TWO NEW JURASSIC BRYOZOA FROM SOUTHERN ENGLAND

by PAUL D. TAYLOR

ABSTRACT. *Reptomultisparsa tumida* sp. nov. and *Reptoclausa porcata* sp. nov. are described respectively from the Bathonian Bradford Clay of Bradford-on-Avon and the Aalenian/Bajocian Inferior Oolite of the Cotswold Hills. The genus *Reptoclausa* was previously known only from the Cretaceous. *Reptoclausa* colonies have autozooecia located on longitudinal ridges which are separated by furrows composed of kenozooecia. This unusual arrangement of zooecia can be explained by the action of physiological growth gradients during colony life.

DURING a revision of some Jurassic Bryozoa from England and Normandy (Taylor 1977) two new species were recognized and are described for the first time in this paper. Both species are encrusting forms belonging to the Order Cyclostomata, the most abundant group of bryozoans during a period of relatively low species diversity. A tentative estimate of known Jurassic bryozoan diversity based on available data suggests the existence of about ninety species belonging to approximately thirty genera, although these figures are undoubtedly an underestimate of total worldwide diversity for three main reasons. First, almost all known Jurassic bryozoans have been described from either England, France, or Germany; they are extremely poorly known from other parts of the world (see Taylor 1977, pp. 336-338). Secondly, high levels of phenotypic variation within species of simple morphology has hindered taxonomic discrimination and quite probably has led to undersplitting. Genetic studies (e.g. Thorpe *et al.* 1978) of living bryozoans are beginning to reveal the presence of 'cryptic' species that are difficult to distinguish morphologically. Thirdly, non-calcified ctenostome bryozoans with a low fossilization potential were perhaps much more common during the Jurassic than is immediately obvious (Voigt 1977; Pohowsky 1978; Taylor 1978). Despite their low apparent diversity Jurassic bryozoans are ubiquitous in marine sediments, which accumulated in aerobic environments containing firm substrates (e.g. brachiopod shells) suitable for colony attachment. Some species developed erect growth from an attached base but the commonest species were totally encrusting, as are the two new species described here.

Type and figured specimens are housed in the British Museum (Natural History) (BMNH).

FAMILIAL CLASSIFICATION OF JURASSIC TUBULOPORINID BRYOZOA

The order Cyclostomata was represented in the Jurassic by two suborders, the Tubuloporina and the Cerioporina. Six major Jurassic families of the Tubuloporina may be distinguished: Stomatoporidae, Oncousoeciidae, Macroeciidae (= Multisparidae), Plagioeciidae, Theonoidae, and Frondiporidae. The stomatoporids are typically encrusting uniserial or narrow multiserial ('ribbon-shaped') genera, apparently lacking the larval brooding polymorphs known as gonozooids which characterize the other tubuloporinid families. Oncousoecids have branching adnate colonies and gonozooids with minute ooeciopores. Macroecid and plagioecid genera developed a variety of convergent colony forms, both erect (e.g. '*Entalophora*', '*Pustulopora*') and encrusting (e.g. '*Berenicea*'), but the two families may be distinguished from one another by the structure of their gonozooids. Macroecid gonozooids are longitudinally elongate and possess comparatively large ooeciopores (the orifice through which the larvae were released). Plagioecid gonozooids are broad, bulbous and possess

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ooeciopores which are considerably smaller than the apertures of autozooids in the same colony. In both the theonoids and the frondiporids, groups of contiguous autozooidal apertures form fascicles elevated above the general level of the colony surface. Frondiporid zooids are typically longer than those of theonoids and, whereas zooidal budding occurred within the lengthening frondiporid fascicles, within-fascicle zooidal budding is not known in the theonoids.

SYSTEMATIC PALAEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder TUBULOPORINA Milne-Edwards, 1838
Family MACROECIIDAE Canu, 1918
Genus REPTOMULTISPARSA d'Orbigny, 1853

(see Walter 1969, p. 75, for a revised generic diagnosis)

Reptomultisparsa tumida sp. nov.

Plate 88, fig. 1; text-fig. 1

Derivation of name. The trivial name *tumida* refers to the broad, swollen appearance of the gonozooecia.

