BRYOZOA FROM THE JURASSIC PORTLAND BEDS OF ENGLAND

by P. D. TAYLOR

ABSTRACT. The Portlandian deposits of southern England contain a moderately abundant, low diversity bryozoan fauna. One new species, *Microecia southwellensis*, is described, and established species, apart from penetrant ctenostomes, are revised. The genus *Elaphopora* is considered invalid and *E. cervina* Lang is referred to *Mesenteripora*. The ecological niche usually occupied in the Jurassic by the cyclostome *Stomatopora* was filled by the earliest known cheilostome bryozoan, *Pyriporopsis portlandensis* Pohowsky, during most of Portlandian times. Animals grazing the surfaces of bivalve shells for food may have affected the bryozoans encrusting these shells.

BEDS of Portlandian age, although not renowned for their bryozoans, contain a moderately abundant fauna of low species diversity. The principal importance of this fauna lies in the occurrence of the only cheilostome bryozoan yet recorded from the Jurassic. *Pyriporopsis portlandensis* Pohowsky, or a closely related species, is likely to have been ancestral to the diverse cheilostomes which dominate present-day bryozoan faunas. With the exception of a few boring ctenostomes (see Pohowsky 1978), all previously described Portlandian bryozoans are cyclostomes. From the French Portlandian of the Boulonnais, d'Orbigny (1851) described *Diastopora tenuis* and Michelin (in Fitton 1839) described *Heteropora fittoni* (see Sauvage 1888), while from the British Portlandian Gregory (1896*a*) described *Berenicea portlandica* and Lang (1925) described *Berenicea damnatorum* and *Elaphopora cervina*. Following a stratigraphical revision of the Portlandian (Wimbledon and Cope 1978) and a sedimentological study of the stage within the type area (Townson 1975), a revision of British Portlandian bryozoans is opportune.

Unless otherwise stated, specimen numbers are British Museum (Natural History) registration numbers.

SYSTEMATIC DESCRIPTIONS

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder TUBULOPORINA Milne-Edwards, 1838
Family ONCOUSOECIIDAE Canu, 1918
Genus MICROECIA Canu, 1918

Type species. *Diastopora sarniensis* Norman, 1864.

Microecia southwellensis sp. nov.

Plate 121, figs. 1, 2

Holotype. D 52652 (Pl. 121, figs. 1, 2) Basal Shell Bed (*kerberus* Zone), Portland Stone, Freshwater Bay (SY 692703), Isle of Portland.

Paratypes. D 52653 (text-fig. 1), D 52654, D 52655 (three specimens) Basal Shell Bed, Freshwater Bay. D 52656 (eight specimens) Basal Shell Bed, Wallsend Cove (SY 677700), Isle of Portland. D 52657 Wockley Micritic Member (*kerberus* Zone), Portland Stone, Chicksgrove Quarry (ST 962296), Tisbury, Wiltshire. D 32676 Portland Sands, *Exogyra* Bed (*albani* Zone), Mutton Cove, Isle of Portland.

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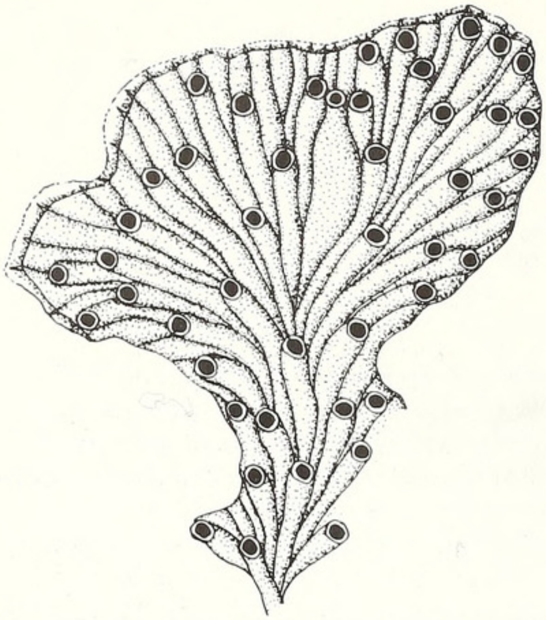
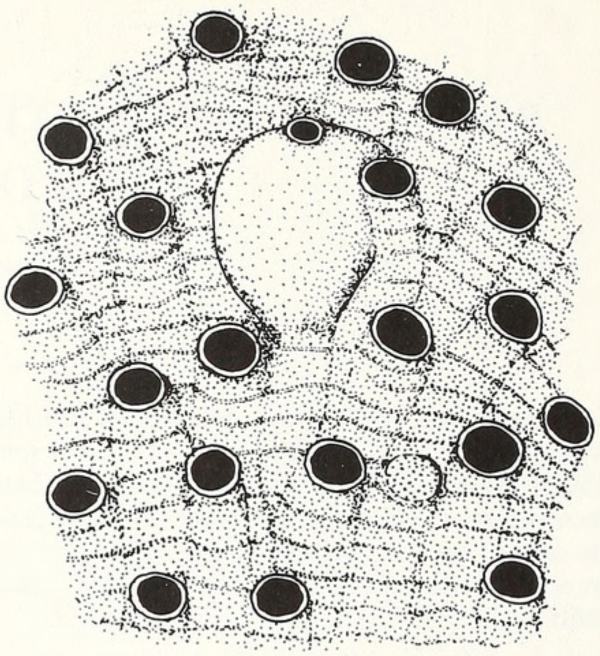


TEXT-FIG. 1. *Microecia southwellensis* sp. nov. Lobe of a colony showing slender autozooecia and a broader gonozooecium. D 52653 Basal Shell Bed (*kerberus* Zone), Portland Stone, Freshwater Bay, Isle of Portland. ×24.



TEXT-FIG. 2. *Hyporosopora portlandica* (Gregory). Autozooecia surrounding a globose gonozooecium. D 52661 Basal Shell Bed (*kerberus* Zone), Portland Stone, Freshwater Bay, Isle of Portland. ×54.

