the laboratory the effect of the chimneys is to create a turbulence that causes water to be reworked by the colony.

Massive corallophyllic cheilostomes also showed type VI patterning. The large (up to several cm in diam) bracket shaped colonies of *Gemelliporidra multilamellosa* were found attached to the sides of ledges and under large coral heads at Galeta Reef. In this position the concave polypide-covered surface faced downward and SCUBA observations showed the very large (mean lophophore diam $= 850$ μm, 24 tentacles) polypides were oriented into the channels between the regularly spaced mounds formed by frontal budding of the skeleton.

Species in Which Polypides Have Some Form of Group Actions

Several species with various types of behavior patterns also appeared to show united activities of several polypides at once that indicated an even greater degree of behavioral (neurophysiological) integration.

Some of these group actions appear to be associated with rejection. In *Reteporellina evelinae* it was noted that group retractions occurred when it was necessary to clear the space between the branches of a large particle. This is probably one of the simplest types of unified activity.

Celleporaria albirostris forms brilliant cerise incrustations on the undersides of foliaceous corals at Galeta. The skeleton of the colony is molded in a regular series of knobs and channels. The polypides are oriented along the channels so that these form the incurrent or through-current pathways, and the knobs mark the excurrent channels. Long spines formed by the zooecial skeletons project upward among the introverts of the expanded polypides, but do not extend above the lophophores so their function in creating turbulence or channelling water is uncertain. The system for channelling water currents is regularly structured, and the greater length of the introvert makes scanning and changing polypide orientation to the temporary cluster type of behavior possible when this is advantageous (as when not all polypides are expanded). There also seems to be a trend toward unified action by polypides in which a whole group of polypides can be seen to undergo an avoidance retraction with writhing of the tentacles. Since there was at no time a predator or large particles observable that would have disturbed them, it seems possible that

this activity might somehow aid in processing water and moving it through the colony. In addition, several times a group of about six polypides was observed waving or bending the lophophores in the same direction at once. Such action could also be important in directing current flow.

Other species also showed unified polypide activity. For example, in the lunulitiform cheilostome *Discoporella umbellata depressa* which has a highly integrated type VI colony pattern, the polypides can be observed to execute a rapid action in which the two abanal tentacles move sharply outward, and then return to the normal expansion. This action could perhaps serve to push the current toward the upper (or lower when the colony is convex surface down) rows of zooids.

Discussion

Probably the most important implication of this work is that there is a greater range in polypide morphology and a greater variety of behavioral activity in marine ectoprocts than was previously suspected, with similar behavioral and associated morphological features occurring (apparently independently) in more than one order.

Although the ectoproct lophophore may be simple in comparison with those of phoronids and brachiopods, there has apparently been a strong trend in subsequent evolution toward development of more complex lophophores. The presumption is that the original lophophore structure was, as it is today in many small forms (including stoloniferous ctenostomes and cyclostomes), of the equi-tentacled type. This grade of construction has developed in both small and large species. In the large species the ends of the tentacles may be held stiffly, so that the lophophore is still a cup-shape, or the free ends may be flexed in and then out, giving the lophophore a campanulate shape.

In the obliquely truncate grade of construction the lophophore has lost its radial symmetry, becoming obliquely truncated in

an anal-abanal (adneural-abneural) direction, and therefore, bilaterally symmetrical. This shape develops in only some polypides in colonies that are organized to form current-enhancing cells. In colonies where the pattern of skeletal growth positions polypides so as to cause the maximum undirectional current flow, the lophophores of all the polypides are often slightly obliquely truncate.

In some cheilostomes the large and many-tentacled lophophore may be more elaborate, having the ends of some of the tentacles shortened and bent more sharply outwards so that a scalloped edge is apparent.