Holotype. BMNH D13346 Bathonian, Bradford Clay (*discus* Zone), Bradford-on-Avon, Wiltshire.

Paratypes. BMNH D52651a–c, Bathonian, Bradford Clay, locality unknown. Other specimens in the authors collection are from the Bathonian White Limestone Formation of Foss Cross, Gloucestershire.

Diagnosis. *Reptomultisparsa* with delicate unilamellar zoaria; autozooecia with maximum width midway along their frontal walls and possessing small apertures; gonozooecia broad and inflated.

Description. Zoaria (Pl. 88, fig. 1) are unilamellar, fan-shaped, or discoidal (bereniciform). Zooecia arise at divisions of existing interzooecial walls on a basal lamina.

Autozooecia have moderately long frontal walls characteristically attaining maximum width midway along their length. Interzooecial walls form conspicuous traces on the relatively flat zoarial surface. The small, circular autozooecial apertures are widely spaced and have raised rims but lack distinct peristomes.

Kenozooecia may occur around gonozooecial borders. Their proximal portions are identical to those of autozooecia but the kenozooecia are truncated distally by gonozooecial dilation and consequently lack an aperture.

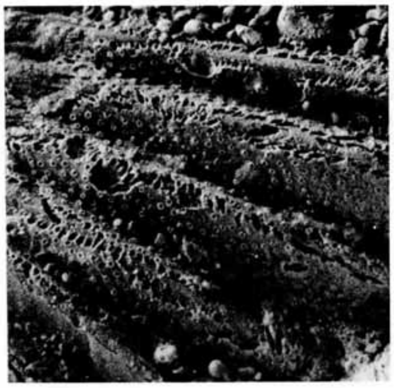
Gonozooecia (text-fig. 1) have narrow proximal portions and well-defined inflated distal portions with a circular to oval shape. The sub-terminal ooeciopores lack ooeciostomes and are transversely elongate and slightly smaller than autozooecial apertures.

EXPLANATION OF PLATE 88

Fig. 1. *Reptomultisparsa tumida* sp. nov. BMNH D13346, Holotype colony, Bathonian, Bradford Clay, Bradford-on-Avon, ×7.

Figs. 2–6. *Reptoclausa porcata* sp. nov. 2, BMNH B4855, immature colony prior to ridge development, Bajocian, Lower Ragstone, Cold Comfort, ×7. 3–5, BMNH D8724, Holotype, Aalenian, Pea Grit, Birdlip. 3, intracolony overgrowth by a new layer of zooecia, ×11. 4, furrow occupied by kenozooecia (centre right), ×13. 5, autozooecia with rounded distal terminations, ×30. 6, BMNH D10091, zoarium showing conspicuous furrows and ridges with a ridge dichotomy, Aalenian, Pea Grit, Crickley Hill, ×8.

Figs. 1 and 2 are of ammonium chloride coated specimens.



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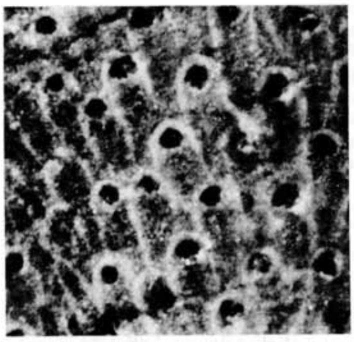

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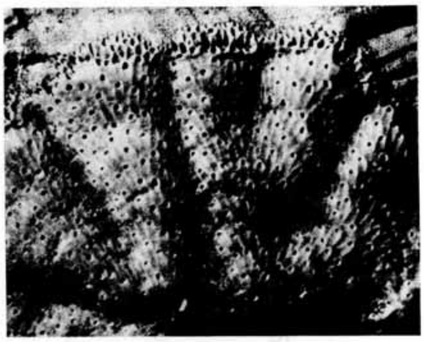

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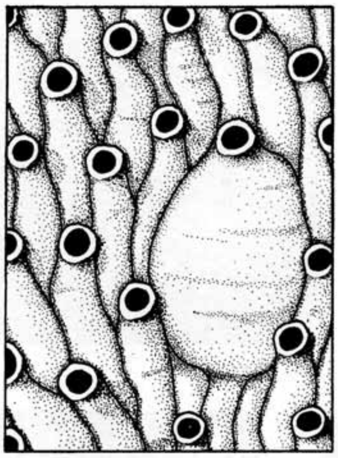
TAYLOR, Jurassic Bryozoa



TEXT-FIG. 1. *Reptomultisparsa tumida* sp. nov. BMNH D13346 (holotype), Upper Bathonian, Bradford Clay, Bradford-on-Avon, Wiltshire. A group of autozooecia and a bulbous gonozooecium. ×38.