Diagnosis. *Microecia* with adnate branching colonies typically irregular and lobate; autozooecia long and slender with small apertures; gonozooecia long, moderately inflated with small, slightly transversely elongate ooeciopores.

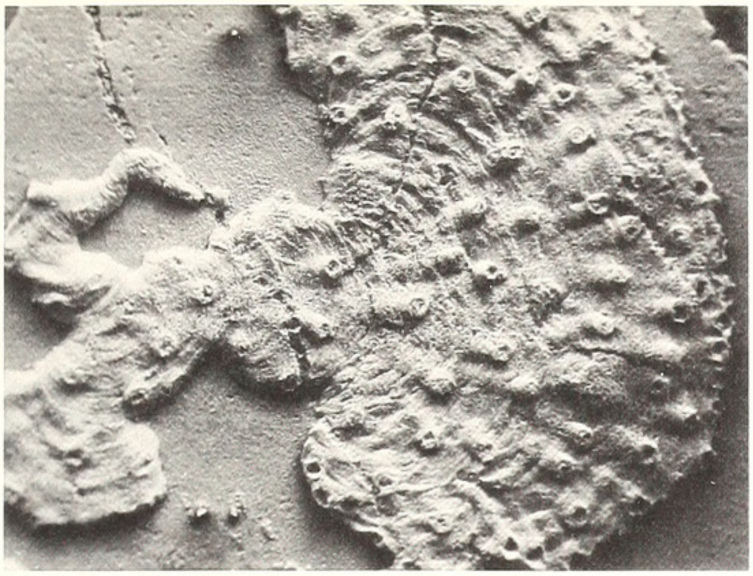
Description. Adnate branching colonies with multiserial ribbons of zooecia (probosciniform). Colony shape tends to be irregular (Pl. 121, fig. 1); colonies may be strongly asymmetrical or possess lobate expansions isolated by regions of occluded growth margin. Arrangement of pseudopores in transverse rows on the colony surface may give colonies a banded appearance. Autozooecia are long, slender and have small apertures which are usually slightly longitudinally elongate (text-fig. 1). Astogenetic variation in autozooecial size is very marked; there is a conspicuous increase in size away from the colony origin within the primary zone of astogenetic change. No ontogenetic zonation is evident and terminal diaphragms have not been observed. Kenozooecia are rare but may occur in the proximity of lateral walls bordering colony branches. Gonozooecia are elongate, moderately inflated and have transversely elliptical ooeciopores (Pl. 121, fig. 2) situated in a slightly subterminal position.

EXPLANATION OF PLATE 121

Figs. 1–2. *Microecia southwellensis* sp. nov. Holotype. D 52652 Basal Shell Bed (*kerberus* Zone), Portland Stone, Freshwater Bay, Isle of Portland. 1. General view showing the irregular form of the colony, ×18. 2. Gonozooecium with ooeciopore (arrowed); growth direction is from left to right, ×55.

Figs. 3–6. *Hyporosopora portlandica* (Gregory). 3–5. D 52658 Wockley Micritic Member (*kerberus* Zone), Portland Stone, Chicksgrove Quarry, Tisbury, Wiltshire. 3. Autozooecia and ridged colony surface, ×40. 4. General view, ×25. 5. Colony growth margin showing interzooecial walls rising from the advancing basal lamina, ×100. 6. D 52659 Basal Shell Bed (*kerberus* Zone), Portland Stone, Freshwater Bay, Isle of Portland, two coalescing fan-shaped subcolonies (origins arrowed) formed by frontal budding through existing autozooecial apertures and spreading over the colony surface, ×70.

All figures are scanning electron micrographs.



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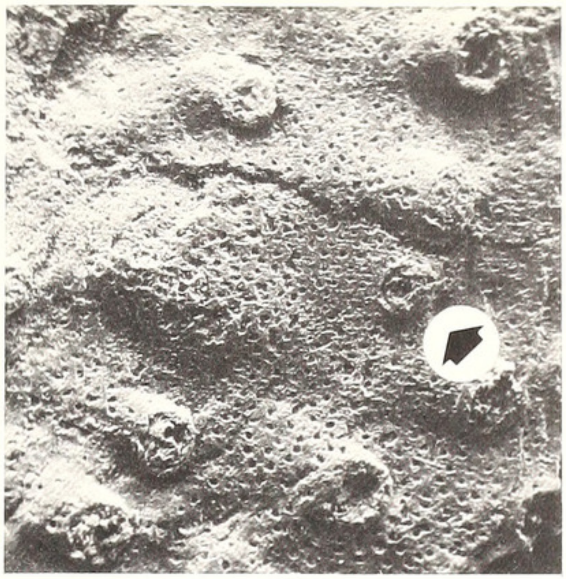

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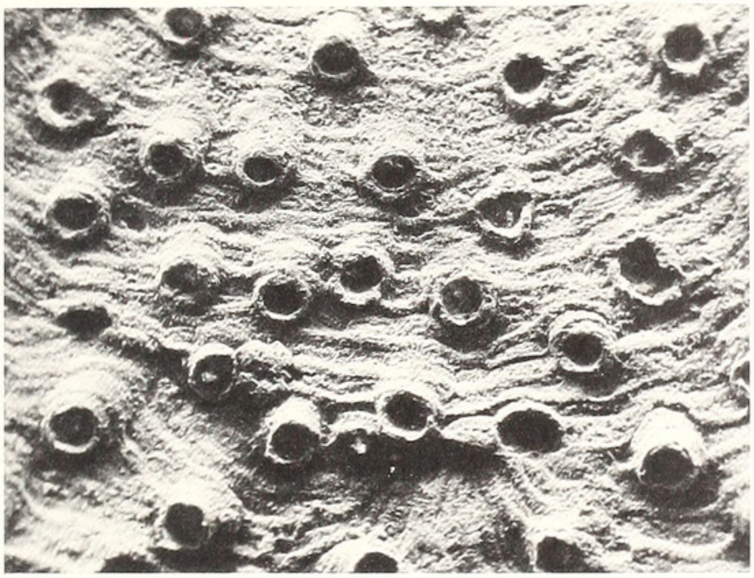