The strongest trend toward bilateral lophophore symmetry is shown by species with bent-tentacled or campylonemidan lophophores. This development for the directing of afferent and efferent currents has developed in all three marine bryozoan orders. In colonies with individualized behavior patterns (e.g. *Aeverrillia*, *Valkeria*, *Victorella*), it has apparently developed to aid the individual in processing water in very low current situations, e.g. among hydroid stems, or in sheltered estuarine habitats. In other species, e.g. *Reteporellina* and *Lichenopora*, it is linked with the development of a strongly unidirectional colonial current flow. In still other forms (*Discoporella*) a slightly campylonemidan lophophore seems linked with a behavioral action (widening of the ventral tentacles) that serves to distribute feeding currents regularly over the colony.

Thus, variation in lophophore shape appears to have a functional significance. The presence of such variation within the structures imposed by the microscopic size of individual marine gymnolaemate and stenolaemate bryozoans, indicates that the lophophore has undergone a radiation in size and shape. This radiation has been associated with behavioral developments and with increase of colony coordination in channelling feeding currents. The development and radiation of tentacle sensory structures may parallel the trends in lophophore development, i.e. one would expect more

sophisticated sensory structures, especially abfrontal structures, in those forms which demonstrate the highest degree of behavioral integration, but the comparative morphology of sensory structures is still too little known for speculation.

Measurements on lophophore dimensions (of species from several localities and all three marine orders) has also indicated the amount of variation that occurs and what its significance might be. Ryland (1975) analyzed lophophore parameters in a single community of marine bryozoans from the New Zealand intertidal. His study showed that while lophophore dimension varied from species to species, dominance of a very few species ensured that most lophophores in the community were in a much more restricted range. Though Ryland did not measure mouth size directly he concluded that the restricted size range of most lophophores in the community indicated that most species were utilizing a common food resource, consisting of particles within a similarly restricted size range. My study, on the other hand, has considered the lophophore dimensions of as many bryozoans as possible from a variety of habitats in tropical and subtropical localities in an attempt to discover the range of variation possible and the relationships between polypide size and feeding activity. The range of variation found, in fact, is similar to that found by Ryland in his New Zealand population (in my samples tentacle number ranged from 8–31, tentacle length from 124–859 μm and lophophore diam from 187–1,012 μm, versus 8–25, 200–900 μm, and 250–1,000 μm for bryozoans from Echinoderm Reef Flat). But, I have emphasized that this range in lophophore dimensions means that the largest species has a much greater size range of particles available to it (up to 90 μm) than does the smallest (less than 20 μm), and that the size differential, *in conjunction with* the behavioral differences observed, indicates considerable potential for partial separation of food resources among marine bryozoans.

Trends in Individual Behavior

In general larger size seemed indicative of more complex tentacle flicking activity— e.g. larger polypides exhibited a greater range of reactions, moving tentacles fast to slow, or making movements involving various lengths of the tentacle in connection with maneuvers for the ingestion or rejection of particles. However, among small polypides, only those of the cheilostomes seemed to be capable of complex actions. In the small cheilostome species the action of the tentacles in batting or rolling particles into the mouth played an important role in feeding whereas in small ctenostomes and cyclostomes ciliary activity was the most important component of feeding behavior.

The function of some of the individual behavioral action is still not known but the significance of others is obvious. For example, many species attempt to put the distal ends of the tentacles together to form a cage. But only in the larger species, particularly *Bugula neritina*, does this seem to have evolved into a specialized method of capturing prey. Small species could not get the ends of the tentacles completely together or twisted in place, and with only a small number of tentacles there were large gaps between the tentacles through which active prey could escape.

Some widespread and elaborate individual activities seemed to be associated with the rejection of particles. Some species showed a special rejection action; in others there was an avoidance retraction with the lophophore being pulled partway back in the zooid to avoid big particles of debris. Different species could reject particles in streams from the rejection tract, puffs, or between the bases of the tentacles, and some could utilize a combination of methods depending on the size and concentration of the particles.

