LIFE HISTORIES OF SOME MESOZOIC ENCRUSTING CYCLOSTOME BRYOZOANS

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ABSTRACT. Single-layered, multiserial cyclostome bryozoans are almost ubiqitous as encrusters of Mesozoic hard substrata but little attention has been paid previously to the attributes of their life histories obtainable from their fossil skeletons. Colonies from 'populations' of one Triassic, five Jurassic and nine Cretaceous species from England and Slovakia are here studied using an image analyser to record colony size and shape, and the number, location and sizes of larval brood chambers. Survivorship curves relative to colony size demonstrate varying patterns of mortality for different species. None of the species shows evidence of a fixed maximum colony size. Some species were capable of producing frontal, or more commonly, peripheral subcolonies. These species typically have smaller colonies than species without subcolonies. Colony size at the onset of female sexual reproduction was found to be relatively constant in some species but variable in most, possibly indicating that an environmental cue triggered reproduction. Most colonies reproduced only once (semelparity) and apparently died shortly afterwards, but a few survived to reproduce a second time (iteroparity). No correlation among species was found between skeletal measures of reproductive effort and colony size. Flexibility in life history patterns predominate in the 15 studied species, the one notable exception being *Actinopora disticha* which was relatively deterministic.

SENESCENCE is not a necessary attribute of the life history of clonal organisms (Sackville Hamilton *et al.* 1987 and references therein; Orive 1995), and indeed the ages attained by some plants, corals, and bryozoans have been shown to be very great, up to at least 13000 years for plants (Cook 1983). These organisms show no signs of clonal senescence and are, at least in comparison with solitary organisms, potentially immortal except for the ever-present possibility of death from extrinsic, environmental causes.

Despite apparent potential immortality, clonal organisms exhibit a wide spectrum of life histories. Some have strongly deterministic growth and may have brief, truncated life-spans, sometimes with clonal senescence (e.g. Chadwick-Furman and Weissman 1995), while others may be longer-lived and have chaotic growth patterns that are disrupted locally by small-scale biotic and abiotic environmental perturbations. Some clonal organisms track an environment through directed growth; for example, they are capable of maintaining local growth trajectories indefinitely within long-lived stationary or slowly migrating environments (e.g. Lasker 1983). However, most clonal taxa fall between such extremes and have their life-spans determined by seasonal changes or limited by site-specific interactions or disturbances.

Bryozoans are exclusively clonal, and they are common to abundant in many marine benthic environments. Among Recent calcified bryozoans, the gymnolaemate order Cheilostomata is by far the more diverse, abundant, and conspicuous. Consequently, cheilostomes have been studied more frequently relative to other bryozoans and much more is known about aspects of their life histories (Gordon 1970; Eggleston 1972; Dudley 1973; Hayward and Ryland 1975; Mawatari 1975; Dyrynda and Ryland 1982; Winston and Jackson 1984; Jackson and Wertheimer 1985; Harvell and Grosberg 1988; Karande and Udhayakumar 1992; Hunter and Hughes 1993; Bishop 1994).

The other calcified bryozoans, the stenolaemate order Cyclostomata, are less diverse, abundant, and conspicuous than cheilostomes in Recent communities. Life-history information on living cyclostome bryozoans is limited and consists predominantly of data on embryo formation and larval longevity for a few species (Harmer 1896; Borg 1926). Data on growth rates (Vail and Wass

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1981*b*), longevities (Winston 1985), relationships between colony growth habits and reproduction (Taylor 1979; McKinney 1983), and reproductive schedules (Ryland 1963) are extremely sparse for living and fossil stenolaemates.

Life histories of extinct benthic marine organisms represented in the fossil record cannot be known to the same level of detail as for living organisms. With very few exceptions, such as daily to annual banding in corals (e.g. Johnson and Nudds 1975), there are few practical ways to measure growth rates of individuals. Furthermore, population parameters are difficult to obtain because it is seldom possible to be sure that fossil skeletons preserved on a single bedding plane were actually coeval (Flessa *et al.* 1993) and there are several processes that, potentially, can selectively remove skeletons, resulting in biased size distributions (see below). However, given the limitations imposed by working with death assemblages that may span an unknown amount of time, one can determine certain aspects of life history if taphonomic effects have not biased the sample. Where size can be taken as an adequate surrogate for age, survivorship curves can be constructed. Colony shape, and capacity and frequency of asexual reproduction can be determined, and, where sexual reproduction is reflected in skeletal structures, size at reproduction, aspects of reproductive effort, and survival beyond reproduction can be quantified.

A variety of growth habits has been produced by bryozoans, which reflect functional, phylogenetic, and life-history differences (McKinney and Jackson 1989). Single-layered, encrusting, multiserial cyclostome colonies belonging to diverse species are common on small hard substrata, such as skeletons of other benthic invertebrates, lithic clasts and hardgrounds, particularly in the Mesozoic (e.g. Brood 1972; Hölder 1972; Palmer and Fürsich 1974, 1981; Mayoral and Sequeiros 1981; Wilson 1986; Walter 1989; Palmer and Wilson 1990; Martill and Hudson 1991; Taylor and Michalik 1991; Bertling 1994). These colonies generally grow radially by budding new zooids around their perimeters. Spread of the colony is commonly interrupted by microenvironmental conditions including crowding and competitive contacts, predation or small-scale obstructions. Colonies in some species develop subcolonies usually along their periphery. Colonies that have not generated subcolonies are here referred to as 'solitary' colonies. Those that have generated subcolonies are referred to as 'compound' colonies, with the original portion referred to as the 'parent' colony and each subcolony as a 'daughter'. Subcolonies originate from a small number of zooids in the parent colony and may either grow away from the parent colony or develop radial growth and overlap the parent colony. In a few species, subcolonies may develop from local regions within the interior of the parent colony rather than from some point around the perimeter, so that as the subcolony develops it is 'stacked' above the parent.

In this paper, life history-related characteristics of 15 species of encrusting, Mesozoic cyclostomes are described and compared, and their implications for the life-histories of these species are discussed. This is one of an informal series of papers that will build information on the diversity and range of cyclostome life histories through time so that eventually the pattern of long-term changes can be documented and analysed for constraints and possible causes.

MATERIAL AND METHODS

This study is based predominantly on suites of specimens from the collections of The Natural History Museum, London (BMNH); other figured or mentioned specimens are from the Sedgwick Museum, University of Cambridge (SM), and the Slovak National Museum, Bratislava, Slovakia (SNM). All available specimens of encrusting Mesozoic cyclostomes in the BMNH collections were examined, and suitably preserved species represented by a sufficient number of specimens and for which collecting bias was thought to be minimal were included in this study. Some of the specimens had been previously catalogued individually, but the majority were in uncurated samples derived from various sources. Most of the uncurated Cretaceous material was collected from the Chalk by C. T. A. Gaster and A. W. Rowe in the late 19th and early 20th centuries. Triassic and Jurassic specimens were collected by us. Several specimens of *Plagioecia* sp. 2 encrusting a single valve of

TABLE 1. Occurrence data for species included in this study.

Species	Location	Stratigraphical horizon	Number of specimens
Actinopora disticha (von Hagenow)	Northfleet, Kent	*coranguinum* Zone	120
Liripora complanata (Roemer)	Seaford and Offham Hill, Lewes, East Sussex	*cortestudinarium* Zone	51
'*Mesonopora*' *laguncula* (Voigt)	Northfleet, Kent	*coranguinum* Zone	43
Plagioecia aff. *carinata* (Levinsen)	Northfleet, Kent	*coranguinum* Zone	19
Discocavea irregularis (d'Orbigny)	Northfleet, Kent; Wanborough, Wiltshire; Eastbourne, and Seaford, East Sussex; West Horsley, Surrey; Norwich, Norfolk	*coranguinum* Zone *mucronata* Zone	146
Hyporosopora dilatata (d'Orbigny)	Stanton Harcourt, Oxfordshire	Oxford Clay (Callovian/Oxfordian)	45
	Warboys Clay Pit, Cambridgeshire	Oxford and Ampthill clays (Oxfordian)	93
Plagioecia? *reniformis* (Gregory)	Northfleet, Kent	*coranguinum* Zone	52
Eurystrotos aff. *acanthina* (Gregory)	Northfleet, Kent	*coranguinum* Zone	19
Hyporosopora sp.	Stanton Harcourt, Oxfordshire	Oxford Clay (Callovian/Oxfordian)	14
'*Mesonopora*' sp.	Seaford and Offham Hill, Lewes, East Sussex; Luton, Chatham, Kent Northfleet, Kent	*cortestudinarium* Zone *coranguinum* Zone	161
Plagioecia sp. 1 (zooids 200 μm width)*	Stanton Harcourt, Oxfordshire	Oxford Clay (Callovian/Oxfordian)	18
Plagioecia sp. 2 (zooids 100 μm width)	Stanton Harcourt, Oxfordshire	Oxford Clay (Callovian/Oxfordian)	14
	Warboys Clay Pit, Cambridgeshire; St Ives, Cambridgeshire	Oxford and Ampthill clays (Oxfordian) Oxford Clay	47
Plagioecia cf. *disciformis* (von Hagnow)	Seaford and Offham Hill, Lewes, East Sussex	*cortestudinarium* Zone	27
Reptomultisparsa hybensis (Prantl)	Viper Pit, Hybe, Slovakia	Hybe Beds (Rhaetian)	88
Reptomultisparsa sp.	Stanton Harcourt, Oxfordshire	Oxford Clay (Callovian/Oxfordian)	6

* Species illustrated in Martill and Hudson (1991, pl. 34, figs 3 and 5).

Gryphaea dilatata (Sowerby) from the Oxford Clay of St Ives, Huntingdonshire (SM J26482) were also included in the study.

Each of these collections of individual species was treated as a death assemblage that was unaffected or minimally affected by taphonomic processes or collecting bias. There may have been

TABLE 2. Summary of colony size attributes. Measurements are in mm and mm² and are given as mean/median. See Table 1 for number of specimens used for determining statistical characteristics.

Species	Diameters			Area	Curve relating area to max. diam.
	Max.	Min.	Ratio		
Actinopora disticha	3·6/3·5	2·9/2·9	0·81/0·83	9·1/7·5	$Y = 0{\cdot}644X^{1{\cdot}512}$
Liripora complanata	5·2/4·6	4·4/4·1	0·85/0·89	18·7/14·0	$Y = 1{\cdot}024X^{1{\cdot}700}$
'*Mesonopora*' *laguncula*	12·0/10·8	9·8/10·0	0·82/0·93	102·8/77·6	$Y = 1{\cdot}160X^{1{\cdot}750}$
Plagioecia aff. *carinata*	13·2/13·3	9·6/10·1	0·73/0·76	99·6/88·6	$Y = 0{\cdot}383X^{2{\cdot}111}$
Discocavea irregularis	3·5/2·8	3·1/2·5	0·89/0·89	10·5/5·5	$Y = 0{\cdot}715X^{1{\cdot}938}$
Hyporosopora dilatata (Stanton Harcourt)	11·9/11·0	8·9/8·6	0·75/0·78	109·3/100·3	$Y = 0{\cdot}747X^{1{\cdot}562}$
Hyporosopora dilatata (Warboys Clay Pit)	8·2/5·5	6·2/4·4	0·76/0·80	49·4/21·9	$Y = 0{\cdot}699X^{1{\cdot}851}$
Plagioecia? *reniformis*	9·3/8·9	7·1/6·7	0·76/0·75	69·2/55·8	$Y = 0{\cdot}687X^{1{\cdot}860}$
Eurystrotos aff. *acanthina*	4·3/4·3	3·6/3·7	0·84/0·86	13·0/12·5	$Y = 0{\cdot}751X^{1{\cdot}855}$
Hyporosopora sp.	8·1/8·0	7·3/7·3	0·90/0·91	47·1/33·5	$Y = 0{\cdot}685X^{1{\cdot}975}$
'*Mesonopora*' sp.	6·6/5·5	5·5/5·0	0·83/0·91	45·4/23·6	$Y = 0{\cdot}763X^{1{\cdot}901}$
Plagioecia sp. 1	6·7/6·4	6·0/5·8	0·90/0·91	33·2/29·2	$Y = 0{\cdot}698X^{1{\cdot}996}$
Plagioecia sp. 2 (Stanton Harcourt)	6·5/6·1	4·8/4·7	0·74/0·77	23·9/21·7	$Y = 1{\cdot}100X^{1{\cdot}585}$
Plagioecia sp. 2 (Cambridgeshire)	4·0/3·6	3·4/3·1	0·85/0·86	12·2/8·9	$Y = 0{\cdot}675X^{2{\cdot}000}$
Plagioecia cf. *disciformis*	2·3/2·0	2·0/1·7	0·87/0·85	4·4/2·4	$Y = 0{\cdot}649X^{2{\cdot}016}$
Reptomultisparsa hybensis	4·5/3·9	3·7/3·5	0·92/0·90	15·6/10·1	$Y = 0{\cdot}607X^{2{\cdot}005}$
Reptomultisparsa sp.	12·7/13·2	10·3/11·2	0·81/0·85	150·0/189·1	$Y = 0{\cdot}753X^{1{\cdot}905}$

taphonomic loss of some of the smallest colonies through abrasive grazing by durophagous echinoids prior to burial, although grazing damage of the general shell surfaces on which the colonies grew was not conspicuous, and very small cyclostome colonies of one to a few zooids were found among the materials from most sites.

Fine-grained matrix and whole fossils characterize the Cretaceous chalks, Jurassic clays, and Triassic silty marls from which the suites of specimens were collected, implying local origin of the fossils and low kinetic energy at the site of deposition. Taphonomic bias due to selective abrasion and transportation is therefore unlikely.

The cyclostome colonies grew as permanent encrustations on solid calcitic substrata, including brachiopods, echinoids and ostreoid bivalves. Cyclostomes too have calcite skeletons (Poluzzi and Sartori 1975). In all lithologies from which suites of specimens were collected the calcite skeletons are well-preserved, so taphonomic bias due to selective dissolution of the smallest specimens is unlikely, especially inasmuch as the colonies were bonded to relatively large substrata of the same composition.

In summary, although preferential loss of small colonies may have occurred so that the proportion of colonies in the smallest potential sizes is underrepresented (as is thought to be the case for most fossil assemblages; Craig and Oertal 1966), there is no evidence in any of the studied assemblages for selective removal of small colonies by durophagous grazers, nor from mechanical abrasion or transportation, nor preferential dissolution. The cyclostome assemblages are therefore treated as taphonomically unbiased, time-averaged death assemblages.

Collecting bias is also thought to have relatively small impact on size distributions, with the following exception. A. W. Rowe and C. T. A. Gaster, who made the bulk of the Cretaceous collections, kept a wide variety of colony sizes and shapes, giving the appearance that they kept all

TABLE 3. Summary of colony reproductive attributes. Measurements are in mm and mm² and are given as minimum/mean/median for ancestrula to ooeciopore and mean/median for ooeciopore to colony edge. Square brackets include number of observations.