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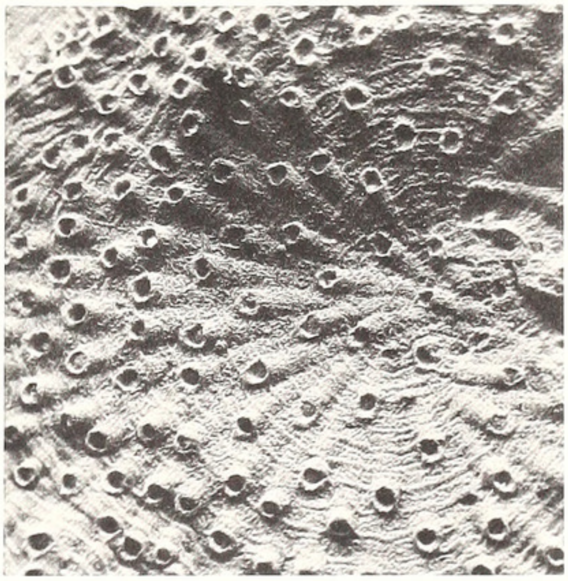

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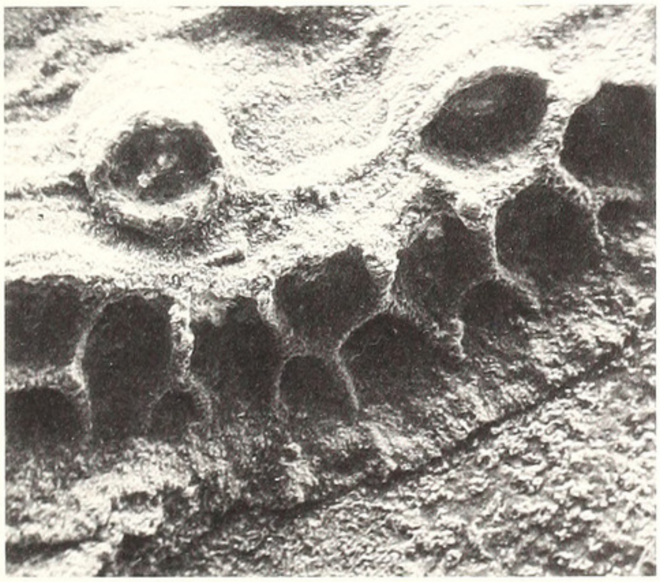

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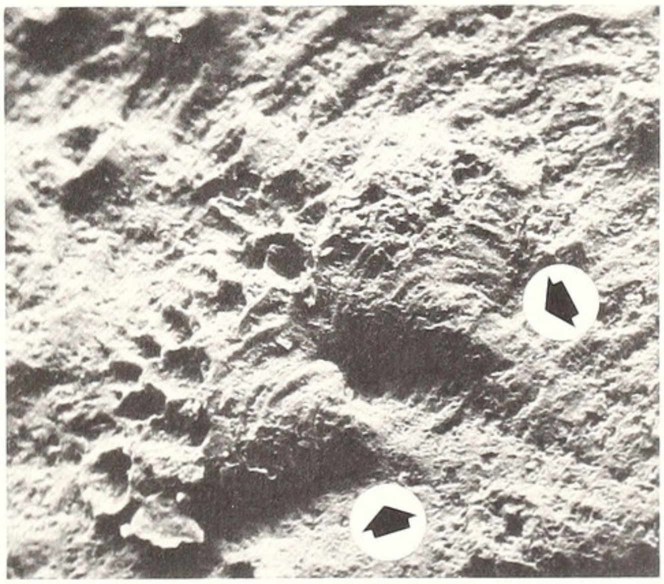

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TAYLOR, Portlandian Bryozoa

TABLE 1. Zooecial dimensions (mm) in *Microecia southwellensis* sp. nov. In addition to the mean value (x̄), observed range (r) is given when sufficient determinations were made. Abbreviations: pd, protoecium diameter; fwl, autozooecium frontal wall length; fww, autozooecium frontal wall width (maximum); law, longitudinal autozooecium aperture width; taw, transverse autozooecium aperture width; tgl, total gonozooecium length (external); gw, gonozooecium width (maximum); low, longitudinal ooeciopore width; tow, transverse ooeciopore width.

	Ancestrula	Autozooecia		Gonozooecia	
Character	x̄	x̄	r	x̄	r
pd	0·14	—	—	—	—
fwl/tgl	0·24	0·81	0·60–1·10	0·91	0·56–1.23
fww/gw	0·10	0·16	0·13–0·20	0·35	0·30–0·44
law/low	0·05	0·08	—	0·04	—
taw/tow	0·05	0·08	—	0·05	—

Remarks. Assignment of this new species to *Microecia*, a genus with an extant type-species, is based largely on the form of the gonozooecia. Colonies of *M. southwellensis* are common in the Basal Shell Bed of the Isle of Portland and it is surprising that the species has remained undescribed. Their straggly form and very slender autozooecia clearly distinguish *M. southwellensis* colonies from the typically discoidal and strongly ridged colonies of *Hyporosopora portlandica* which is also common in the Basal Shell Bed.

Known stratigraphical range. Portlandian, *albani* to *kerberus* Zones.

Family PLAGIOECIIDAE Canu, 1918
Genus HYPOROSOPORA Canu and Bassler, 1929

Type species. Hyporosopora typica Canu and Bassler, 1929.

Emended diagnosis. Plagioeciidae with exclusively adnate colonies in which zooecia bud from a basal lamina; gonozooecia are globular, subtriangular or boomerang-shaped and have inflated frontal walls and small, transversely elliptical ooeciopores.