Dimensions. See Table 1.

Remarks. The relatively broad and inflated gonozooecia of *Reptomultisparsa tumida* distinguish it from other species in the genus, and the subterminal position of the ooeciostome contrasts with the terminal ooeciostomes developed in plagioecids with similar bereniciform colonies.

Stratigraphical range. Upper Bathonian.

TABLE 1. Dimensions (in mm) of *Reptomultisparsa tumida* zooecia. Abbreviations of morphological characters: law, longitudinal autozooecial aperture width; taw, transverse autozooecial aperture width; fwl, autozooecial frontal wall length; fww, autozooecial frontal wall width (maximum); tgl, total gonozooecial frontal wall length; igl, length of inflated portion of the gonozooecial frontal wall; gw, gonozooecial frontal wall width (maximum); low, longitudinal ooeciopore width; tow, transverse ooeciopore width. Abbreviations of statistical functions: Nc, number of colonies from which measurements were taken; Nz, number of zooecia measured; x̄, mean value; Rc, range of colony means; Rz, total range of values.

	Nc	Nz	x̄	Rc	Rz
law	3	55	0·08	0·08	0·06–0·10
taw	3	55	0·08	0·08	0·06–0·09
fwl	3	55	0·67	0·63–0·69	0·46–0·88
fww	3	55	0·18	0·17–0·19	0·14–0·21
tgl	3	3	1·44	1·20–1·82	1·20–1·82
igl	3	6	1·11	0·92–1·34	0·86–1·34
gw	3	6	0·62	0·53–0·67	0·51–0·80
low	3	5	0·06	0·06	0·05–0·07
tow	3	5	0·07	0·06–0·08	0·06–0·10

Genus REPTOCLAUSA d'Orbigny, 1853

Reptoclausa porcata sp. nov.

Plate 88, figs. 2–6; text-fig. 2

?1894 *Berenicea allaudi* (Sauvage); Gregory, p. 60.
1896*a* *Berenicea Allaudi* (Sauvage); Gregory, p. 44 (*partim.*).
1896*b* *Berenicea allaudi* (Sauvage); Gregory, p. 77 (*partim.*), pl. 3, fig. 6.
1969 *Idmonea triquetra* Lamouroux; Walter, p. 52 (*partim.*), pl. 3, figs. 11–13 only.

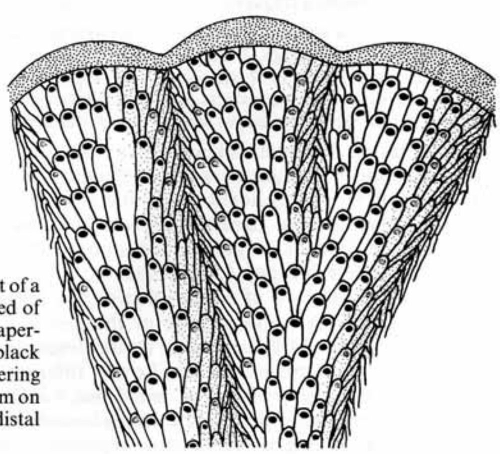
Derivation of name. The trivial name *porcata* refers to the ridged and furrowed form of the zoarium.

Holotype. BMNH D8724, Aalenian, Pea Grit (*murchisonae* Zone), Birdlip, Gloucestershire.