Species	Brood chamber shape (width/length)	Ancestrula to ooeciopore	Ooeciopore to *colony edge* Values (SD)	% area as gonozooids in fertile colonies	%fertile colonies
Actinopora disticha	7·1	0·6/1·1/1·0	0·4/0·4 (0·24)	5·4	34·6
	[41]	[41]	[41]	[27]	[78]
Liripora complanata	1·21	0·9/2·5/2·7	0·4/0·3 (0·24)	1·1	21·9
	[6]	[7]	[7]	[7]	[32]
'*Mesonopora*' *laguncula*	0·9	2·8/4·5/4·4	1·5/1·4 (0·42)	2·8	32·2
	[20]	[20]	[20]	[10]	[31]
Plagioecia aff. *carinata*	3·3	6·1/6·4/6·4	1·0/1·0 (–)	1·4	5·3
	[2]	[2]	[2]	[1]	[19]
Discocavea irregularis	irregular	0·7/0·7/0·7	0·6/0·6 (–)	23·0	2·5
	[2]	[2]	[2]	[1]	[40]
Hyporosopora dilatata	1·0	2·6/6·3/6·7	1·8/1·4 (1·71)	2·6	26·1
(Stanton Harcourt)	[29]	[29]	[29]	[11]	[42]
Hyporosopora dilatata	1·1	2·2/6·0/4·9	1·8/1·8 (0·97)	3·3	23·3
(Warboys)	[19]	[19]	[19]	[10]	[43]
Plagioecia? *reniformis*	1·6	1·9/3·5/3·1	0·9/0·7 (0·78)	0·8	55
	[59]	[58]	[58]	[22]	[40]
Eurystrotos aff. *acanthina*	1·6	0·9/1·8/2·2	0·3/0·2 (–)	3·5	63·2
	[19]	[19]	[19]	[11]	[16]
Hyporosopora sp.	0·7	2·3/4·0/3·7	1·4/1·2 (1·08)	6·0	57·1
	[42]	[42]	[42]	[8]	[14]
'*Mesonopora*' sp.	3·0	1·1/3·3/2·9	0·8/0·7 (0·62)	6·5	29·7
	[94]	[95]	[97]	[41]	[138]
Plagioecia sp. 1	3·0	2·1/3·1/2·9	1·1/0·9 (0·75)	6·8	88·2
	[46]	[46]	[46]	[16]	[18]
Plagioecia sp. 2	2·4	1·4/2·9/2·7	1·1/0·6 (1·28)	6·8	71·4
(Stanton Harcourt)	[34]	[34]	[34]	[10]	[14]
Plagioecia sp. 2	3·0	1·3/1·8/1·5	0·7/0·7 (0·24)	5·4	21
(Cambridgeshire)	[9]	[9]	[9]	[6]	[34]
Plagioecia cf. *disciformis*	2·5	1·0/1·3/1·3	0·3/0·3 (0·05)	5·5	11·1
	[4]	[4]	[4]	[3]	[277]
Reptomultisparsa hybensis	0·3	2·0/3·6/3·7	0·9/0·8 (0·54)	2·5	14·8
	[12]	[12]	[12]	[4]	[27]
Reptomultisparsa sp.	0·8	8·2/9·4/9·0	2·2/2·1 (0·39)	1·9	33·3
	[6]	[6]	[6]	[2]	[6]

colonies encountered. Quite possibly, however, colonies less than 1 mm diameter may have been overlooked more commonly than the larger colonies. This potential bias in the collections has been compensated in part because where multiple encrusting cyclostomes are present on a single echinoid test or bivalve shell or fragment used in this study, each was assigned to species and used, whether or not the colonies had been marked by the original collectors.

The Triassic species *Reptomultisparsa hybensis* was collected by one of us (PDT), and all specimens encountered were kept. All substrates potentially encrusted by *R. hybensis* were collected, returned to the laboratory for cleaning and retained if encrusted. Collection of *R. hybensis* was therefore not selective. Data on colony size distributrions for species collected from the Oxford Clay

at Stanton Harcourt are not used, because specimens were screened in the field and only the more informative or well-preserved specimens kept, so that size bias may have been introduced.

Material of two species, *Hyporosopora dilatata* and *Plagioecia* sp. 2, was collected specifically for this project from the Oxford/Ampthill clays at Warboys Clay Pit, near Peterborough, Cambridgeshire. Between 300 and 400 specimens of *Gryphaea* and other oysters were collected without selectivity, brought back to the laboratory, and scanned for encrusting bryozoans. All encrusted bivalves were kept, and all colonies of the two bryozoan species were used in the study.

Localities, stratigraphical horizons, and number of specimens of species used in this study are given in Table 1. It should be stressed that in most cases it has not been possible to establish the name for a species with complete confidence and precision because the systematics of Mesozoic encrusting cyclostomes is very poorly understood. Most of the species erected by 19th century authors, including d'Orbigny, Reuss and Roemer, were inadequately described and illustrated, and have never been revised using modern techniques such as SEM. In addition, the morphology of the gonozooid is crucial in generic identification and extremely valuable in distinguishing between species with similar autozooidal morphologies. However, gonozooidal characters are unknown in many species because gonozooids are lacking in the type specimens. Differences between species can be very subtle, and confident species determination is often only possible when type specimens are available for direct comparison.

Colony sizes (maximum and minimum diameters, area, perimeter), diameters of zooidal apertures (ten measured per specimen), distances between centres of neighbouring zooidal apertures (ten measured per specimen), number of gonozooids, brood chamber sizes (maximum and minimum diameters, area), total area of brood chambers per colony, ancestrula to ooeciopore distances, and ooeciopore to colony edge distances were determined for each colony, using an ImageAnalyst system. Some quantitative characteristics of individual colonies were calculated, including

1. Average radius = $(\text{area}/\pi)^{0.5}$
2. Excess perimeter = perimeter − (2) (average radius) (π)
3. Relative amount of excess perimeter = excess perimeter/((2) (radius) (π))

INDIVIDUAL SPECIES

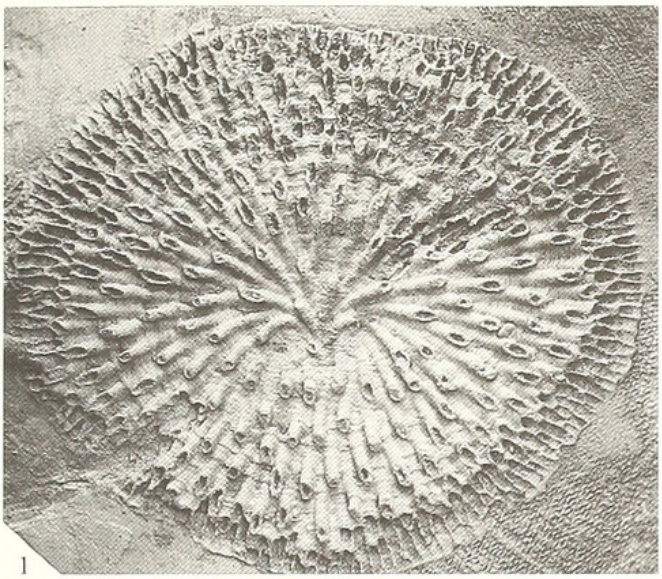
Life history characteristics of individual species of Mesozoic encrusting cyclostomes are summarized in Table 2 (colony size attributes) and Table 3 (data on reproductive effort). Descriptions of the attributes of representative species for which the largest number of specimens is available are given below.

EXPLANATION OF PLATE 1

Figs 1–4. *Reptomultisparsa hybensis* (Prantl, 1938); Triassic, Rhaetian, Hybe Beds; Hybe, Slovakia. 1–2, SNM 19779. 1, infertile, sub-circular colony with circumferential growing edge; ×10. 2, cluster of colonies including two small colonies, bottom left and bottom right, the former fan-shaped prior to the development of a circumferential growing edge, and the latter being overgrown by a larger colony; ×12. 3–4, SNM Z-20655. 3, colony with lobe growing with a gonozooid towards the top left; ×10. 4, detail of the longitudinally elongate gonozooid; × 22.

Figs 5–6. *Hyporosopora dilatata* (d'Orbigny, 1850); Jurassic, Callovian/Oxfordian, Oxford Clay; Stanton Harcourt, Oxfordshire. 5, BMNH D58679; regular colony with circumferential growing edge; abraded gonozooids are developed close to the growing edge lower left and lower right; ×7. 6, BMNH D59266; irregular colony abutting a serpulid and small cemented bivalves; a gonozooid is present in the lower left near the growing edge; ×5·6.

All are back-scattered scanning electron micrographs of uncoated specimens, except figures 5 and 6 which are light photomicrographs.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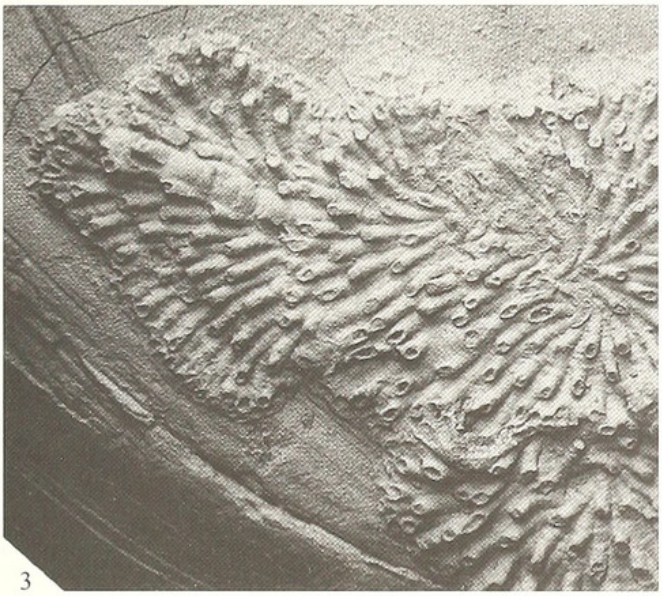
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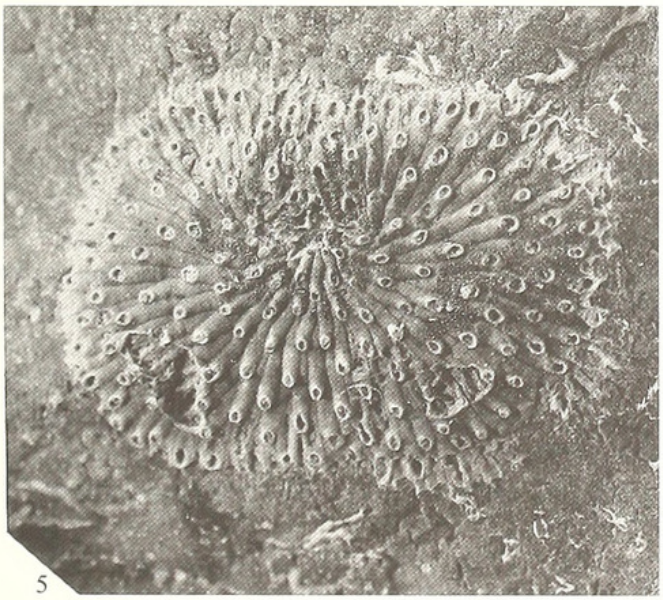
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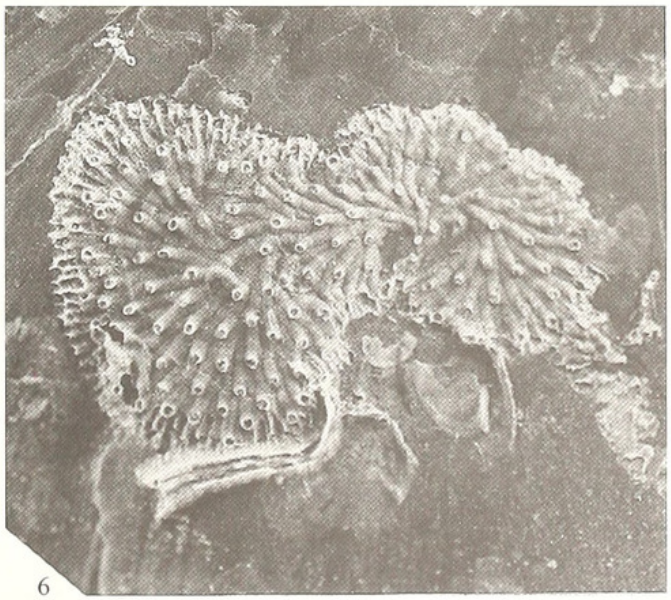
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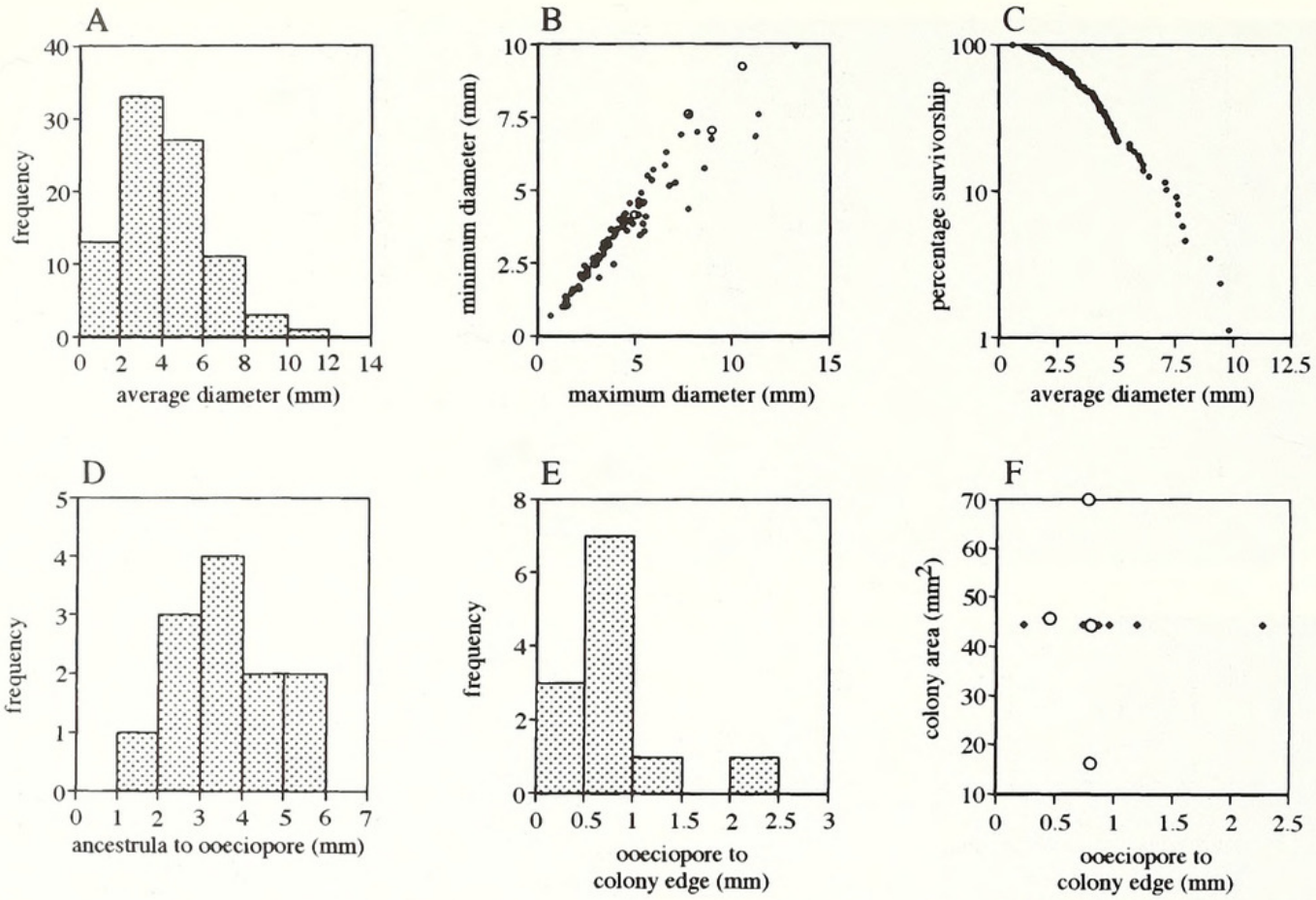
McKINNEY and TAYLOR, *Reptomultisparsa*, *Hyporosopora*