Remarks. Hyporosopora has been considered to be synonymous with *Plagioecia* Canu 1918 by Walter (1969). However, colonies of the extant type-species of *Plagioecia*, *Berenicea patina* Lamarck 1816, have gonozooecia with extremely broad frontal walls pierced by autozooecial apertures. These gonozooecia contrast with those of so-called *Plagioecia* from the Jurassic.

Hyporosopora portlandica (Gregory 1896)

Plate 121, figs. 3–6, Plate 122, fig. 2

1896*a* *Berenicea portlandica*, sp. n.; Gregory, p. 43.
1896*b* *Berenicea portlandica*, Gregory; Gregory, p. 83, pl. 3, fig. 5.
1979 *Hyporosopora portlandica* (Gregory); Taylor, fig. 3.

Holotype. D 1853 Portland Oolite, Tisbury, Wiltshire. This is the only specimen mentioned by Gregory and it is therefore accepted as the holotype.

Other material. D 7585 locality and horizon unknown. D 20286–91, 93–97, 99–303 Portlandian Oyster Bed, Tilly Whim Caves, Durlston Head, Swanage (mentioned by Woodward 1910). D 47325 Portlandian, probably either Tisbury or Portland (figured by Taylor 1979, fig. 3). D 52658 (Pl. 121, figs. 3–5), D 52669 (7) Wockley Micritic Member, Chicksgrove Quarry, Tisbury. D 52659 (Pl. 121, fig. 6), D 52661 (text-fig. 2), D 52663 (7) Basal Shell Bed, Freshwater Bay, Portland. D 52660 (Pl. 122, fig. 2), D 52662 (sample) Basal Shell Bed, Wallsend Cove, Portland. D 52664 (4) Basal Shell Bed (fallen blocks), Grove Cliff (SY 703719), Portland. D 52665 (2) Portland Stone (fallen blocks), West Weare Cliffs (SY 681725), Portland. D 52666 (4) Roach (*anguiformis* Zone), top Portland Stone, Kingbarrow Quarry (SY 690729), Portland. D 52667 (4) Basal Shell Bed, Chalbury Quarry (SY 693838), Dorset. D 52668 (3) *Exogyra* Bed (*albani* Zone), Portland Sand, Plaisters Lane (SY 697843), Sutton Poyntz, Dorset. D 52673 Arkells Bed J-J1, (*kerberus* Zone), Portland Stone (fallen block), St. Albans Head (SY 959754), Purbeck, Dorset.

Emended diagnosis. Hyporosopora with the zoarial surface crossed by numerous transverse ridges; frontally-budded subcolonies frequent; autozooecia are small and often have transversely elongate apertures; gonozooecia are globular to subtriangular in shape.

Description. Zoaria are adnate, fan-shaped to discoidal (bereniciform), commonly unilamellar but occasionally multilamellar. Zooecia were budded at distal growth margins (Pl. 121, fig. 5) where established interzooecial walls divided on a basal lamina. Multilamellar growth usually resulted from the formation, by frontal budding (cf. cheilostome bryozoans, Banta 1972), of a fan-shaped or discoidal subcolony on the surface of the parent colony (Pl. 121, fig. 6). Overgrowth of the parent colony by peripheral fan-shaped subcolonies and spiral overgrowth around pivot points (Taylor 1976) were further ways in which multilamellar growth could be achieved. Regularly-spaced ridges (0·05–0·10 mm apart) of low profile ornament the zoarial surface transverse to growth direction (Pl. 122, fig. 2) and separate bands of pseudoporous frontal wall. Autozooecia are small and their limits often poorly defined on the colony surface. Autozooecial apertures (Pl. 121, figs. 3, 4) small, most being slightly transversely elongate, although longitudinally elongate apertures may occur in astogenetically early autozooecia. The protoecium averages 0·13 mm in diameter and the ancestrula 0·34 mm in length. Ontogenetic zonation of autozooecia not obvious; terminal diaphragms appear to be irregularly distributed and long peristomes are not preserved. Kenozooecia lacking apertures may occur at both intrazoarial and interzoarial anastomoses. Gonozooecia are subcircular (text-fig. 2) to subtriangular (Taylor 1979, fig. 3) in outline, inflated and devoid of the transverse ridges which elsewhere ornament the zoarial surface. Their small, transversely elongate ooeciopores may be occluded and their tapering ooeciostomes are slightly beyond the inflated portion of the gonozooecium.

Remarks. Colonies of *H. portlandica* are distinguished from other Portlandian bryozoans by their ridged surfaces. This species is by far the most abundant bryozoan in the British Portlandian. Only two other species of encrusting Jurassic bryozoans possess ridged colony surfaces: *Mesenteripora undulata* Michelin and *Mesenteripora? enstonensis* (Pitt and Thomas). *H. portlandica* differs from both by the typically transverse elongation of its autozooecial apertures and by the occurrence of frontal budding. Branching fragments of the cyclostome *Mesenteripora cervina* (Lang) may represent an erect growth stage of *H. portlandica* which would transfer *H. portlandica* into *Mesenteripora* and place *M. cervina* in synonymy with *M. portlandica.*

Known stratigraphical range. Portlandian, *albani* to *anguiformis* Zones.

TABLE 2. Zooecial dimensions (mm) in *Hyporosopora portlandica* (Gregory). Abbreviations as in Table 1 with the following additions: Nz, number of zooecia measured; Nc, number of colonies; Rz, range of zooecial measurements; Rc, range of colony mean values; igl, length of inflated portion of gonozooecium.

Character	Nz	Nc	$\bar{x}$	Rz	Rc
fwl	60	4	0·49	0·32–0·80	0·44–0·56
fww	75	5	0·15	0·11–0·19	0·14–0·17
law	140	10	0·08	0·05–0·11	0·07–0·10
taw	140	10	0·09	0·07–0·13	0·08–0·11
tgl	17	9	0·97	0·69–1·31	0·69–1·24
igl	29	12	0·57	0·32–0·83	0·36–0·83
gw	29	12	0·61	0·23–0·95	0·30–0·95
low	19	8	0·04	0·03–0·07	0·04–0·06
tow	19	8	0·06	0·05–0·07	0·05–0·07

Hyporosopora sp.