Colony Behavior

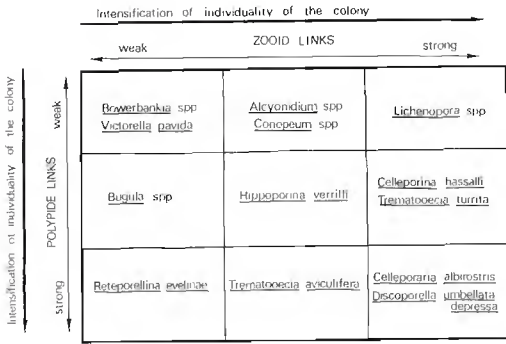Of the species studied the ctenostome species appeared most limited in the ex-

Intensification of individuality of the colony

	ZOOID LINKS	
weak		strong
Bowerbankia spp Victorella pavida	Alcyonidium spp Conopeum spp	Lichenopora spp
Bugula spp	Hippoporina verrilli	Celleporina hassalli Trematooecia turrita
Reteporellina evelinae	Trematooecia aviculifera	Celleporaria albirostris Discoporella umbellata depressa

(left axis: Intensification of individuality of the colony — POLYPIDE LINKS — weak / strong)

Figure 15. Levels of morphological and behavioral integration (with respect to feeding and current producing activities).

pression of colony-wide behavior patterns (chiefly type I and type II), though individual behavior could be quite complex (e.g. *Sundanella*). Carnose ctenostomes and several species of encrusting cheilostomes showed temporary clustering of zooids, apparently a trend for increasing current flow (and enhancing turbulence) in colonies where zooids are contiguous.

With massive encrusting forms the trend is toward increasing the efficiency in channelling the water through the colony, and by creating more turbulence, perhaps bringing a greater number of particles in. This can be accomplished in several ways: by orientation by the polypides alone, by orientation of polypides and formation of rough skeletal clusters, and by more regularly patterned arrangements of mounds and channels, carried to the extreme in something like *Lichenopora intricata*.

The ability of these organisms to manipulate water currents is one of the most striking observations of the study. The function of many colony patterns and behavioral activities appears to be to create turbulent water flow. In order to separate food particles from the water column all these animals have to have some method of changing water flow as it passes over the colony. In species living in very still water environments (e.g. sea-grass beds, inside dead mollusk shells, and in other cryptic habitats),

the problem is to create some turbulence and movement of the water to begin with. In species living in high-energy environments the problem is to change the flow in the immediate vicinity of the colony from laminar to turbulent. The whirlpool patterns set up by colonies observed in the laboratory that appear to be reworking of the water, are apparently necessary in nature to get food particles out of the macro-currents into a microenvironment from which the animals can extract them.

In the most highly integrated colonies studied, joint actions of groups of polypides aided in rejection of particles and processing of water currents. These colonies appeared to be approaching by various means the stage of integration described by Beklemishev (1970) in which "cormidia" or colonial organs are composed of several individuals. According to Beklemishev colonies can become more integrated in three ways, by weakening of zooid individuality, by intensification of colony individuality, and by the development of cormidia for the fulfillment of colony functions. With respect to feeding behavior and manipulation of feeding currents various types of bryozoan colonies can perhaps be considered as a matrix, in which the degree of integration increases by the increasing linkage between zooids (in the sense of closeness of spacing, contiguity, and regularity of patterning, as all bryozoans are connected, anyway), and by increasing of linkage between polypides, as shown by increasing colony control of polypide orientation (scanning = weak; temporary = moderate; fixed = strong), and by the increasing degree of behavioral integration as indicated by unified activities of the polypides. Such a matrix (Figure 15), while no doubt too simplified to cover all cases, does give a picture of the position of different types of colonies studied.

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LITERATURE CITED

Banta, W. C., F. K. McKinney, and R. L. Zimmer. 1974. Bryozoan monticules: excurrent water outlets? Science 185: 783–784.