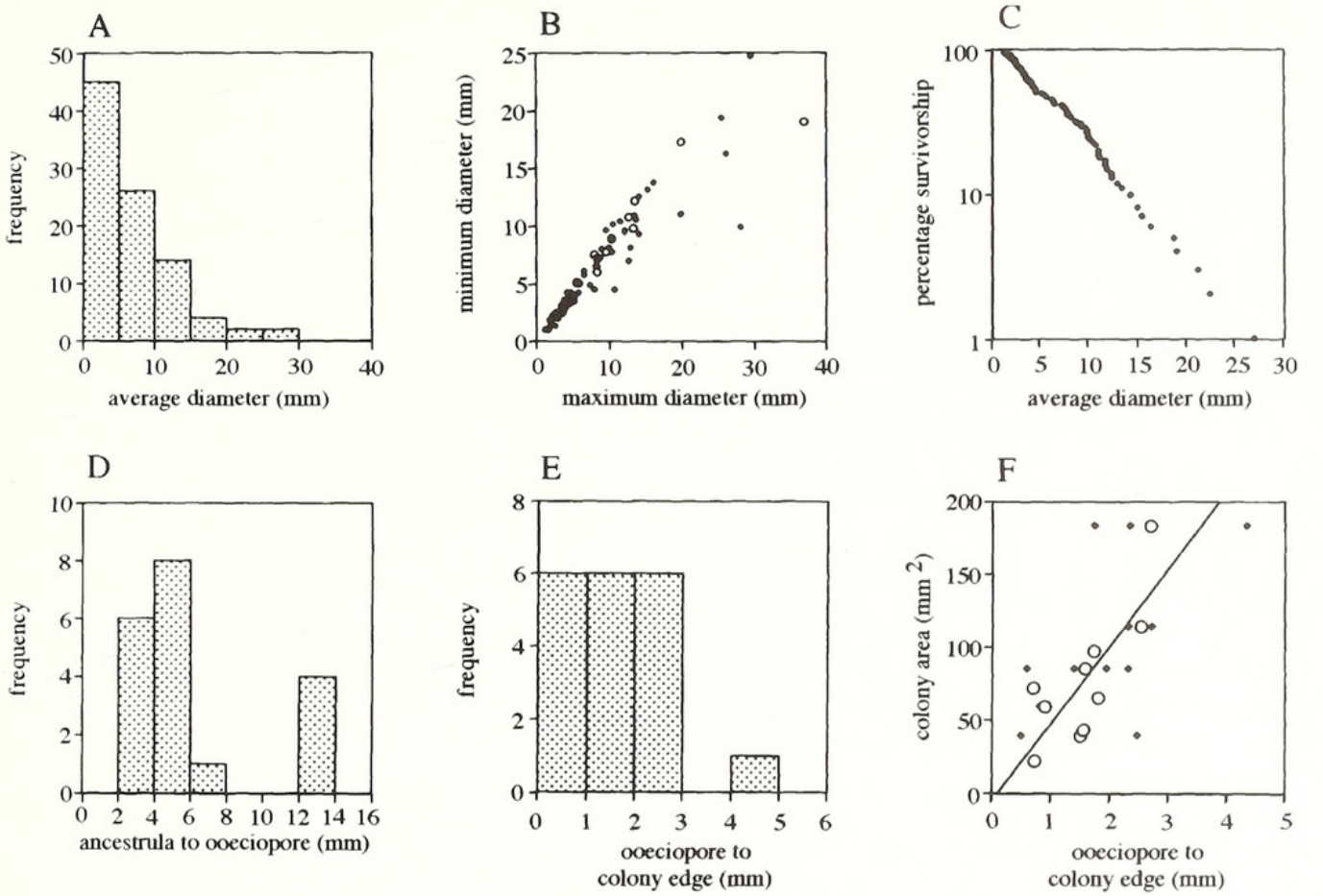
TEXT-FIG. 1. Graphs summarizing quantitative data on *Reptomultisparsa hybensis* (Prantl, 1938). A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles represent infertile colonies and open circles colonies with complete gonozooids present. C, percentage survivorship based on size (average diameters). D, histogram of distances between point of origin of colonies (i.e. protoecium of ancestrula) and ooeciopores. E, histogram of distances between ooeciopores and the nearest edge of the colony. F, plot of distances between ooeciopores and the nearest edge of the colony, versus colony area; horizontal alignment of points on this plot represents multiple values observed on a single colony; mean value for the colony is given as a open circle.

Triassic species

Reptomultisparsa hybensis. *R. hybensis* (Prantl, 1938) colonies grew as typically small, circular to somewhat irregularly shaped (Text-fig. 1A–B) sheets in which autozooidal apertures were isolated and quincuncially arranged. Minimum colony diameter averaged 83 per cent. of the maximum diameter. Most small but few large colonies were essentially circular (Pl. 1, fig. 1); minimum diameter of the least circular colony was 56 per cent. of the maximum diameter, due to growth interference with a conspecific colony growing on the same substratum. In general, irregularity in shape was due at least in part to growth interference, which is clearly seen in several colonies that abut or overgrow but do not fuse with conspecifics (Pl. 1, fig. 2). Subcolonies were not developed, although irregular lobes occur in some colonies (Pl. 1, fig. 3).

Coefficient of variation for mean diameter of colonies is 53 (for number (N) of colony measurements for this and other species, see Table 1). Plotted as percentage survivorship on a logarithmic axis (Text-fig. 1C), average diameters of colonies show an increasing death rate up to approximately 5 mm, with somewhat irregular but near-constant death rate for larger colonies ($Y = 231{\cdot}3*10^{-0{\cdot}198X}$).

Minimum diameter of colonies with fully developed gonozooids was 4·2 mm (minimum area = 16·3 mm^2), and gonozooids were present in four of the 27 colonies (15 per cent.) equal to or greater



TEXT-FIG. 2. Graphs summarizing quantitative data on *Hyporosopora dilatata* (d'Orbigny, 1850). A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles represent infertile colonies and open circles colonies with complete gonozooids present. C, percentage survivorship based on size (average diameters). D, histogram of distances between point of origin of colonies (i.e. protoecium of ancestrula) and ooeciopores. E, histogram of distances between ooeciopores and the nearest edge of the colony. F, plot of distances between ooeciopores and the nearest edge of the colony, versus colony area; solid dots represent individual measurements, and open circles represent pooled data for each colony with two or more ooeciopores; regression, $Y = -5{\cdot}04 + 52{\cdot}75X$.

than 4·2 mm in minimum diameter (Text-fig. 1B). Minimum distance from ancestrula to ooeciopore was 2·0 mm, and mean distance 3·6 mm (Text-fig. 1D; for number (N) of skeletal reproductive features of this and other species, see Table 3). Brood chambers (gonozooids) are much longer than broad, and most are close to the colony margin (Pl. 1, fig. 4). The ooeciopore is an average of 0·9 mm from the outer edge of the developing zooids along the colony margin, with a range of 0·2–2·3 mm (Text-fig. 1E).

There is no apparent correlation between colony area and distance between ooeciopore and colony margin (Text-fig. 1F; $r = -0{\cdot}094$, $p = 0{\cdot}906$, $N = 4$, using mean values from each colony with multiple gonozooids and observed values for colonies with a single gonozooid). Nine brood chambers occurred in one large colony and, with the exception of a single chamber located midway between the protoecium and colony margin, they occurred about 1 mm from the colony margin. The single chamber located mid-way was not included in the calculation of mean value of distance between ooeciopores and colony margin. No correlation between colony area and number of gonozooids in fertile colonies was seen in the very small sample of fertile colonies ($r = 0{\cdot}013$, $p = 0{\cdot}987$, $N = 4$).

Minimum diameter of fertile colonies averaged 7·0 mm, while that of non-fertile colonies that had reached or exceeded the size of the smallest fertile colony averaged 5·3 mm. The difference is not

significant (Mann-Whitney U = 29, p = 0·246, N = 29), but only a small number of fertile colonies is present in the sample.

Jurassic species

Hyporosopora dilatata. Data presented here are for specimens collected from Warboys Clay Pit, Cambridgeshire. Colonies of *H. dilatata* (d'Orbigny, 1850) commonly grew to relatively large sizes (Text-fig. 2A). Early colony growth produced gradually widening fans (Pl. 2, fig. 5) that within about 1 mm flared laterally so that both sides of the fan recurved and engulfed the proximal part of the ancestrula (protoecium). Subsequent growth produced sub-circular colonies (Pl. 1, fig. 5) except that with increasing size colonies often became somewhat irregular in shape (Text-fig. 2B). Autozooidal apertures in *H. dilatata* are isolated and quincuncially arranged. Colonies included in this study encrust valves of the bivalve *Gryphaea*. They did not develop subcolonies, although a few have irregular lobes with a constricted region connecting the lobe(s) with the original part of the colony (Pl. 1, fig. 6).

Minimum diameter averages 75 per cent. of maximum diameter. Coefficient of variation for mean diameter of these colonies is 79. Plotted as percentage survivorship on a logarithmic axis, the average diameters of colonies shows a remarkably constant death rate with increasing size (Text-fig. 2C).

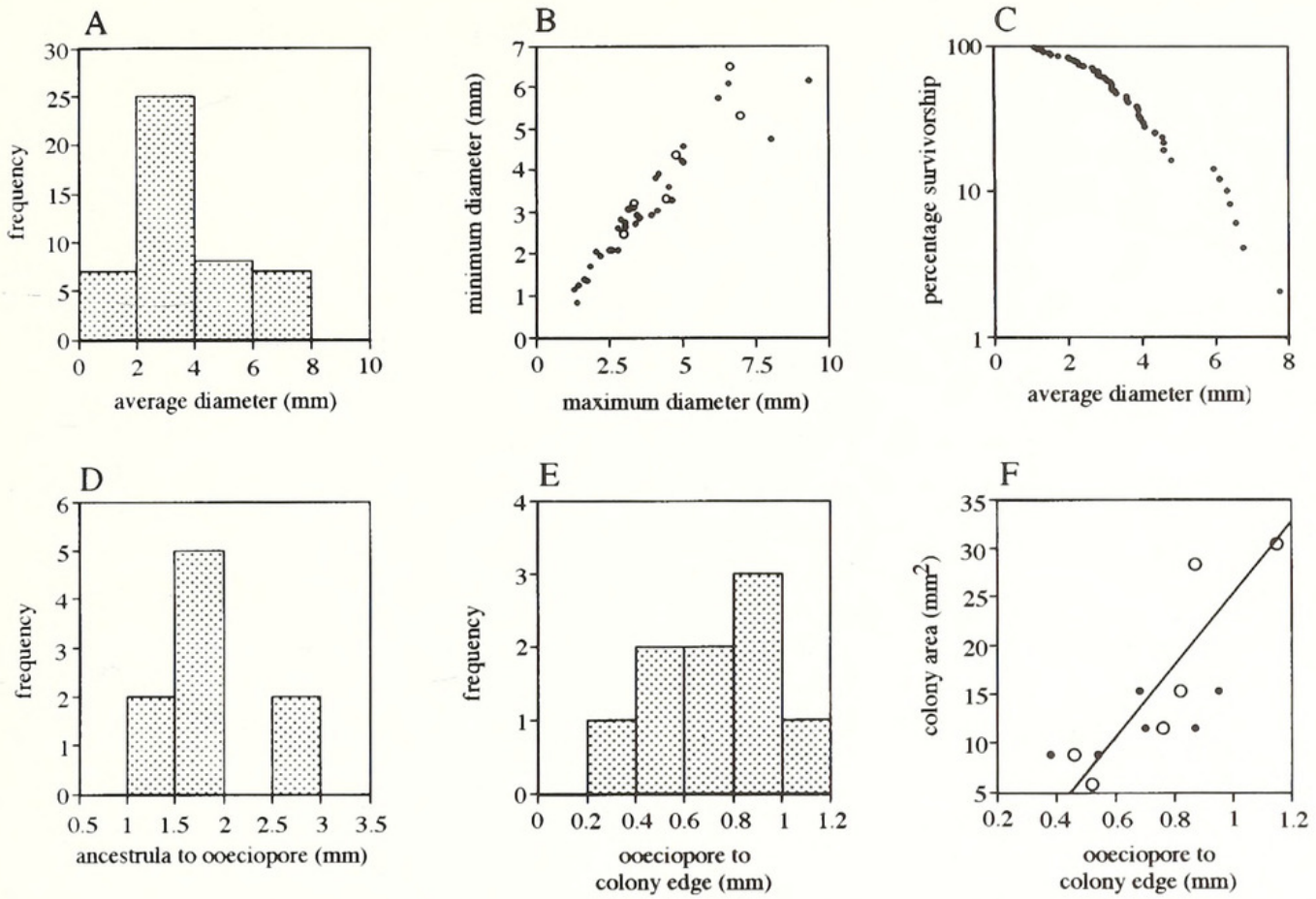
Minimum diameter of colonies with fully developed gonozooids was 5·1 mm (minimum area was 22·0 mm^2), and gonozooids were present in ten of the 43 colonies (23 per cent.) equal to or greater than 5·1 mm in diameter (Text-fig. 2B). Minimum distance from protoecium to ooeciopore is 2·2 mm, and the mean is 6·0 mm (Text-fig. 2D). There was no difference in mean minimum diameter of fertile colonies (10·4 mm) and of non-fertile colonies (10·1 mm) that had reached the 5·1 mm minimum diameter for fertile colonies (Mann-Whitney U = 163, p = 0·954, N = 43).

The ooeciopore is located at about the midpoint of the dilated part of the gonozooid (Pl. 2, fig. 6), averaging 1·8 mm from the outer edge of the developing zooids along the colony margin (Text-fig. 2E). There is moderate (r = 0·783, N = 10) but significant (p < 0·007) positive correlation between colony area and distance between ooeciopore and colony margin; although colonies grew only a short distance beyond completion of the brood chamber, the distance of continued growth was on average greater for larger colonies (Text-fig. 2F). This distance varied between 0·5 mm and 4·4 mm in the specimens available.

Brood chambers are approximately equidimensional and are close to the colony margin. Fertile colonies had one to four brood chambers, and where two or more occur within a single colony, they are approximately equidistant from the edge of the colony. Among fertile colonies, there is a marginally significant correlation between colony area and number of fully developed gonozooids (r = 0·176, p = 0·094, N = 10).

Plagioecia *sp. 2*. Except where otherwise specified, data presented for this species are for specimens collected from Warboys Clay Pit, Cambridgeshire. This species grew as typically small, essentially circular patches (Text-fig. 3A–B), formed by rapid expansion of an initially fan-shaped colony and coalesence of the two edges of the fan where they met and overgrew the early zooids of the colony (Pl. 2, fig. 2). Autozooidal apertures are isolated and quincuncially arranged. Minimum diameter of colonies averages 83 per cent. of maximum diameter, and the majority, even the largest colonies (Pl. 2, fig. 1), are near this ratio.

Coefficient of variation for mean diameter of colonies is 42. Percentage survivorship plotted on a logarithmic scale shows increasing death rate up to about 4 mm average diameter, then an abrupt reduction in death rate followed by relatively slow increase in death rate for the larger colonies (Text-fig. 3C). Subcolonies (Pl. 2, fig. 4) were produced in a small proportion of the colonies from Stanton Harcourt. They formed at the perimeter of the parent colony, originating from single zooids that functioned as pseudoancestrulae, from which a well-defined fan of zooids extended and gave rise to a radially expanding daughter colony.



TEXT-FIG. 3. Graphs summarizing quantitative data on *Plagioecia* sp. 2. A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles represent infertile colonies and open circles colonies with complete gonozooids present. C, percentage survivorship based on size (average diameters). D, histogram of distances between point of origin of colonies (i.e. protoecium of ancestrula) and ooeciopores. E, histogram of distances between ooeciopores and the nearest edge of the colony. F, plot of distances between ooeciopores and the nearest edge of the colony, versus colony area; solid dots represent individual measurements, and open circles represent pooled data for each colony with two or more ooeciopores; regression, $Y = -11{\cdot}19 + 36{\cdot}54X$.