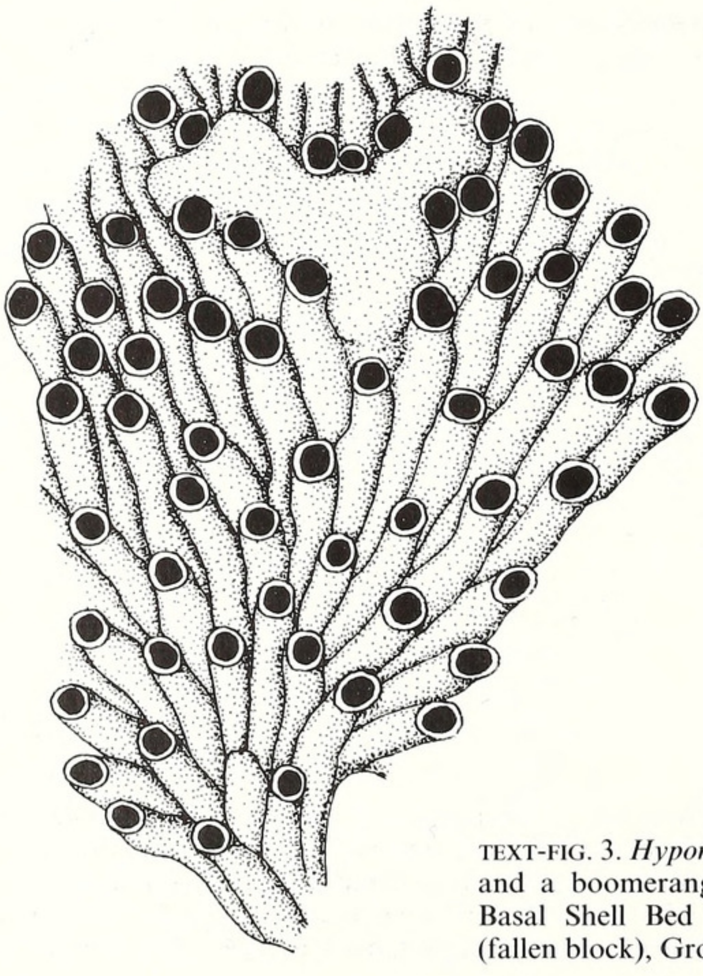
Text-fig. 3

?1851 *Diastopora tenuis*, d'Orb [sp. nov.]; d'Orbigny, p. 55.
?1888 *Rosacilla tenuis*, Orb.; Sauvage, p. 48, pl. 4, figs. 8, 9.
?1925 *Berenicea damnatorum*, new species; Lang, p. 164, text-fig. 4.

Material. D 52672 *Exogyra* Bed (*albani* Zone), Portland Sand, Plaisters Lane, Sutton Poyntz, Dorset. D 52670 Basal Shell Bed, Wallsend Cove, Portland. D 52671 (text-fig. 3) Basal Shell Bed (fallen block), Grove Cliff, Portland.

Description. Adnate fan-shaped or discoidal colonies (bereniciform) with zooecial budding from a basal lamina. Autozooecia are small with an average frontal wall length of 0·50 mm and width of 0·16 mm. Their small apertures are about 0·07–0·10 mm in diameter. Gonozooecia (text-fig. 3) are subtriangular, inflated, about 0·60 mm long, 0·90 mm wide and have small ooeciopores which are transversely elongate (0·05 × 0·07 mm).

Remarks. Colonies of a species of *Hyporosopora* lacking transverse ridges (distinguishing them from *H. portlandica*) occur sporadically in the British Portlandian. They may be equivalent to d'Orbigny's (1851) French Portlandian species *Diastopora tenuis* or to Lang's (1925) *Berenicea damnatorum*. The former species was unassigned by Walter (1969, p. 217) in his revision of French Jurassic bryozoans and Lang's solitary specimen (D 31734) of *B. damnatorum* is too poorly-preserved to permit identification. This Portlandian species of *Hyporosopora* compares with two species recorded from the Middle Jurassic, *H. typica* Canu and Bassler 1929 and *H. parvipora* (Canu and Bassler 1929). Insufficient material prohibits a more certain comparison.



TEXT-FIG. 3. *Hyporosopora* sp. A group of autozooecia and a boomerang-shaped gonozooecium. D 52671 Basal Shell Bed (*kerberus* Zone), Portland Stone (fallen block), Grove Cliff, Isle of Portland. × 28.

Genus MESENTERIPORA de Blainville, 1830

Type species. Mesenteripora michelini de Blainville 1830.

Emended diagnosis. Plagioeciidae with initially adnate zoaria from which erect branches or fronds may arise; zooecia bud from a basal lamina in adnate portions and from both sides of a lamina of interior wall in erect portions of the colony.

Remarks. Plagioeciid species capable of developing erect growth by budding zooecia from both sides of an upright lamina of interior wall (lacking cuticle) are referred to the genus *Mesenteripora.* Erect portions of colonies may be frondose (eschariform) or branching and elliptical (adeoniform) to subcircular (vinculariiform) in cross-section. *Elaphopora* Lang 1925 is a junior synonym of *Mesenteripora. E. cervina* from the Portlandian is the type-species of *Elaphopora* and no other species have been referred to the genus either by Lang or any subsequent workers. *Elaphopora* was apparently founded for erect cyclostomes displaying the following three characteristics: elliptical cross-sectional shape of branches, transverse ridges ornamenting the branch surface, branch division at close intervals. The first two characteristics are know in *Mesenteripora* and the third characteristic seems ecologically controlled and unsuitable for generic division. Consequently, *Elaphopora* is considered to be an invalid genus.