Beklemishev, W. N. 1970. Principles of Comparative Anatomy of Invertebrates (Transl. 3d Russian ed., Moscow, 1964, by J. M. MacLennan; Z. Kabata, ed.) University of Chicago Press, Chicago. 1: 490 pp., and 2: 532 pp.

Borg, F. 1926. Studies on recent cyclostomatous Bryozoa. Zool. Bidrag. Uppsala 10: 181–507.

Bullivant, J. S. 1967. Aspects of feeding of the bryozoan *Zoobotryon verticillatum* (Delle Chiaje). Ph.D. Thesis. University of Southern California. 165 pp.

————. 1968. The method of feeding of lophophorates (Bryozoa. Phoronida, Brachiopoda). N. Z. J. Mar. Freshwat. Res. 2: 135–146.

Dudley, J. E. 1973. Observations on the reproduction, early larval development, and colony astogeny of *Conopeum tenuissimum* (Canu). Chesapeake Sci. 14: 270–278.

Farre, A. 1837. Observations on the minute structure of some of the higher forms of polypi, with view of a more natural arrangement of the class. Phil. Trans. Roy. Soc. London 127: 387–426.

Gordon, D. P. 1974. Microarchitecture and function of the lophophore in the bryozoan *Cryptosula pallasiana*. Mar. Biol. 27: 147–163.

Grant, R. E. 1827. Observations on the structure and nature of Flustrae. Edinburgh New Philos. J. 3: 107–342.

Hincks, T. 1880. A history of the British marine Polyzoa. Van Voorst. London. 1: 601 pp., and 2: 83 pl.

Hyman, L. H. 1959. The invertebrates. V. 5. McGraw-Hill. New York. 783 pp.

Jebram, D. 1973. Preliminary observations on the influences of food and other factors on the growth of Bryozoa. Kieler Meeresforsch. 29: 50–57.

Kraepelin, K. 1887. Die deutschen Susswasserbryozoen. I. Anatomisch-systematischer Teil. Abhandl. Geb. Naturw., Hrsg. v. Naturw. Ver. Hamburg 10: 1–168.

Lister, J. J. 1834. Some observations on the structure and functions of tubular and cellular polypi, and of ascidiae. Phil. Trans. Roy. Soc. London 124: 365–388.

Loppens, K. 1908. Les bryozoaires d'eau douce. Ann. Biol. Lacustre 3: 141–188.

Lutaud, G. 1955. Sur la ciliature du tentacule chez les bryozaires chilostomes. Arch. Zool. Exp. Gen. 92: 13–19.

————. 1973. L'innervation du lophophore chez le bryozoaire chilostome *Electra pilosa* (L.). Z. Zellforsch. 140: 217–234.

Mangum, C. P., and T. J. M. Schopf. 1967. Is an ectoproct possible? Nature 213: 264–266.

Marshall, S. M. 1973. Respiration and feeding in copepods. Adv. Mar. Biol. 11: 57–120.

Parsons, T. R., and R. J. LeBrasseur. 1970. The availability of food to different trophic levels in the marine food chain. Pages 325–343 *in* J. H. Steele, ed. Marine Food Chains. University of California Press. Berkeley. 551 pp.

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. Proc. 9th Europ. Mar. Biol. Symp.: 363–393.

Silén, L. 1944. On the division and movements of the alimentary canal of the Bryozoa. Ark. Zool. 35A: 1–41.

Smith, L. W. 1973. Ultrastructure of the tentacles of *Flustrellidra hispida* (Fabricius). Pages 335–343 in G. P. Larwood. ed. Living and Fossil Bryozoa. Academic Press. New York. 634 pp.

Strathmann, R. R. 1973. Function of lateral cilia in suspension feeding of lophophorates (Brachiopoda, Phoronida, Ectoprocta). Mar. Biol. 23: 129–136.

Winston, J. E. In press. "Feeding," *in* R. M. Woollacott and R. L. Zimmer, eds. The Biology of Bryozoans. Academic Press. New York.