Minimum diameter of colonies with fully developed gonozooids was 2·5 mm (Text-fig. 3B; minimum area 5·8 mm^2), and gonozooids were present in six of the 29 colonies (21 per cent.) equal to or greater than 2·5 mm in minimum diameter. Minimum distance from ancestrula to ooeciopore is 1·3 mm, and mean distance is 1·8 mm (Text-fig. 3D). Brood chambers are up to four times broader than long (Pl. 2, fig. 3), and are elongated parallel to nearby colony margins. The ooeciopore is located on the distal side of the brood chamber, averaging 0·7 mm from the outer edge of the developing zooids along the colony margin (Text-fig. 3E). Distance between ooeciopore and colony margin is highly correlated with colony area (Text-fig. 3F; $r = 0{\cdot}880$, $p = 0{\cdot}021$, $N = 6$). Up to two brood chambers were noted per colony, although there was no correlation between colony area and number of brood chambers ($r = 0{\cdot}164$, $p = 0{\cdot}311$) based on the small sample ($N = 6$) of fertile colonies from Cambridgeshire.

Fertile colonies had a mean minimum diameter of 4·2 mm and mean area of 16·7 mm^2 at time of death, and non-fertile colonies at least 2·5 mm in minimum diameter (the minimum observed diameter of fertile colonies) had a mean minimum diameter of 3·9 mm and mean area of 13·6 mm^2. The differences in size are not significant (Mann-Whitney U test: minimum diameter, $U = 57{\cdot}0$, $p = 0{\cdot}518$; area, $U = 55{\cdot}0$, $p = 0{\cdot}451$; $N = 29$).

Cretaceous species

Actinopora disticha. Colonies of *A. disticha* (von Hagenow, 1851) grew as small, essentially circular patches (Text-fig. 4A–B; Pl. 3, figs 1, 3) in which autozooidal apertures are arranged in biserial, radiating fascicles. Specimens included in this study encrusted shells of inoceramid bivalves and echinoid tests. For solitary colonies and parental portions of compound colonies, minimum diameter averages 91·3 per cent. of maximum diameter. Coefficient of variation for mean diameter of these colonies that did not given rise to subcolonies is 49. Plotted as percentage survivorship on a logarithmic scale, the average diameters of solitary colonies and parent portions of compound colonies show an increasing death rate up to about 5 mm, with a few large outliers that have diameters greater than 5 mm (Text-fig. 4C).

Subcolonies (Pl. 3, fig. 2) extended from a marginal pseudoancestrular zooid in the parent colonies and were produced in 37 of 107 colonies (35 per cent.) equal to or greater than 1·2 mm in diameter, which was the smallest colony found to have produced a daughter subcolony. Mean diameter for production of subcolonies was approximately 3·0 mm (standard deviation = 0·98 mm, N = 37), with near-normal distribution except left-truncated at the point of the smallest parent colony (Text-fig. 4D). Usually only one daughter subcolony was produced. Rarely more than one first-generation daughter subcolony was budded from the parent, and only one definite and two or three ambiguous instances of budding of second-generation subcolonies were found.

Colonies that did not produce subcolonies were usually circular, although a few of the largest were oval (Text-fig. 4B). Subcolonies were initially fan-shaped, with lateral walls of the fan formed of exterior wall. They then became essentially circular where the growth zone at the outer end of the fan flared and recurved laterally, joining and fusing over the proximal part of the cone. Continued growth of subcolonies occurred around the entire periphery. Local production of subcolonies around the colony perimeter therefore resulted in unequal colony diameters (Text-fig. 4B) and substantially lengthened the perimeter (Text-fig. 4E) such that where subcolonies are present there is a larger perimeter than would be necessary to enclose the total area of the colony were it circular (Text-fig. 4F).

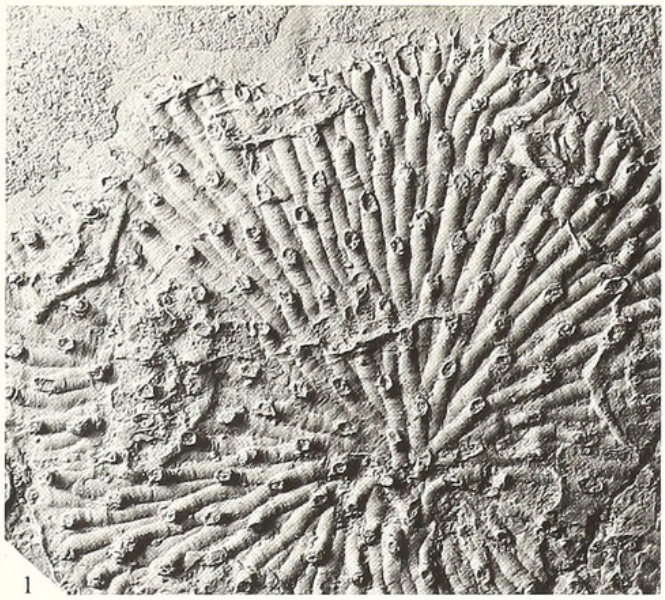
Minimum diameter of colonies with fully developed gonozooids was 2·2 mm (minimum area = 2·0 mm^2), and gonozooids were present in 27 of the 74 colonies (35 per cent.) equal to or greater than 2·2 mm in diameter (Text-fig. 4G). Minimum distance from protoecium to ooeciopore was 0·6 mm, and the mean 1·1 mm (Text-fig. 4H). Brood chambers are much broader than long, and are located close to and parallel with the colony margin. Fertile colonies had only a single brood chamber, or where multiple brood chambers were developed, they were in a single ring (Pl. 3, fig. 3), having formed simultaneously around the colony perimeter. In a few colonies the entire circumference was occupied by two or three brood chambers joined at their lateral ends. The ooeciopore (Pl. 3, fig. 4) is located on the distal side of the brood chamber, averaging 0·4 mm from the outer edge of the developing zooids along the colony margin (Text-fig. 4I). There is a moderate ($r = 0{\cdot}573$; $N = 27$) but significant ($p < 0{\cdot}002$) positive correlation between colony area and

EXPLANATION OF PLATE 2

Figs 1–4. *Plagioecia* sp. 2; BMNH D59445; Jurassic, Callovian/Oxfordian, Oxford Clay; Stanton Harcourt, Oxfordshire. 1, part of a large colony with two rings of collapsed gonozooids; × 12. 2, central area of the same colony with the earliest zooids overgrown; × 40. 3, transversely elongate gonozooid with crushed frontal wall; × 60. 4, peripheral subcolony; × 40.

Figs 5–6. *Hyporosopora dilatata* (d'Orbigny, 1850). 5, BMNH D49316; Jurassic, Oxfordian, Oxford Clay; Warboys, Cambridgeshire; small fan-shaped colony with ancestrula (top right) not overgrown; × 14. 6, BMNH D58664; Jurassic, Callovian/Oxfordian, Oxford Clay; Stanton Harcourt, Oxfordshire; gonozooid with crushed frontal wall; × 30.

All are back-scattered scanning electron micrographs of uncoated specimens.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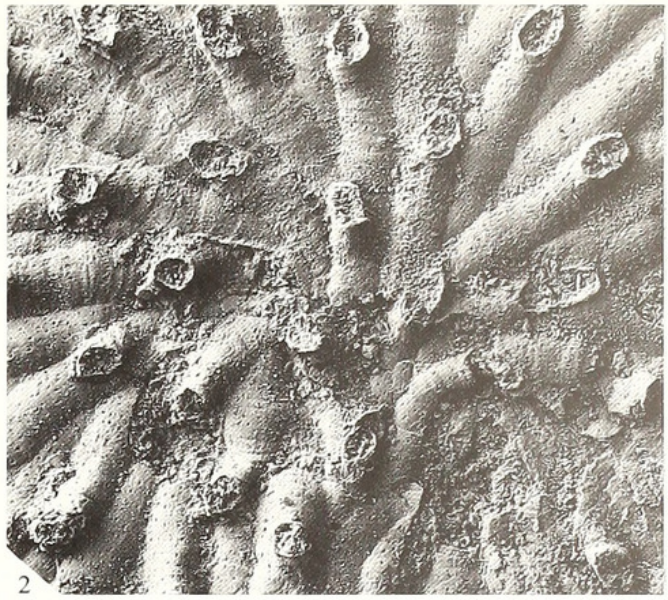
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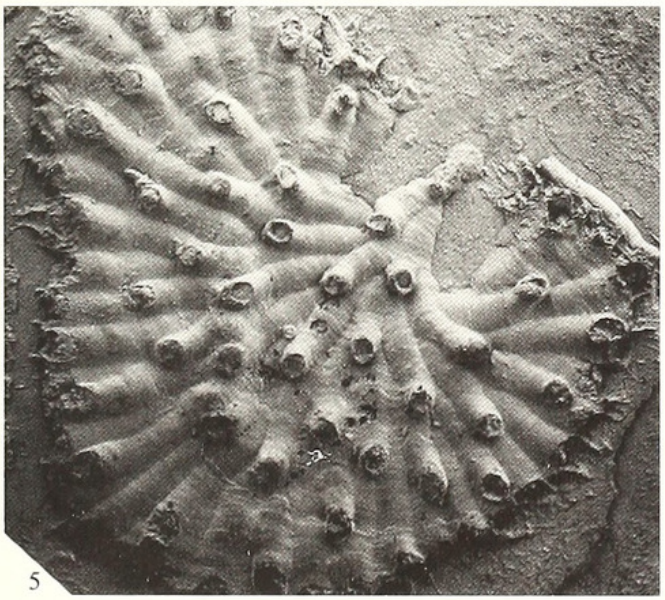
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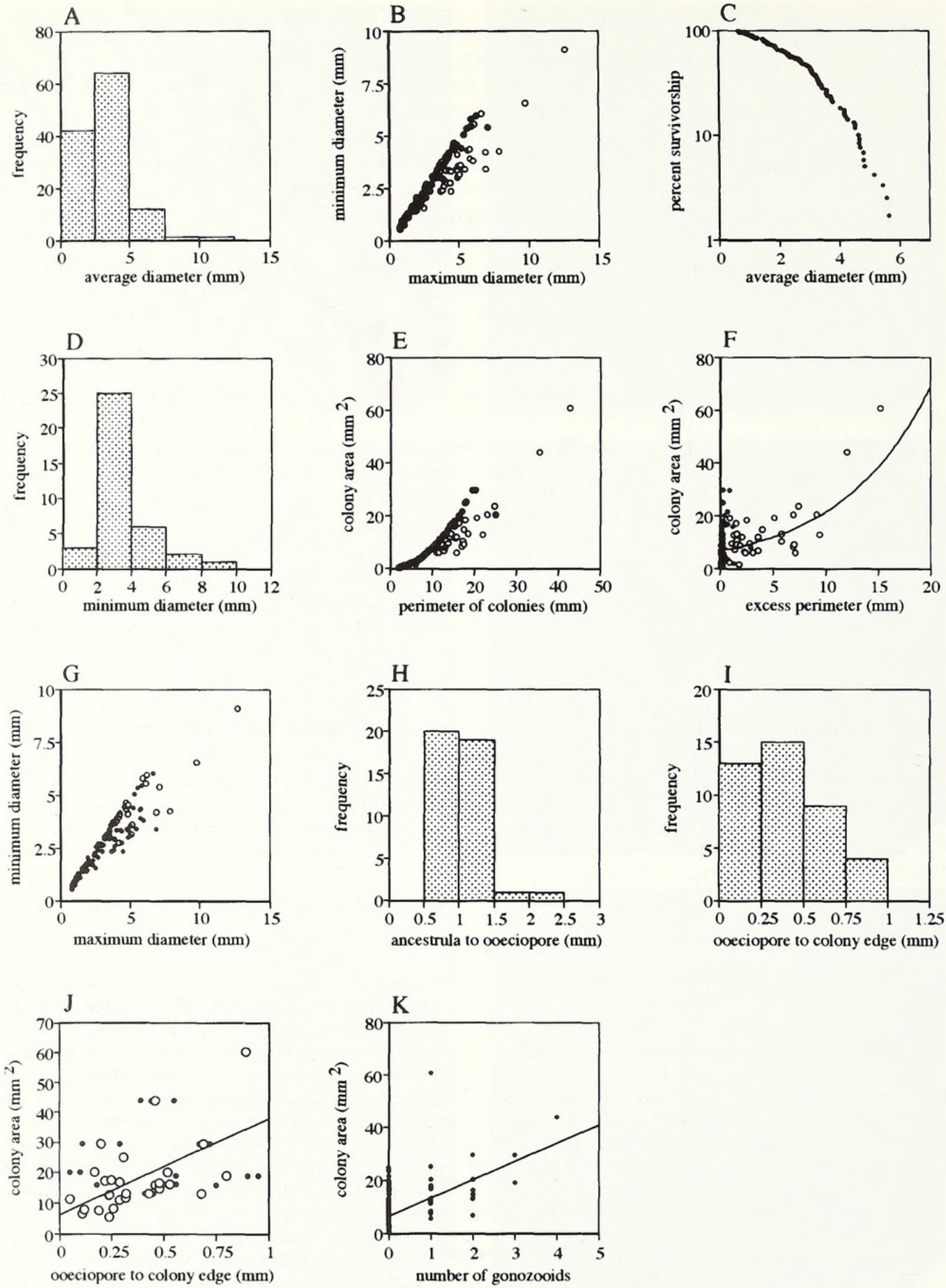
McKINNEY and TAYLOR, *Plagioecia*, *Hyporosopora*



TEXT-FIG. 4. For caption see opposite.

distance between ooeciopore and colony margin; while colonies grew only a short distance beyond completion of the brood chamber (e.g. Pl. 3, fig. 3), the distance of continued growth was on average greater for larger colonies (Text-fig. 4J). This distance varied between 0·05 mm and 0·95 mm in the specimens available. Up to four brood chambers were noted per colony, in most instances with relatively large fertile colonies having more brood chambers (Text-fig. 4K, r = 0·576, p 0·000).

Fertile colonies had a mean minimum diameter of 4·4 mm and mean area of 18·0 mm^2 at time of death, and nonfertile colonies that had minimum diameter of at least 2·2 mm (the minimum observed diameter of fertile colonies) had a mean minimum diameter of 3·5 mm and mean area of 11·1 mm^2. The differences in size are significant (Mann-Whitney U test: minimum diameter, U = 333, p = 0·0007; area, U = 338, p = 0·012; N = 74).

Among the colonies that were large enough to bear gonozooids, 28 had produced subcolonies, and of these nine had both subcolonies and gonozooids. There is no indication that either mode of reproduction is preferentially associated with or precluded by the other (X^2 = 0·3667, p = 0·5434, N = 74).

Discocavea irregularis. Colonies of *D. irregularis* (d'Orbigny, 1851) grew as typically small, circular colonies (Text-fig. 5A–B; Pl. 3, fig. 5) in which autozooids radiate from the central region and are deflected obliquely upward, away from the substratum by new zooids budding basally around the colony perimeter of the mound-shaped colony. Because of the elongated cylindrical shape of the zooids and their divergence, the colony has a slight central depression atop the overall mound shape that is devoid of zooidal apertures. Throughout the remainder of the colony, zooidal apertures are slightly separated from one another and arranged in variably defined radial rows. For solitary colonies and parental portions of colonies that developed subcolonies, minimum diameter averages 91 per cent. of maximum diameter. Coefficient of variation for mean diameter of such colonies is 57. Plotted as percentage survivorship on a logarithmic scale, the average diameters of colonies show an increasing death rate, with minor inflections in the curve (Text-fig. 5C).