Mesenteripora cervina (Lang, 1925)

Plate 122, fig. 1

1925 *Elaphopora cervina*, new species; Lang, p. 166, text-figs. 5, 6.
1953 *Elaphopora cervina* Lang, 1926 [sic]; Bassler, p. G43, fig. 13, *4*.

Holotype. D 31729 Basal Shell Bed (*kerberus* Zone), Portland Stone, Portland (Pl. 122, fig. 1).

Other material. D 52674 Portland Freestone Member (*?anguiformis* Zone), St. Albans Head, Dorset (text-fig. 4). A further four specimens (D 31730–D 31733) mentioned by Lang (1925) appear to be lost.

TEXT-FIG. 4. *Mesenteripora cervina* (Lang). Part of a branch showing autozooecia and ornament of transverse ridges. Portland Freestone Member (*?anguiformis* Zone), St. Albans Head, Dorset. × 12.

TEXT-FIG. 5. *Pyriporopsis portlandensis* Pohowsky. Dividing and intersecting branches composed of autozooecia with large apertures. D 52679 Wockley Micritic Member (*kerberus* Zone), Portland Stone, Chicksgrove Quarry, Tisbury, Wiltshire. × 19.

Emended diagnosis. *Mesenteripora* with elliptical to subcircular branches ornamented by ridges transverse to growth direction; autozooecia have circular or transversely elongate apertures, gonozooecia are long and attain maximum width at their distal edge.

Description. Zoarial branches are erect and have a circular or elliptical cross-section. Branches dichotomise and successive dichotomies may be closely-spaced (as in the holotype). Zooecia bud from both sides of a narrow lamina (interior wall). Transverse ridges ornament branch surfaces (text-fig. 4) and are spaced about 0·10 to 0·15 mm apart. Autozooecia have frontal walls of variable length and apertures which tend to be slightly transversely elongate, have thick rims and may be occluded by terminal diaphragms level with the zooecial frontal wall. Gonozooecia are elongate, attaining a maximum width at their distal edge.

TABLE 3. Zooecial dimensions (mm) in *Mesenteripora cervina* (Lang). Abbreviations as in Tables 1 and 2.

Character	Nz	Nc	x	Rz	Rc
fww	11	2	0·58	0·40–0·76	0·43–0·72
fwl	11	2	0·24	0·21–0·27	0·24
law	11	2	0·12	0·10–0·13	0·11–0·12
taw	11	2	0·13	0·11–0·14	0·12–0·13
tgl	1	1	1·65	—	—
gw	1	1	0·70	—	—

Remarks. Neither of the available specimens preserve the zoarial base but, by comparison with other Jurassic tubuloporinids, this is likely to be an adnate multiserial expansion of the bereniciform type. The presence of transverse ridges in *M. cervina* raises the possibility that the 'species' represents the erect branches of encrusting *Hyporosopora portlandica* colonies. Discrepancies in zooecial size between *M. cervina* and *H. portlandica* are to be expected in the transition between encrusting and erect growth (see Taylor 1977, p. 78). However, confirmation of a synonymy between *M. cervina* and *H. portlandica* awaits the find of a specimen preserving both encrusting and erect stages of growth. None of the numerous *H. portlandica* specimens examined, many of which are comparatively large and seemingly 'mature' colonies, display any indication of erect growth.

Known stratigraphical range. Portlandian, *okusensis* to *anguiformis* Zone (Lang 1925 mentions the occurrence of this species in the Whit Bed which is *anguiformis* Zone).

EXPLANATION OF PLATE 122

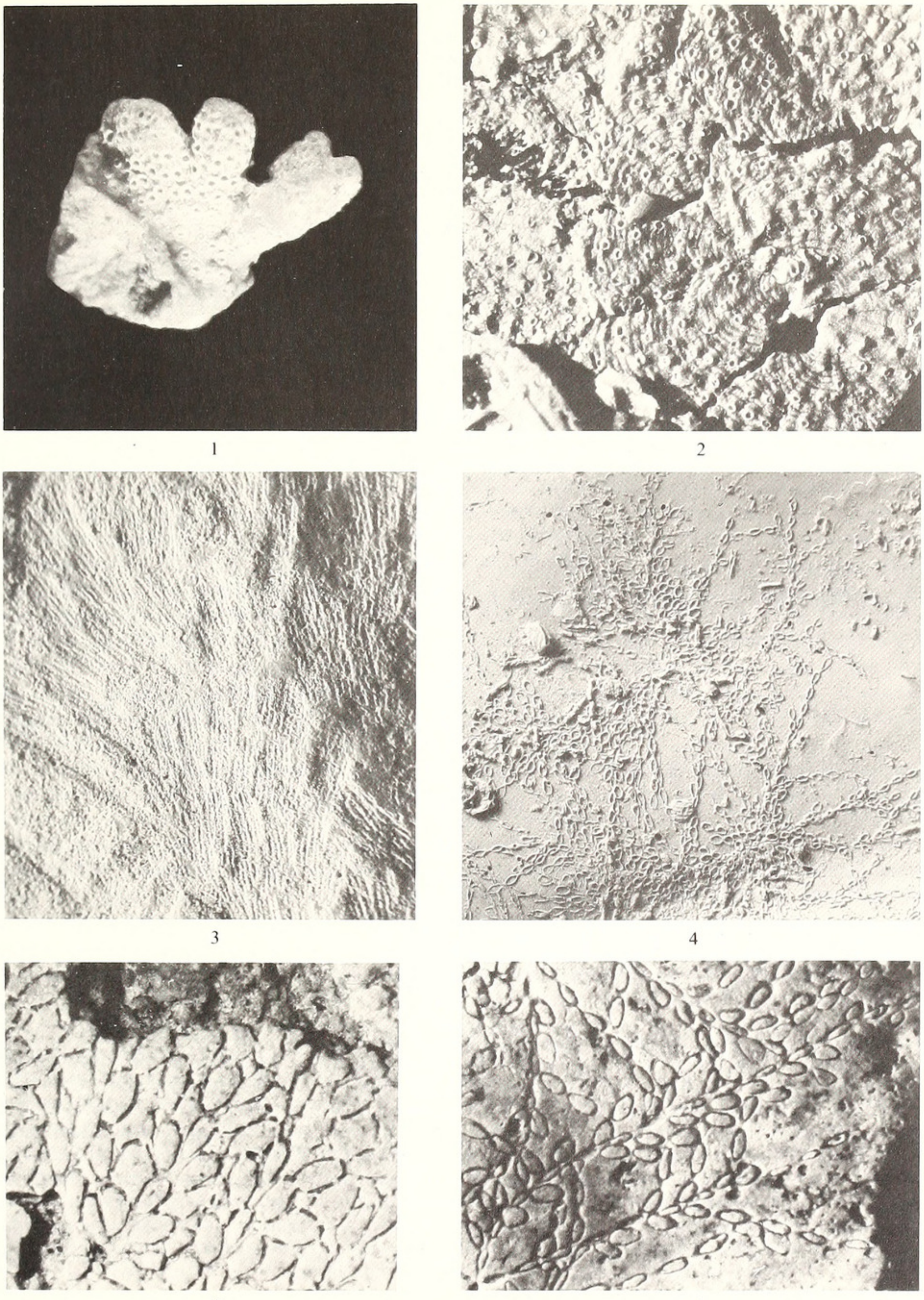
Fig. 1. *Mesenteripora cervina* (Lang). Holotype. D 31729 Basal Shell Bed (*kerberus* Zone), Portland Stone, Isle of Portland, ×9.