Paratypes. BMNH D7526a–b, Aalenian, Pea Grit (*murchisonae* Zone), near Stroud, Gloucestershire. BMNH D31586, Aalenian, Lower Limestone (*murchisonae* Zone), Crickley Hill, Gloucestershire. BMNH B2290a–c, Inferior Oolite, Crickley Hill, Gloucestershire. BMNH B4855, Lower Ragstone (*discites* Zone), Cold Comfort, Gloucestershire. BMNH D1795, Inferior Oolite, ?locality. BMNH D10091, Pea Grit (*murchisonae* Zone), Crickley Hill, Gloucestershire. BMNH D30002a–c, Lower Limestone (*murchisonae* Zone), Kimsbury, Painswick, Gloucestershire.

Diagnosis. *Reptoclausa* with continuous autozooecial ridges separated by furrows of kenozooecia; zoaria commonly unilamellar, occasionally multilamellar.

Description. Zoaria are adnate, fan-shaped (Pl. 88, fig. 2) to discoidal, commonly unilamellar but occasionally multilamellar (Pl. 88, fig. 3). Zooecia arise where existing interzooecial walls divide on a basal lamina at the colony growth margin. Rounded ridges of low profile cross the zoarial surface parallel to the direction of growth and form lobate projections where they meet the colony growth margin (Pl. 88, fig. 6). Ridge crests are about 2 mm apart and new ridges appear at dichotomies of established ridges. Ridges are occupied by autozooecia orientated with their long axes slightly divergent from the ridge crest. Zooecium size, particularly width, decreases progressively away from ridges towards intervening furrows occupied by kenozooecia (text-fig. 2). Multilamellar growth was achieved either by spiral overgrowth around irregularly distributed pivot points (Taylor 1976), or by a process, comparable with the frontal budding known in cheilostomes (Banta 1972), in which an overgrowing zooecium arose from an autozooecial aperture to initiate a fan-shaped expansion on the zoarial surface. The first zooecium of each new frontally budded layer has a short frontal wall and a longitudinally elongate aperture.



TEXT-FIG. 2. Semidiagrammatic representation of part of a *Reptoclausa porcata* colony showing ridges composed of autozooecia and furrows of kenozooecia lacking apertures. Open autozooecial apertures are shown in black and the occluded apertures of autozooecia bordering kenozooecial furrows are stippled. The large zooecium on the left-hand ridge is a gonozooecium. The lobate distal growth margin is evenly stippled. Approx. × 18.

Frontal walls of autozooecia are thick, have rounded distal terminations (Pl. 88, fig. 5), and are clearly defined by traces of vertical interzooecial walls on the zoarial surface. Autozooecial apertures are slightly transversely elongate. Thin-walled peristomes are preserved only when immured by intracolony overgrowths. Terminal diaphragms, level with the frontal walls, frequently occlude zooecia, particularly those situated at boundaries between ridges and furrows (text-fig. 2). Ontogenetic zonation (Silén and Harmelin 1974) of autozooecia is not apparent.

Kenozooecia, occurring regularly in furrows between autozooecial ridges (Pl. 88, fig. 4), have narrow frontal walls defined by the faint traces on the zoarial surface of their vertical interzooecial walls. Less elongate kenozooecia may occur at growth margin anastomoses and in the vicinity of zoarial lateral walls.

Gonozooecia are developed in about 50% of the zoaria examined. They are elongate, slightly dilated in width and inflated, and are situated on zoarial ridges. The transversely elongate ooeciopores are about the same size as autozooecial apertures.

Dimensions. See Table 2.

TABLE 2. Dimensions (in mm) of *Reptoclausa porcata* zooecia. Abbreviations as in Table 1.

	Nc	Nz	$\bar{x}$	Rc	Rz
law	5	125	0·10	0·09–0·10	0·07–0·11
taw	5	125	0·10	0·09–0·11	0·08–0·13
fwl	5	125	0·61	0·52–0·66	0·40–0·80
fww	5	125	0·22	0·22–0·23	0·18–0·29
tgl	4	34	1·70	1·62–1·77	1·17–2·25
gw	4	36	0·43	0·37–0·46	0·35–0·59
low	3	19	0·09	0·08–0·09	0·07–0·13
tow	3	19	0·12	0·11–0·14	0·10–0·15