Subcolonies were commonly produced, formed by a local lobe extending from the perimeter of the parent colony which then developed its own radial growth pattern, or by eruptive budding from the upper surface of the parent colony, with a new basal wall formed below the portion that spread laterally over the parent (Pl. 3, fig. 5). The eruptive budding appears to have been centred on the inner portion of the peripheral ring of extending zooids of the colony rather than involving either the most marginal zooids or the inner portion of the colony where zooidal growth had slowed or ceased. Subcolonies were produced in 12 of 121 colonies (10 per cent.) equal to or greater than 1·7 mm in diameter, which was the smallest colony found that had produced a daughter subcolony (Text-fig. 5B). Four of the specimens with subcolonies had developed them by frontal eruptive budding. Mean diameter for production of subcolonies was 4·6 mm (standard deviation = 2·1 mm,

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TEXT-FIG. 4. Graphs summarizing quantitative data on *Actinopora disticha* (von Hagenow, 1851). A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles represent colonies without subcolonies and open circles colonies with subcolonies. C, percentage survivorship based on size (average diameters). D, minimum diameter of parent portion of colony when first subcolony was produced. E, plot of colony perimeter length versus colony area; filled circles represent colonies without subcolonies and open circles colonies with subcolonies. F, plot of excess perimeter above that required to enclose a circle of area equal to the colony, versus colony area; filled circles represent colonies without subcolonies and open circles colonies with subcolonies (regression for colonies with subcolonies, $Y = 6{\cdot}55(10^{0{\cdot}051X})$). G, plot of minimum versus maximum colony diameters; filled circles represent infertile colonies and open circles colonies with complete gonozooids present. H, histogram of distances between point of origin of colonies (i.e. protoecium of ancestrula) and ooeciopores. I, histogram of distances between ooeciopores and the nearest edge of the colony. J, plot of distances between ooeciopores and the nearest edge of the colony, versus colony area; solid dots represent individual measurements, and open circles represent pooled data for each colony with two or more ooeciopores; regression, $Y = 6{\cdot}19 + 31{\cdot}80X$. K, plot of number of brood chambers versus colony area; regression, $Y = 6{\cdot}75 + 6{\cdot}83X$.

N = 12), with a strongly right-skewed distribution (Text-fig. 5D). Multiple daughter subcolonies were commonly produced.

Within the sample studied, brood chambers (Pl. 3, fig. 6) were seen in only three colonies. They are inconspicuous, generally placed centrally, with a porous, interior-walled domal roof enclosing a space over the region where feeding zooids diverged forming the central depression of the colony. Lateral portions of the brood chamber generally extend for some distance along the surface of the colony, between the rows of autozooidal apertures. The position of the ooeciopore is unknown; none of the visible apertures are sufficiently differentiated to be identifiable as ooeciopores. Minimum diameter of fertile colonies ranged from 2·4 mm to 3·1 mm, encompassing the average minimum diameter of all colonies, and none of the three fertile colonies had generated subcolonies.

Liripora complanata. *L. complanata* (Roemer, 1840) grew as small, essentially circular colonies (Text-fig. 6A–B; Pl. 4, figs 2–3) in which autozooidal apertures are arranged in uniserial, radiating fascicles. For solitary colonies and parent portions of compound colonies, minimum diameter averages 93 per cent. of maximum diameter. Coefficient of variation for mean diameter of such colonies is 25·3. Plotted as percentage survivorship on a logarithmic scale, the average diameters of colonies show an increasing death rate up to about 5 mm (Text-fig. 6C), with a decreased, near-constant death rate for colonies greater than 5 mm diameter.

Subcolonies were commonly produced along the perimeter of the parent colony (Pl. 4, figs 2–3). They are present in nine of 24 colonies (38 per cent.) equal to or greater than 3·1 mm in diameter, which was the smallest colony found that had produced a daughter subcolony. Mean diameter for production of subcolonies was 6·1 mm (standard deviation = 1·05 mm, N = 9), with a slightly left-skewed distribution (Text-fig. 6D). Usually only one daughter subcolony was produced per colony.

Subcolonies, immediately following their initiation, developed a circular shape with holo-peripheral growth. Four parent colonies on specimen BMNH D46466 (Pl. 4, figs 2–4) are distributed on the surface of an inoceramid as two pairs. Contact was made between colonies within each pair, growth stopped soon afterwards, and each parental colony then generated a subcolony. It seems possible that the production of subcolonies may have been stimulated either by contact between the parent colonies or by cessation of their growth.

Within the sample studied, gonozooids were produced only in subcolonies, although a single specimen from another locality and horizon (BMNH D45165; *B. mucronata* Zone, Edward's Pit, Mousehold, near Norwich, England), possibly belonging to the same species, has a gonozooid near the edge of the parent colony as well as one in a subcolony. Brood chambers (Pl. 4, fig. 4) are recurved arcuate, broader than long, and are close to and parallel with the colony margin. The position of the ooeciopore is visible in only one specimen, where it is located on the distal side of the brood chamber (Pl. 4, fig. 4).

Minimum diameter of parent colonies with fertile subcolonies is 3·9 mm (Text-fig. 6E; minimum area 12·7 mm^2), and gonozooids were present in seven of the 32 colonies (22 per cent.) equal to or

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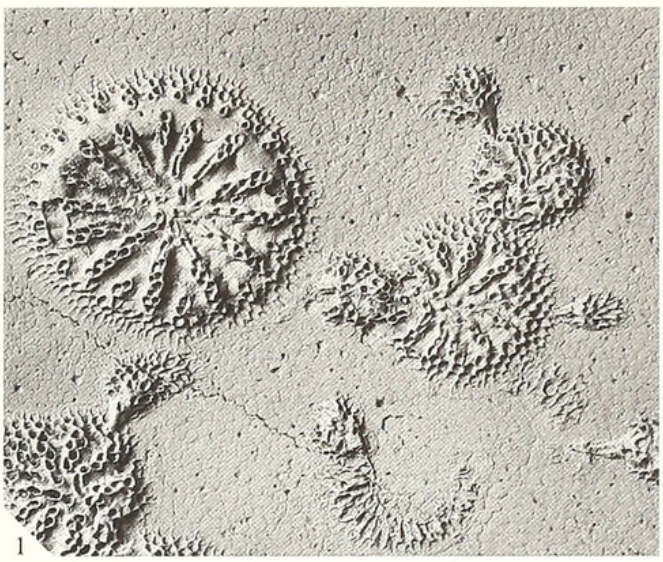
EXPLANATION OF PLATE 3

Figs 1–4. *Actinopora disticha* (von Hagenow, 1851); Cretaceous, Santonian, *coranguinum* Zone, Upper Chalk; Northfleet, Kent. 1–2, BMNH BZ 1838. 1, fertile colony (top left) and several smaller infertile colonies, some with peripheral subcolonies and some abraded; ×6. 2, peripheral subcolony; ×43. 3–4, BMNH BZ 3232. 3, disc-shaped colony with two gonozooids forming a complete ring close to the growing edge; ×10. 4, small ooeciopore of a gonozooid located between radial rows of autozooidal apertures; ×60.

Figs 5–6. *Discocavea irregularis* (d'Orbigny, 1851). 5, BMNH D45080; Cretaceous, Campanian, mucronata Zone, Upper Chalk; Earlham Lime Works, Norwich, Norfolk; colony with raised margins and a frontal subcolony; ×7. 6, BMNH BZ 1839; Cretaceous, Santonian, *coranguinum* Zone, Upper Chalk; Northfleet, Kent; inconspicuous brood chamber made visible by partial loss of its roof; ×45.

All are back-scattered scanning electron micrographs of uncoated specimens.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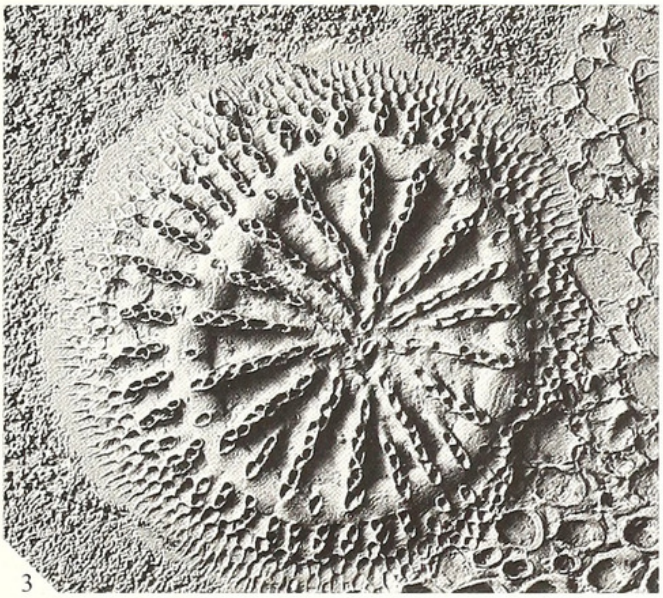
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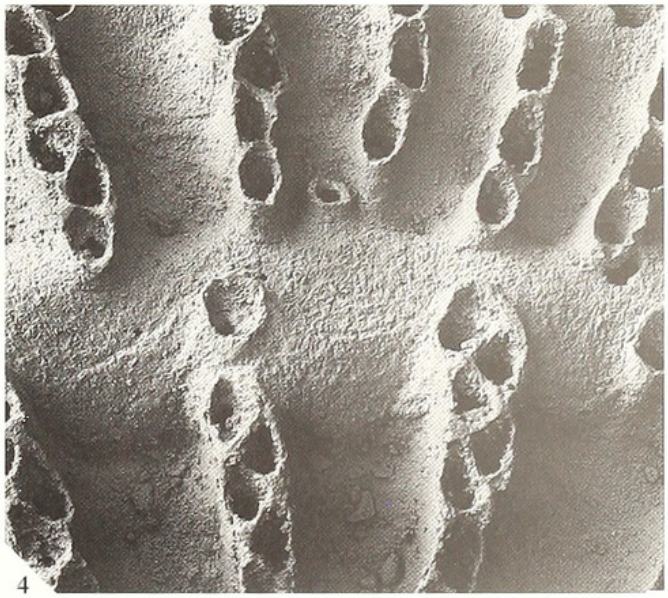
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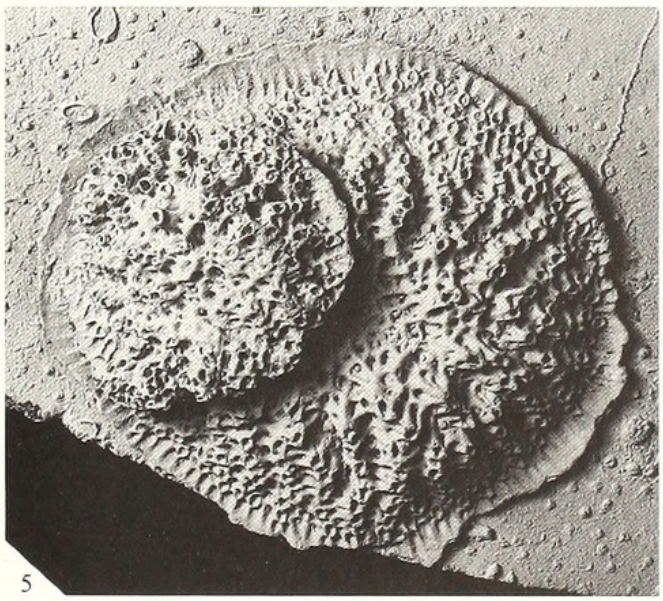
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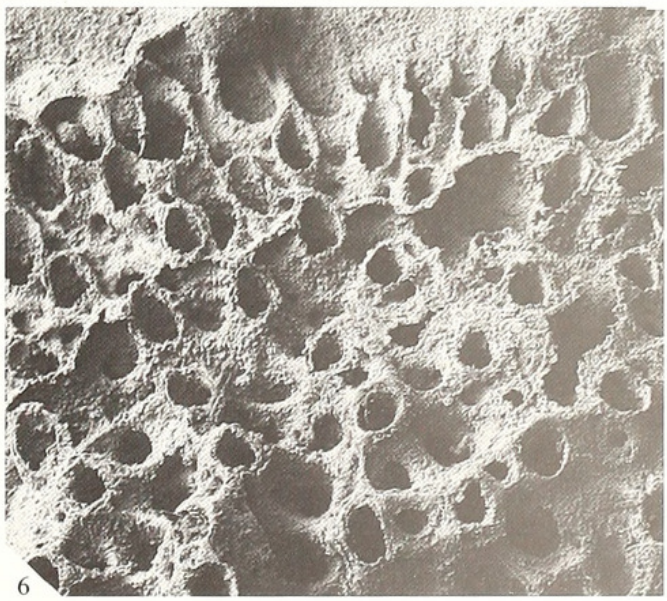
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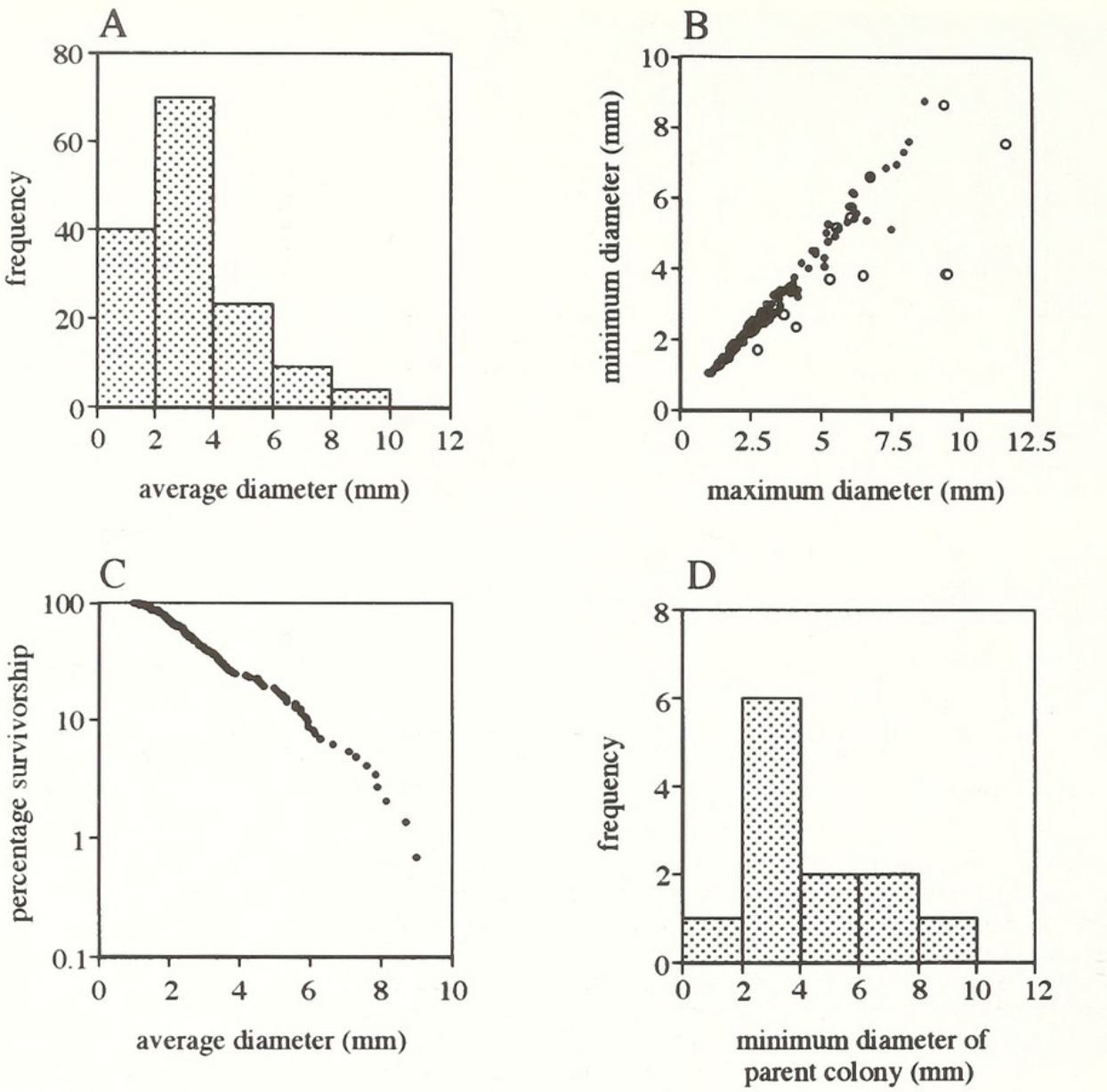
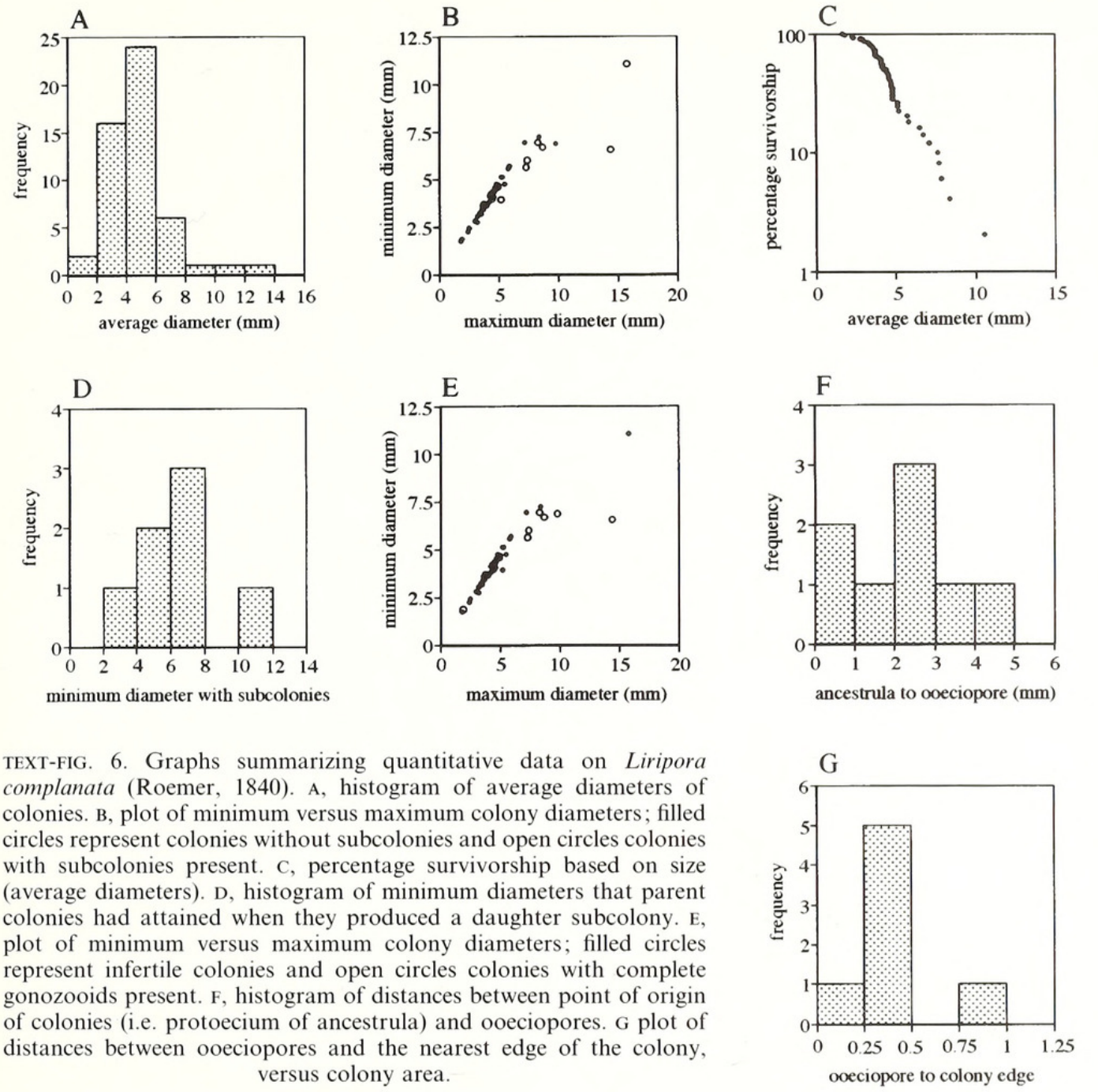
McKINNEY and TAYLOR, *Actinopora*, *Discocavea*