Fig. 2. *Hyporosopora portlandica* (Gregory). D 52660 Basal Shell Bed (*kerberus* Zone), Portland Stone, Wallsend Cove, Isle of Portland. Ridged zoarium showing the typical state of preservation, ×13.

Fig. 3. *Radulichnus* sp. D 52658 Wockley Micritic Member (*kerberus* Zone), Portland Stone, Chicksgrove Quarry, Tisbury, Wiltshire. Gastropod grazing traces on a bivalve shell encrusted by *Hyporosopora portlandica* (Gregory), ×50.

Figs. 4–6. *Pyriporopsis portlandensis* Pohowsky. 4. D 52675 Portlandian, ?locality, latex cast of a colony preserved as a mould on the steinkern of a trigoniid bivalve, ×4. 5. D 52676 Cockly Bed (*okusensis* Zone), Portland Stone, Okus Road Quarry, Swindon, pluriserial portion of a colony preserved as a mould on a bivalve steinkern showing sediment-filled dietellae linking adjacent zooecia, ×16. 6. D 52677 Cockly Bed, Okus Road Quarry, Swindon, uniserial growth in a colony preserved as a mould on a bivalve steinkern, ×10.

Fig. 3 is a scanning electron micrograph, the remainder are light photomicrographs.



TAYLOR, Portlandian Bryozoa

Family STOMATOPORIDAE Pergens and Meunier, 1886
Genus STOMATOPORA Bronn, 1825

Type species. Alecto dichotoma Lamouroux, 1821.

Stomatopora sp.

Material. D 32676 *Exogyra* Bed (*albani* Zone), Mutton Cove, Isle of Portland.

Description. Colony of adnate, bifurcating branches with uniserial rows of zooecia between 0·7 and 0·9 mm in length. Zooecia maintain a fairly constant width (*c.* 0·35 mm) throughout their length and have small apertures of about 0·06–0·09 mm diameter.

Remarks. This unreferred species of *Stomatopora* is represented by a single fragmentary colony which resembles *S. dichotomoides* (d'Orbigny) but is distinguished by its smaller apertural dimensions.

Known stratigraphical range. Portlandian, *albani* Zone.

Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMATA Busk, 1852
Family ELECTRIDAE Stach, 1937
Genus *Pyriporopsis* Pohowsky, 1973

Type species. Pyriporopsis portlandensis Pohowsky, 1973.

Diagnosis. (see Pohowsky 1973).

Pyriporopsis portlandensis Pohowsky 1973

Plate 122, figs. 4–6; text-fig. 5.

1973 *Pyriporopsis portlandensis*, new species; Pohowsky, p. 448, fig. 1, pl. 1, figs. 1–3, 5–6.

Holotype. D 52046 Portland Roach, uppermost Portland Stone, Isle of Portland.

Paratypes. Institute of Geological Sciences (London) 48594 top of Portland Stone, Swindon. D 52047, D 52048 Basal Shell Bed, Portland Stone, west coast of Isle of Portland. D 52049 Portlandian, Aylesbury. D 52050 Portland Roach, quarry west of Easton, Isle of Portland.

Other material. D 52675 Portlandian, ?locality (Pl. 122, fig. 4). D 52676 (Pl. 122, fig. 5), D 52677 (Pl. 122, fig. 6), D 52678 (8) Cockly Bed (*okusensis* Zone), Okus Road Quarry (SU 148836), Swindon, Wiltshire. D 52679 (text-fig. 5) Wockley Micritic Member, Chicksgrove Quarry, Tisbury. D 52680 Roach (*anguiformis* Zone), Portland Stone, Kingbarrow Quarry, Portland.