Remarks. Among the specimens included by Gregory (1869*b*) in *Berenicea allaudi* (Sauvage) are two (BMNH D1794, D1795) belonging to this new species. *Rosacilla allaudi* of Sauvage (1888) is a simple, multiserial tubuloporinidean lacking ridged zoaria and quite distinct from the species figured as *Berenicea allaudi* by Gregory (1896*b*, pl. 3, fig. 6). Walter (1969, p. 52) includes specimens of *Reptoclausa porcata* within *Idmonea triquetra* Lamouroux 1821. *Reptoclausa porcata*, however, differs from *Idmonea triquetra* in the following features:

1, *R. porcata* zoaria have a fan-shaped to discoidal form whereas zoaria of *I. triquetra* consist of dichotomising narrow multiserial branches. 2, The branches of *I. triquetra* have a well-defined triangular cross-section distinct from the rounded ridges of *R. porcata*. 3, Ooeciopores of *I. triquetra* are about half the diameter of *R. porcata* ooeciopores. 4, *I. triquetra* zooecia are usually arranged in distinct rows. Those of *R. porcata* are not usually arranged in rows and have larger frontal wall dimensions.

Furthermore, *R. porcata* is known only from the Upper Aalenian and Lower Bajocian, whereas the probable range of *I. triquetra* is Upper Bajocian to Lower Callovian (Walter 1969).

Hillmer (1971, p. 42) noted the similarity between Lower Cretaceous *Reptoclausa* and two of Walter's (1969) figured *Idmonea triquetra* specimens (BMNH D10091, D31586) which are here included in *R. porcata*. *R. porcata* differs from the Lower Cretaceous type-species of *Reptoclausa*, *R. neocomiensis* d'Orbigny (redescribed by Hillmer 1971), which has autozooecial ridges discontinuous in the direction of colony growth and kenozooecia occupying a larger proportion of the zoarial surface. The known range of the genus *Reptoclausa* is extended back from the Lower Cretaceous into the Middle Jurassic by the description of *R. porcata*.

R. porcata is abundant in the Lower Inferior Oolite of the Cotswolds where, along with *Reptomultisparsa cricopora* and *R. ventricosa*, it is found encrusting a variety of substrates including the large terebratulid brachiopod *Pseudoglossothyris simplex* and limestone intraclasts. Some of the brachiopod-encrusting colonies may represent associations with a living brachiopod because bryozoan growth is frequently found to terminate at a growth line on the brachiopod shell suggesting that growth of both bryozoan and brachiopod were checked simultaneously but, whereas brachiopod growth later recommenced, bryozoan growth did not (Ager 1961).

Stratigraphical range. Upper Aalenian–Lower Bajocian.

Discussion. The morphology of *Reptoclausa porcata* contrasts with that of most other multiserial encrusting tubuloporinideans (e.g. *Reptomultisparsa tumida*) and deserves further consideration. In colonies of *Reptoclausa porcata* zooecium size, particularly frontal wall width, decreases progressively passing from the crests of the ridges to the bottoms of the furrows (text-fig. 2). Ridge crests bear broad autozooecia, furrows are composed of narrow kenozooecia, and the intervening regions between ridge crests and furrows possess comparatively narrow autozooecia typically occluded by terminal diaphragms. This type of morphological gradient perpendicular to the growth direction of the colony suggests the presence during life of a physiological gradient (Bronstein 1939; Anstey *et al*. 1976), perhaps hormonal, which determined zooid structure according to position of budding. Comparatively large zooids were budded at regularly spaced loci along the growing edge of the colony. Here, the zoarium was differentially thickened to give a ridge which formed a lobate projection where it intersected the colony growing edge. These large zooids displayed a dominance over zooids budded between loci causing them to be crowded and reduced in size. The smallest zooids budded between loci were too small to support a functional polypide (gut and tentacles) and thus became kenozooids. It seems that zooids of intermediate size could support only a short-lived polypide whose degeneration was followed by early occlusion of the zooecial aperture by a terminal diaphragm. The functional significance of the unusual arrangement of autozooecia and kenozooecia in *Reptoclausa* is unclear but may relate to the maintenance of efficient colony feeding, with autozooid exhalent currents departing from the colony surface above regions of non-feeding kenozooids (see Taylor 1979).

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