TEXT-FIG. 5. Graphs summarizing quantitative data on *Discocavea irregularis* (d'Orbigny, 1851). A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles representing solitary colonies and open circles representing compound colonies. C, percentage survivorship based on size (average diameters). D, histogram of minimum diameters that parent colonies had attained when they produced a daughter subcolony.

greater than 3·9 mm in diameter. Mean diameter of colonies with fully developed gonozooids is 7·9 mm, which is significantly different from the mean of 4·8 mm for non-fertile colonies equal to or greater in diameter than the 3·9 mm minimum for gonozooid development (Mann-Whitney $U = 41$, $p = 0{\cdot}034$, $N = 32$).

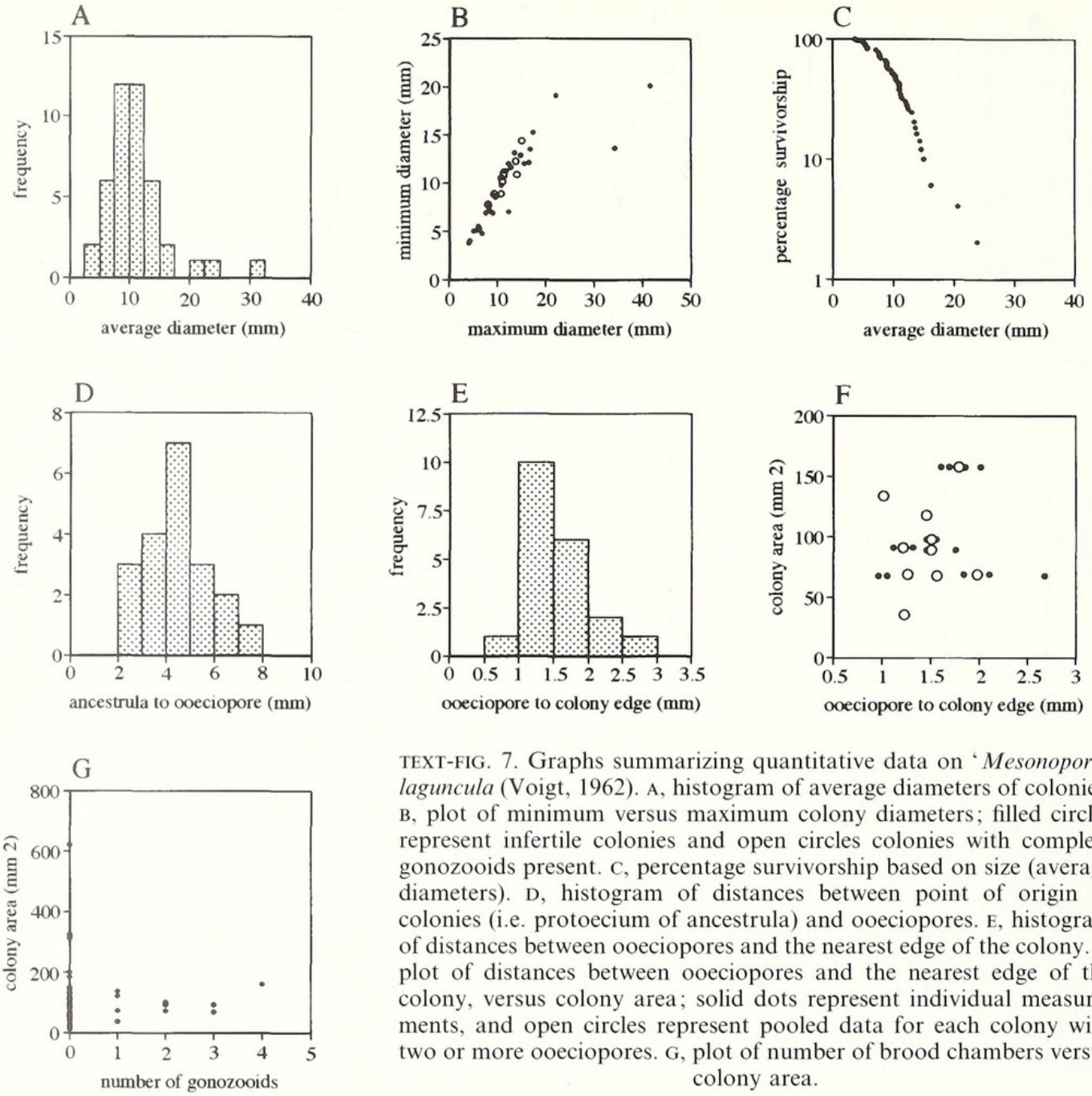
Based on the single preserved ooeciopore and presuming a similar position for ooeciopores of the abraded brood chambers, minimum distance from protoecium of the parent colony to ooeciopore is 1·8 mm, and the mean is 2·8 mm (Text-fig. 6F). Ooeciopores were located on average 0·5 mm from the outer edge of the developing zooids along the subcolony margin when the colony died (Text-fig. 6G). There is no correlation between colony size and distance between ooeciopore and subcolony margin ($r = 0{\cdot}750$, $p = 0{\cdot}589$, $N = 7$); instead, subcolonies, and parent colonies if they were still viable, grew only a short distance beyond completion of the brood chamber. This distance varied between 0·3 mm and 1·0 mm in the specimens available. Only one gonozooid per colony was noted



TEXT-FIG. 6. Graphs summarizing quantitative data on *Liripora complanata* (Roemer, 1840). A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles represent colonies without subcolonies and open circles colonies with subcolonies present. C, percentage survivorship based on size (average diameters). D, histogram of minimum diameters that parent colonies had attained when they produced a daughter subcolony. E, plot of minimum versus maximum colony diameters; filled circles represent infertile colonies and open circles colonies with complete gonozooids present. F, histogram of distances between point of origin of colonies (i.e. protoecium of ancestrula) and ooeciopores. G plot of distances between ooeciopores and the nearest edge of the colony, versus colony area.

where they occurred in the sample studied, although in specimen BMNH D45161, which may belong to *L. complanata*, two gonozooids were present.

'Mesonopora' laguncula. '*M*'. *laguncul*a (Voigt, 1962) grew as small to moderately large, circular to rather irregularly shaped colonies (Text-fig. 7A–B; Pl. 4, fig. 1) in which autozooidal apertures are isolated and quincuncially arranged. Zooids have their greatest external width about mid-way along the length, tapering both proximally and distally. Commonly, autozooids have their distal ends flexed to one side, giving a slightly sinuous external appearance to the zooids (cf. *Serpentipora*; see Brood 1981). Colonies of this species resemble Walter's (1989) concept of *Mesonopora*, but mode of formation of the gonozooid differs from the type species and involves distal and proximal growth of the brood chamber from the maternal zooid. In addition, brood chambers are roughly equidimensional rather than being appreciably broader than long. The species probably belongs to an undescribed genus.

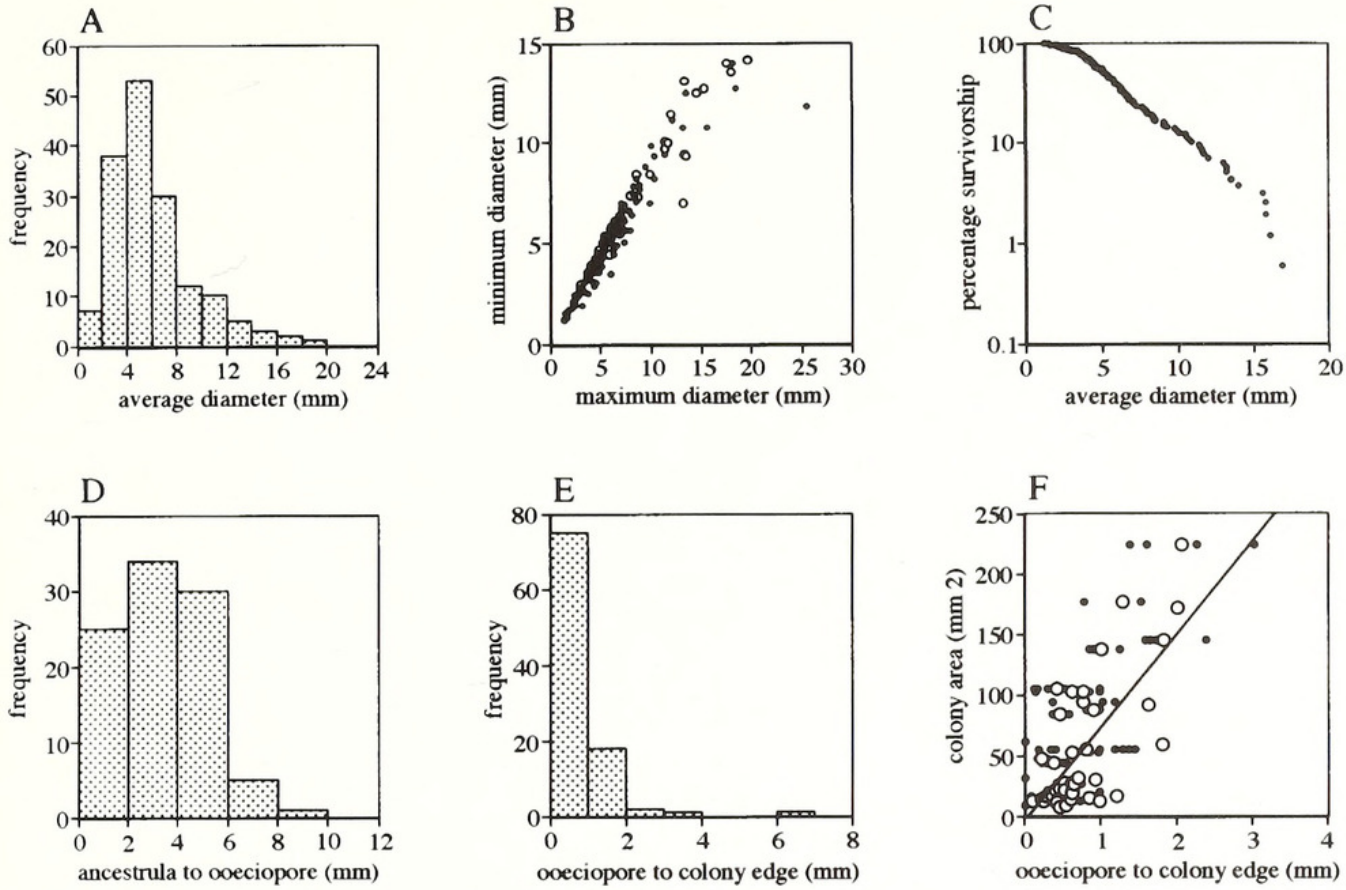


TEXT-FIG. 7. Graphs summarizing quantitative data on '*Mesonopora*' *laguncula* (Voigt, 1962). A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles represent infertile colonies and open circles colonies with complete gonozooids present. C, percentage survivorship based on size (average diameters). D, histogram of distances between point of origin of colonies (i.e. protoecium of ancestrula) and ooeciopores. E, histogram of distances between ooeciopores and the nearest edge of the colony. F, plot of distances between ooeciopores and the nearest edge of the colony, versus colony area; solid dots represent individual measurements, and open circles represent pooled data for each colony with two or more ooeciopores. G, plot of number of brood chambers versus colony area.

Minimum diameter of colonies averages 82 per cent. of their maximum diameter, and the variance is high. Even some large colonies are essentially circular, while maximum diameter of others is over twice minimum diameter. Growth interference is clearly seen in one colony that is slightly irregular in shape, but it is unclear why others became irregularly shaped.