Description. Commonly uniserial, occasionally pluriserial, encrusting colonies composed of chains of autozooecia (Pl. 122, figs. 4, 6) each giving rise to a distal bud and often to one or two disto-lateral buds. Autozooecia are oval to pyriform in shape and have large, longitudinally elongate apertures with rims which bear short, radially-arranged ridges (text-fig. 5). Autozooecial length averages about 0·55 mm, width 0·32 mm, aperture length 0·41 mm and aperture width 0·20 mm. Autozooecia tend to be longer and narrower in uniserial portions of colonies than in crowded pluriserial portions. Lateral walls of autozooecia contain a variable number of chambers, interpreted as dietellae (or pore chambers) by Pohowsky (1973), which either open to the exterior via a small pore or connect with contiguous autozooecia (Pl. 122, fig. 5). Apertures may be closed by a calcareous diaphragm, suggesting polypide degeneration, and the occurrence of one or more concentric zooecial walls within some zooecia is evidence for polypide regeneration. Zones of astogenetic change are defined by an increase in autozooecium length, brought about largely by caudal extension, for the first four to six generations of each linear series of zooecia.

Remarks. This distinctive species has importance as the earliest known cheilostome bryozoan and the only cheilostome found in the Jurassic. The supposed Jurassic cheilostomes described by Gregory

(1894) were shown to be of Cretaceous age by Voigt (1968). The inconspicuous nature of *P. portlandensis* colonies together with their tendency to encrust concave surfaces accounts for the late discovery of such an important bryozoan species.

Known stratigraphical range. Portlandian, *okusensis* to *anguiformis* Zones.

PALAEOECOLOGY

Portlandian bryozoans are found encrusting a variety of shell substrates including ammonites, bivalves, and gastropods. Some may have colonized the shells of living organisms. For example, *Hyporosopora portlandica* colonies are sometimes found to be concentrated around the ventral margins of articulated *Camptonectes lamellosus* shells where the bryozoan colonies may have benefited from the feeding currents of the living bivalve. In other instances, however, post-mortem associations can be demonstrated by the attachment of the bryozoans to internal surfaces of bivalve shells or ammonite body chambers. An associated encrusting epifauna of serpulids (*Glomerula* and *Mucroserpula*) and oysters (e.g. *Nanogyra nana*) apparently competed with the bryozoans for substrate space. The adnate bivalves are commonly found to have overgrown the bryozoans, the bryozoans in turn usually overgrow the serpulids, while competition between bryozoan species usually resulted in overgrowth of *Microecia southwellensis* by *Hyporosopora portlandica*.

Bryozoan-encrusted bivalve shells from the Wockley Micritic Member of Tisbury may be marked by numerous small grooves (Pl. 122, fig. 3), *Radulichnus* Voigt 1977, attributed to the rasping radula of a gastropod or chiton grazing the surface of the shell, perhaps for encrusting algae. The pentaradiate grazing traces of echinoids, *Gnathichnus* Bromley 1975, are also evident on these shells from Tisbury and on bivalve shells from the Basal Shell Bed and Roach of Portland. Bryozoan colonies attached to such shells are often found to be heavily abraded. Most of the zoarium may be missing, with the exception of the basal lamina and stumps of the interzooecial walls. It seems possible that this damage was caused by the same animals which created the trace fossils *Radulichnus* and *Gnathichnus* either incidentally during herbivorous grazing or intentionally during active predation on the bryozoans. In both cases the molluscs and echinoids may have had a significant effect on the encrusting bryozoan fauna. Their activities may account for the absence of large bryozoan colonies and for the success of *Hyporosopora portlandica* with transverse ridges which would have strengthened the zoarium against bioerosion.

Although *Microecia southwellensis* and *Hyporosopora portlandica* are often found encrusting shell exteriors, the cheilostome *Pyriporopsis portlandensis* preferred the cryptic habitats provided by concave shell interiors. *P. portlandensis* colonies are commonly found as impressions on the surfaces of steinkerns of trigoniid bivalves. The cheilostome probably encrusted hidden concave surfaces of disarticulated bivalve shells resting convex upwards on the sea-bed (cf. Bosence 1979). *P. portlandensis* appears to have replaced the cyclostome *Stomatopora* in habitats of this type during most of Portlandian time. Elsewhere in the Jurassic coexistence of *Stomatopora* and bereniciform bryozoans (e.g. *Hyporosopora*) is ubiquitous (Taylor 1979) but *Stomatopora* is significantly rare in Portlandian beds. The first known cheilostome bryozoan may have evolved as a fugitive species which favoured cryptic habitats where competition for substrate space and predation pressure were relatively lax.

A notable feature of all Portlandian bryozoans is the small size of their zooids. This they share with Mesozoic bryozoans found in other chalky, micritic carbonates e.g. the Bathonian White Limestone of Oxfordshire and much of the Chalk. Small zooid size may be an adaptive character developed in tranquil environments of micrite sedimentation where a large surface area: volume ratio would have conferred respiratory and filter-feeding advantages.

DISCUSSION

The low species diversity of British Portlandian bryozoans requires explanation. Other Jurassic carbonate sequences, providing they contain the shells of epifaunal animals for encrustation, may yield bryozoan faunas which are considerably more diverse. Echinoderm diversity is also low in the British Portlandian and certain groups (corals, belemnites, brachiopods) appear to be either very rare or totally absent. Some form of environmental instability may have been responsible for these low diversities (see Hallam, 1975, pp. 213–220). Salinity fluctuations are one possibility (Ager and Wallace 1970) and, in the case of the bryozoans, the absence of pauses in sedimentation sufficient to allow synsedimentary lithification may have been a contributory factor. Jurassic deposits yielding the richest diversities of bryozoans invariably reveal evidence of synsedimentary lithification in the form of hardgrounds and intraclasts. Notable among these are the Upper Aalenian Pea Grit of Gloucestershire (Richardson 1904), the Upper Bajocian Microzoa Beds of Dorset (Walter 1967) and the Upper Bathonian Bradford Clay of Wiltshire (Palmer and Fürsich 1974).

The Portlandian bryozoans are sufficiently distinctive to be potentially valuable in the identification of Portlandian age sediments in Britain. *Hyporosopora portlandica* is a particularly characteristic and common species which occurs only in the Portlandian and *Pyriporopsis portlandensis* may be similarly confined. However, the stratigraphical value of the bryozoans requires testing by studies of Portlandian and contiguous deposits from other parts of the world.

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