Coefficient of variation for mean diameter of colonies is 48. Plotted as percentage survivorship on a logarithmic scale, the average diameters of colonies show an increasing death rate up to about 16 mm (Text-fig. 7C), with three 'Methusalah' colonies that reached diameters in excess of 20 mm.

Colonies grew by a mixture of extension around the entire perimeter and local extension, but they did not produce subcolonies. Some colonies have pronounced growth lines that probably reflect variations in growth rate, including possible temporary growth cessation. Following this, however, resumption of higher growth rates occurred essentially around the entire perimeter, with neither peripheral pseudoancestrular groups producing subcolonies nor frontal budding of subcolonies.



TEXT-FIG. 8. Graphs summarizing quantitative data on '*Mesonopora*' sp. A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles represent infertile colonies and open circles colonies with complete gonozooids present. C, percentage survivorship based on size (average diameters). D, histogram of distances between point of origin of colonies (i.e. protoecium of ancestrula) and ooeciopores. E, histogram of distances between ooeciopores and the nearest edge of the colony. F, plot of distances between ooeciopores and the nearest edge of the colony, versus colony area; solid dots represent individual measurements, and open circles represent pooled data for each colony with two or more ooeciopores; regression, $Y = -3{\cdot}02 + 76{\cdot}79X$. G, plot of number of brood chambers versus colony area.

Minimum diameter of colonies with fully developed gonozooids is 7·7 mm (Text-fig. 7B), minimum area 35·7 mm^2, and gonozooids were present in ten of the 31 colonies (32 per cent.) equal to or greater than 7·7 mm in minimum diameter. Minimum distance from ancestrula to ooeciopore is 2·8 mm, and the mean distance is 4·5 mm (Text-fig. 7D). Brood chambers are approximately equidimensional, are located close to the colony margin (Pl. 4, fig. 1), and where several occur within a single colony are scattered around much of the perimeter. The ooeciopore is located mid-way along the length of the brood chamber, averaging 1·5 mm from the outer edge of the developing zooids along the colony margin (Text-fig. 7E). Distance between the ooeciopore and colony margin varies from about 1 mm in some of the smaller colonies to as much as 2·7 mm in the largest fertile colony (Text-fig. 7F), but there is no correlation between colony area and this distance ($r = 0{\cdot}074$, $p = 0{\cdot}840$, $N = 10$). Up to four brood chambers were noted per colony, with no apparent correlation between colony area and number of brood chambers (Text-fig. 7G; $r = 0{\cdot}350$, $p = 0{\cdot}321$, $N = 10$).

Minimum diameter of fertile colonies averaged 10·5 mm, and their area averaged 92·7 mm^2. Non-fertile colonies that had reached or exceeded the size of the smallest fertile colony averaged 12·1 mm minimum diameter and had an average area of 105·9 mm^2. The differences, however, are not significant (Mann-Whitney U test: minimum diameter, $U = 84{\cdot}5$, $p = 0{\cdot}386$; area, $U = 81$, $p = 0{\cdot}311$; $N = 31$).

'Mesonopora' *sp.* This species grew as small to moderately large, circular to rather irregularly shaped colonies (Text-fig. 8A–B; Pl. 4, fig. 5) in which autozooidal apertures are isolated and quincuncially arranged. As for '*M.*' *laguncula*, colonies of '*Mesonopora*' sp. appear to fit within Walter's (1989) concept of the genus, but mode of formation of the gonozooid differs from the type species, involving distal and proximal growth of the brood chamber from the maternal zooid and envelopment of the surrounding autozooids (Pl. 4, fig. 6). The species probably belongs to the same undescribed genus as '*M.*' *laguncula*.

Minimum diameter of colonies averages 85 per cent. their maximum diameter, and the majority are near this ratio. Even some large colonies are essentially circular, although the maximum diameter of others is over twice the minimum diameter. Irregularity in shape was due at least in part to growth interference, which is clearly seen in some colonies that abut other encrusting organisms (Pl. 5, fig. 5) or that have lifted the growing edge apparently in an attempt to rise over some object or organism that was not preserved (Pl. 4, fig. 5). Other irregularly shaped colonies show no evidence of interference from adjacent organisms or objects.

Coefficient of variation for mean diameter of colonies is 56. Plotted as percentage survivorship on a logarithmic scale, the average diameters of solitary colonies and parent portions in compound colonies show a constant death rate up to about 15 mm (Text-fig. 8C).

True subcolonies were not produced, although in a small percentage of specimens lobes extended locally well beyond the adjacent arrested or more slowly growing colony edge (Pl. 5, fig. 5) and occasionally overgrew older parts of the colony (Pl. 5, fig. 6). These lobes expanded only slightly once established.

Minimum size of colonies with fully developed gonozooids is 2·7 mm (Text-fig. 8B; 6·4 mm^2), and gonozooids were present in 41 of the 138 colonies (30 per cent.) equal to or greater than 2·7 mm in minimum diameter. Minimum distance from ancestrula to ooeciopore is 1·1 mm, and the mean distance is 3·3 mm (Text-fig. 8D). Brood chambers (Pl. 4, fig. 6) are broader than long, are close to and parallel with the colony margin, and may extend around much of the perimeter. The ooeciopore is located on the distal side of the brood chamber, averaging 0·8 mm from the outer edge of the developing zooids along the colony margin (Text-fig. 8E). There is a pronounced positive correlation between colony size and distance between ooeciopore and colony margin ($r = 0{\cdot}705$, $p < 0{\cdot}001$, $N = 41$). Ooeciopores are exactly on the colony margin in some of the smaller colonies, and are

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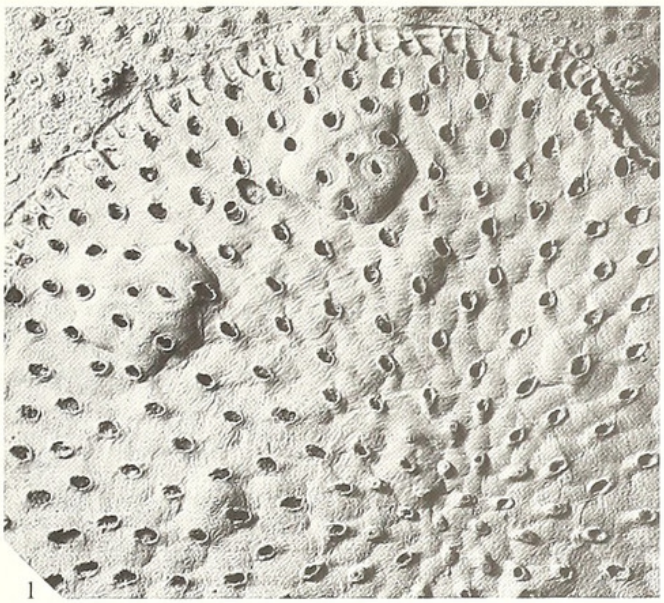
EXPLANATION OF PLATE 4

Fig. 1. '*Mesonopora*' *laguncula* (Voigt, 1962); BMNH BZ 1837; Cretaceous, Santonian, *coranguinum* Zone, Upper Chalk; Northfleet, Kent; part of a colony with two gonozooids visible as swellings centre left and top; × 10.

Figs 2–4. *Liripora complanata* (Roemer, 1840); BMNH D46466; Cretaceous, Coniacian, *cortestudinarium* Zone, Upper Chalk; Seaford, Sussex. 2, two compound colonies, each with a peripheral subcolony; × 7·6. 3, peripheral subcolony (left) overgrowing the margin of the parent colony; × 15. 4, detail of the peripheral subcolony depicted in figure 3 showing the arcuate gonozooid with the ooeciopore immediately left of the hole in the roof; × 41.

Figs 5–6. '*Mesonopora*' sp.; BMNH BZ 1844; Cretaceous, Santonian, *coranguinum* Zone, Upper Chalk; Offham Hill, near Lewes, Sussex. 5, colony with two gonozooids (upper left and centre right) and a ridge (lower right) formed by overgrowth of an obstruction; × 12. 6, transversely elongate gonozooid enveloping several autozooids; × 57.

All are back-scattered scanning electron micrographs of uncoated specimens.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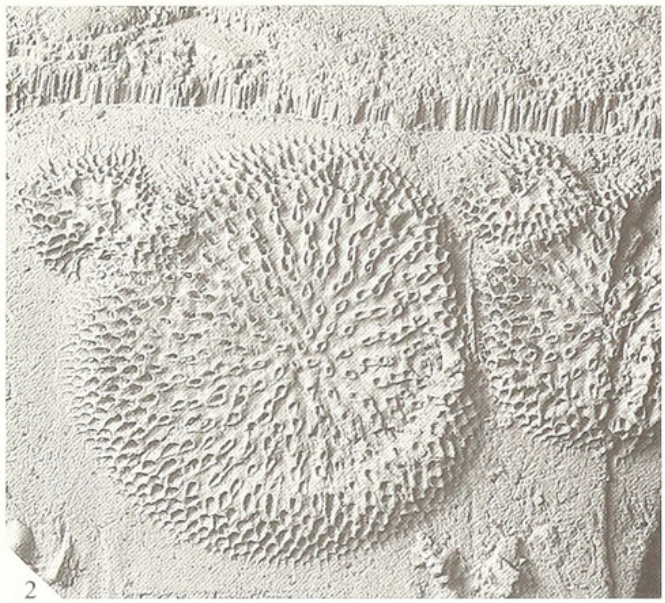
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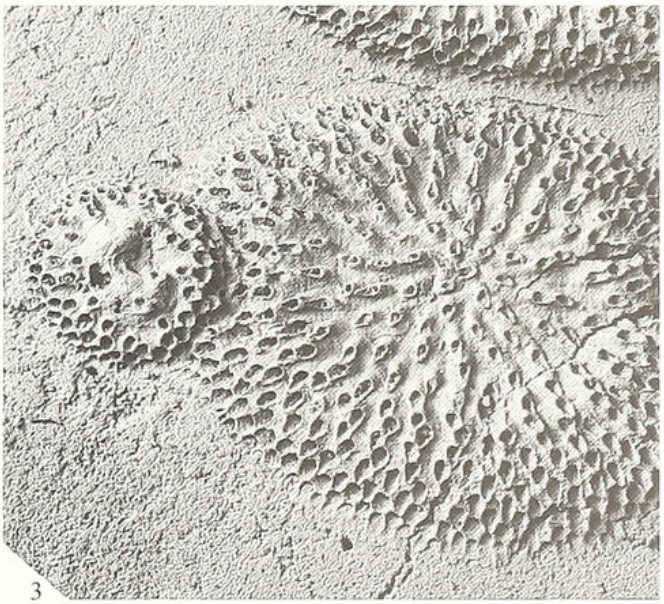
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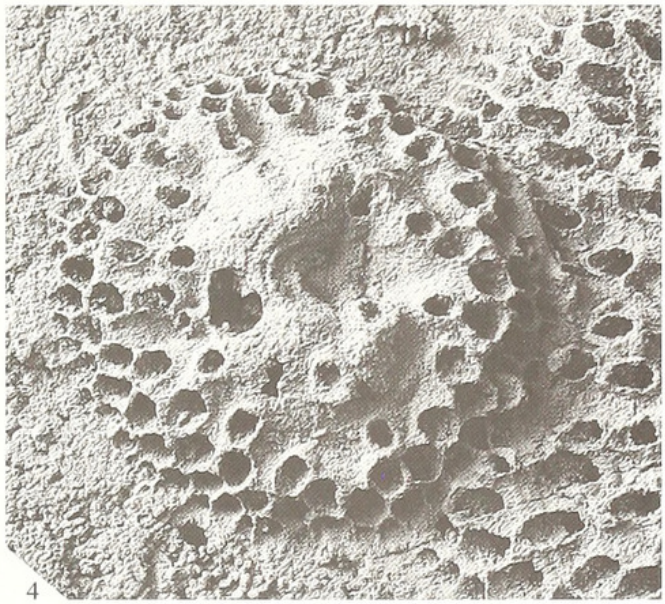
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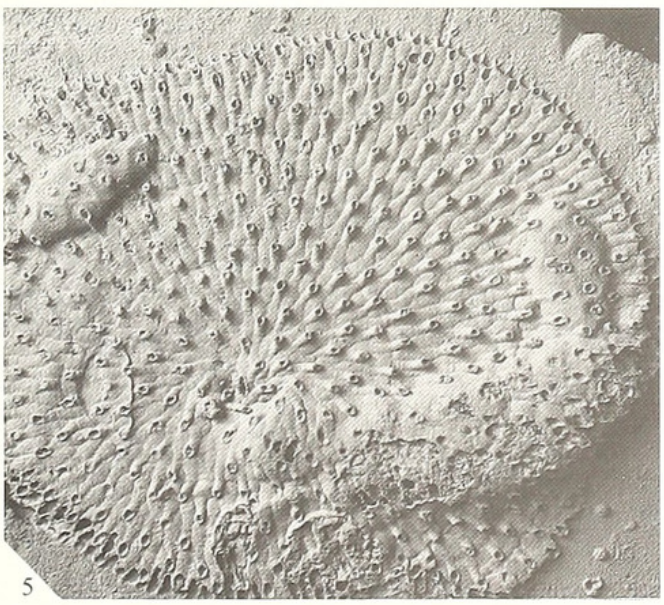
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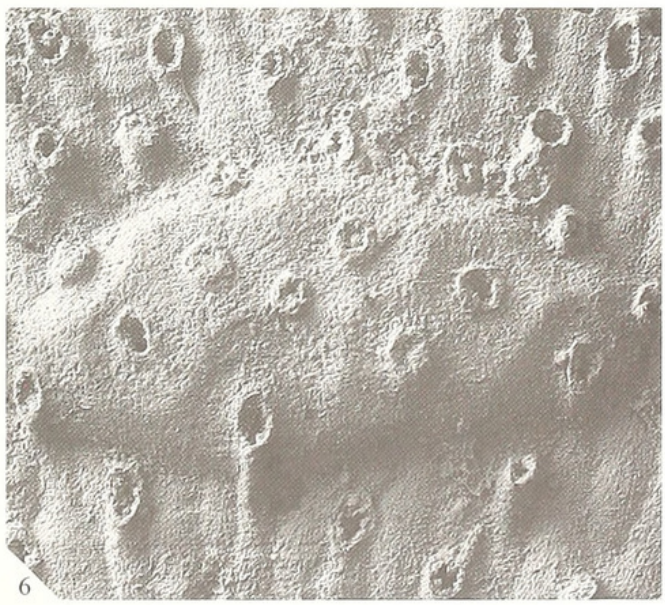
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McKINNEY and TAYLOR, '*Mesonopora*', *Liripora*

rarely more than 2 mm from the margin (Text-fig. 8F). Up to nine brood chambers were noted per colony, with relatively large colonies tending to have the higher number of brood chambers (Text-fig. 8G; $r = 0{\cdot}348$, $p = 0{\cdot}026$, $N = 41$).

The colony with nine brood chambers had them arranged in two rows: an inner circular row of five, and an outer circular row of four, indicating that the colony had undergone two periods of reproduction, with death occurring shortly after completion of the outer circle (ooeciopore to growing edge averaging 0·32 mm for the outer row).

Eleven of the colonies that had grown to 2·7 mm diameter or larger show evidence of interference within a short period before the colony died. This interference comprises abutment against other skeletized encrusters or development of elevated colony margins, although in most cases the objects or organisms encountered were not preserved. Over half (six of 11; 55 per cent.) of these colonies produced brood chambers shortly after contact with the obstruction. This proportion is marginally significantly higher than the fertile proportion (28 per cent.) of colonies of the same size range that show no preserved evidence of growth interference ($X^2 = 3{\cdot}53$, $p = 0{\cdot}06$; $N = 138$).

On one substratum, three approximately equal-sized colonies had fused and continued growing as a single chimaeric colony. Gonozooids were produced in each of the three original colonies at a distance from the ancestrula approximately equal to the distance from the ancestrula to the point of contact with the adjacent colonies, i.e. gonozooid production coincided with fusion.

Fertile colonies had a mean minimum diameter of 7·0 mm and mean area of 53·4 mm^2 at time of death, and nonfertile colonies that had minimum diameters of at least 2·7 mm (the minimum observed diameter of fertile colonies) had a mean minimum diameter of 5·8 mm and mean area of 34·1 mm^2. These differences, however are not significant (Mann-Whitney U test: minimum diameter, $U = 1678{\cdot}5$, $p = 0{\cdot}149$; area, $U = 1677$, $p = 0{\cdot}147$; $N = 41$).

Plagioecia? reniformis. *P.? reniformis* (Gregory, 1899) developed relatively large, circular to somewhat irregularly shaped colonies (Text-fig. 9A–B; Pl. 5, fig. 1) in which autozooidal apertures are isolated and quincuncially arranged. Minimum diameter of colonies averages 76 per cent. of maximum diameter, and the majority are near this ratio. Even the largest colonies, while having generally more irregular outlines than smaller colonies, have an approximately 85 per cent. ratio of width to length. There is no preserved evidence for the cause of the moderate irregularities in colony outlines.

Coefficient of variation for mean diameter of colonies is 41. Plotted as percentage survivorship on a logarithmic scale, the average diameters of colonies show an increasing death rate up to about 10 mm, at which point death rate decreased and then gradually increased (Text-fig. 9C). No colonies smaller than 3 mm diameter were found.

True subcolonies were not produced, although in a small percentage of specimens, local lobes (Pl. 5, fig. 3) extend well beyond the adjacent arrested or more slowly growing colony edge. The lobes have highly irregular shapes. Some lobes expanded only slightly once established but others

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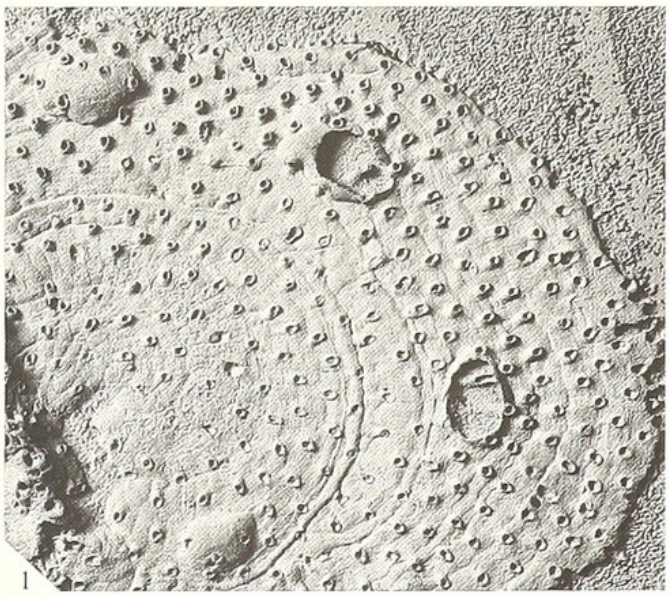
EXPLANATION OF PLATE 5

Figs 1–4. *Plagioecia? reniformis* (Gregory, 1899); Cretaceous, Santonian, *coranguinum* Zone, Upper Chalk; Northfleet, Kent. 1–2, BMNH BZ 1836. 1, part of a colony with conspicuous growth checks and four visible gonozooids, two having broken roofs; ×7·5. 2, gonozooid showing bulbous roof penetrated by a few autozooids and small distal ooeciopore (top centre); ×50. 3–4, BMNH BZ 1835. 3, broad lobe extending from the growing edge; ×21. 4, growth irregularity comprising a spiral lobe of zooids growing across a truncated former growing edge; ×22.

Figs 5–6. '*Mesonopora*' sp.; BMNH BZ 1051; Cretaceous, Santonian, *coranguinum* Zone, Upper Chalk; Northfleet, Kent. 5, lobate colony encrusting an echinoid test together with a stomatoporid bryozoan and a brachiopod (bottom right); ×11. 6, spiralling lobe overgrowing older parts of the colony; ×26.

All are back-scattered scanning electron micrographs of uncoated specimens.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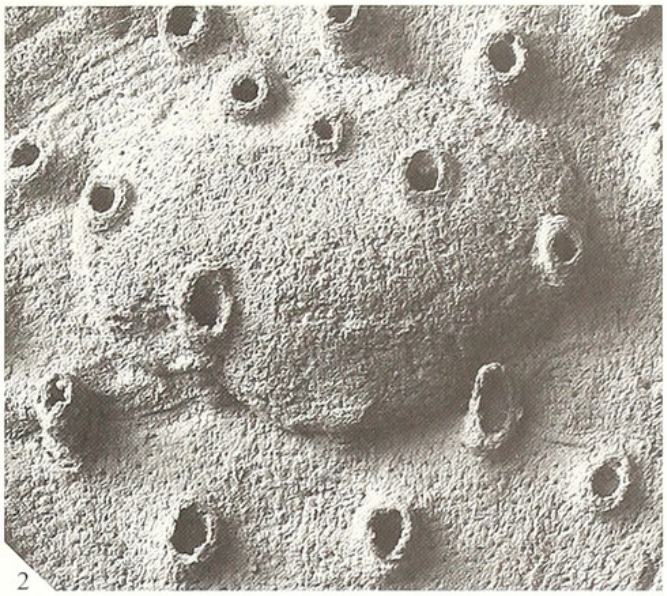
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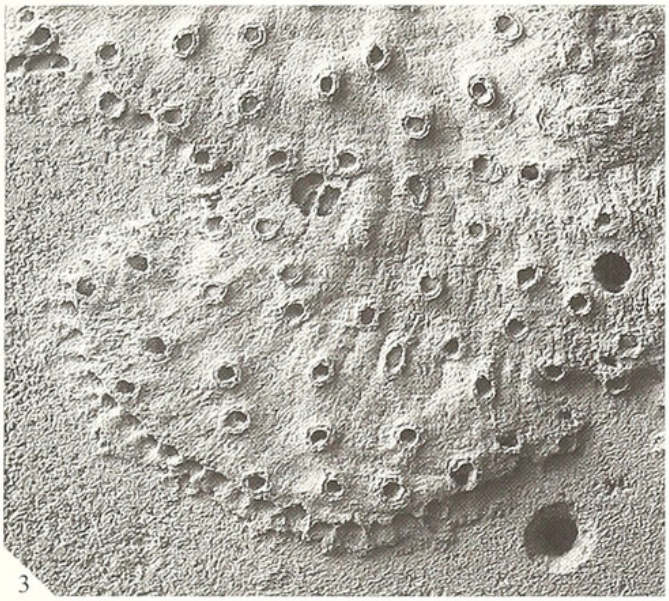
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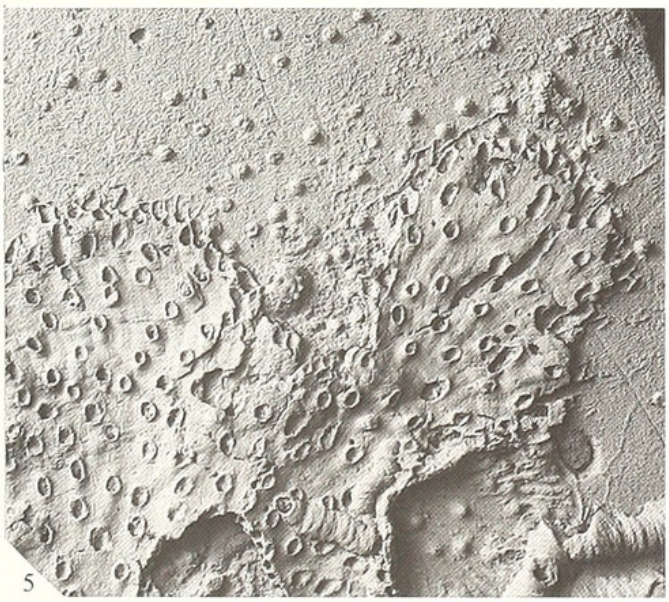
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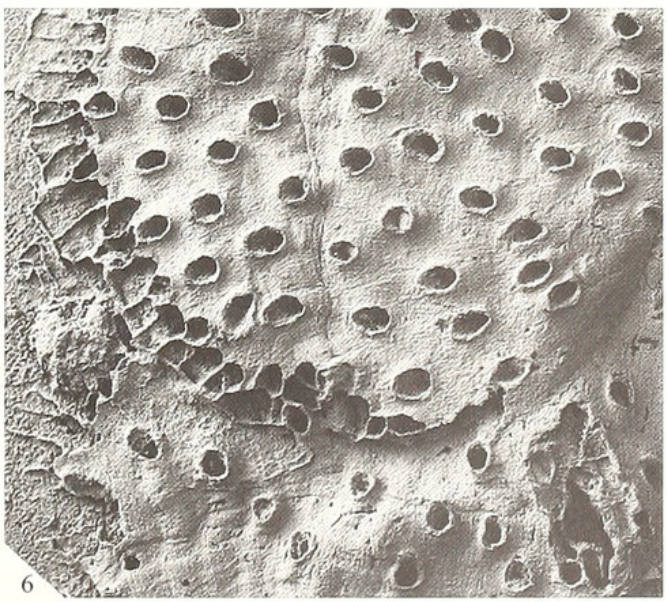
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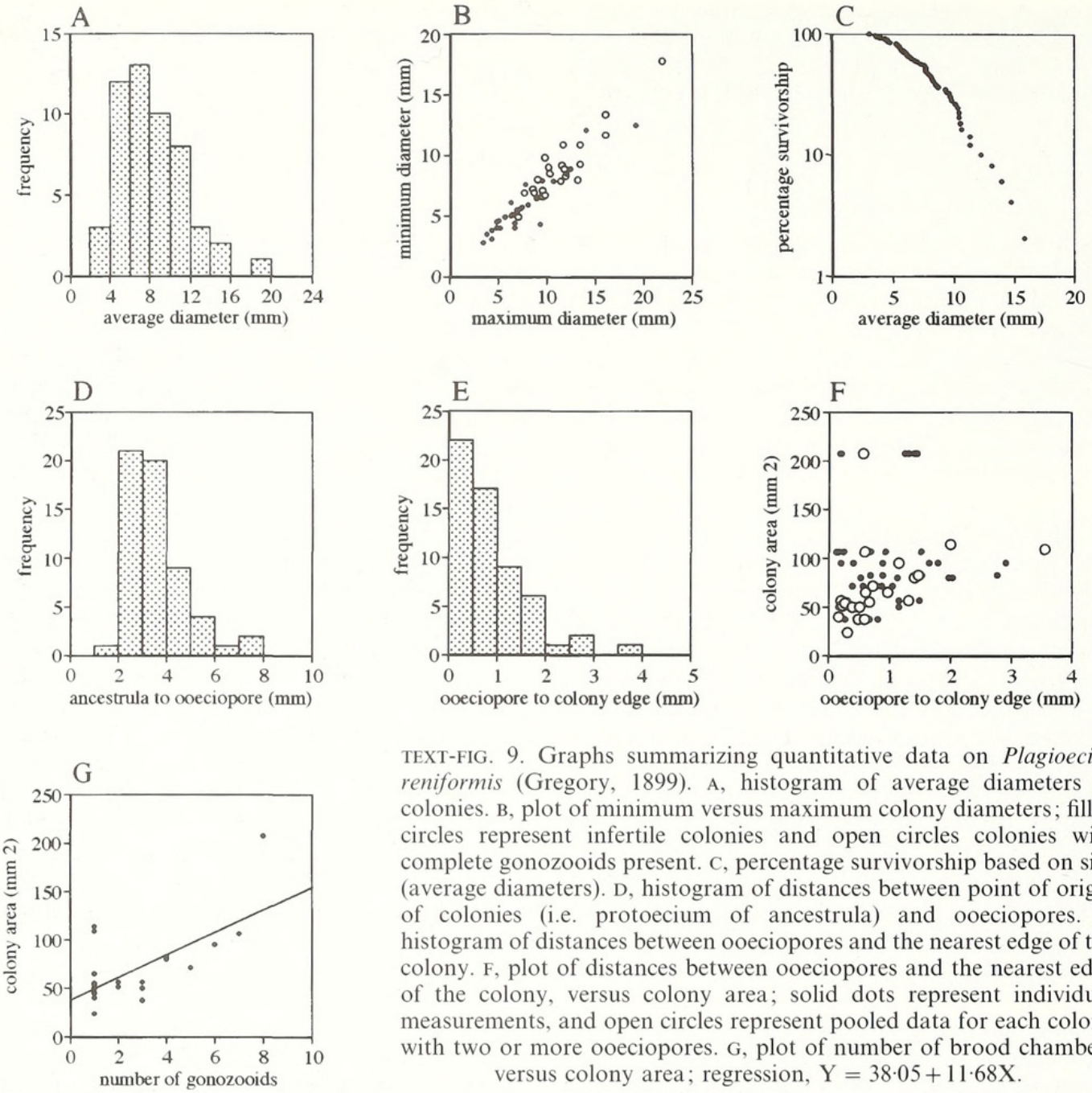
McKINNEY and TAYLOR, *Plagioecia*?, '*Mesonopora*'



TEXT-FIG. 9. Graphs summarizing quantitative data on *Plagioecia*? *reniformis* (Gregory, 1899). A, histogram of average diameters of colonies. B, plot of minimum versus maximum colony diameters; filled circles represent infertile colonies and open circles colonies with complete gonozooids present. C, percentage survivorship based on size (average diameters). D, histogram of distances between point of origin of colonies (i.e. protoecium of ancestrula) and ooeciopores. E, histogram of distances between ooeciopores and the nearest edge of the colony. F, plot of distances between ooeciopores and the nearest edge of the colony, versus colony area; solid dots represent individual measurements, and open circles represent pooled data for each colony with two or more ooeciopores. G, plot of number of brood chambers versus colony area; regression, $Y = 38{\cdot}05 + 11{\cdot}68X$.

expanded so much that the growth margin recurved (Pl. 5, fig. 4) and locally overgrew or truncated the adjacent margin of the colony.

Minimum diameter of colonies with fully developed gonozooids was 4·8 mm (Text-fig. 9B; minimum area 23·0 mm^2), and gonozooids were present in 22 of the 40 colonies (55 per cent.) equal to or greater than 4·8 mm in minimum diameter. Minimum distance from ancestrula to ooeciopore is 1·9 mm, and the mean distance is 3·5 mm (Text-fig. 9D). Brood chambers (Pl. 5, fig. 2) are up to twice as broad as long; the long axis is parallel with the nearby colony margin. The ooeciopore is located on the distal side of the brood chamber, averaging 0·9 mm from the outer edge of the developing zooids along the colony margin (Text-fig. 9E). There is no correlation between colony size and distance between ooeciopore and colony margin (Text-fig. 9F; $r = 0{\cdot}378$, $p = 0{\cdot}091$, $N = 22$). Up to eight brood chambers were noted per colony, with relatively large colonies tending to have the higher number of brood chambers (Text-fig. 9G; $r = 0{\cdot}639$, $p < 0{\cdot}001$, $N = 22$).

Fertile colonies had a mean minimum diameter of 9·0 mm and mean area of 69·9 mm^2 at time of

death, and non-fertile colonies that had minimum diameter of at least 4·8 mm (the minimum observed diameter of fertile colonies) had a mean minimum diameter of 7·0 mm and mean area of 47·0 mm^2. The differences in size are significant (Mann-Whitney U test: minimum diameter, $U = 95$, $p = 0{\cdot}005$; area, $U = 103$, $p = 0{\cdot}010$; $N = 40$).

DISCUSSION

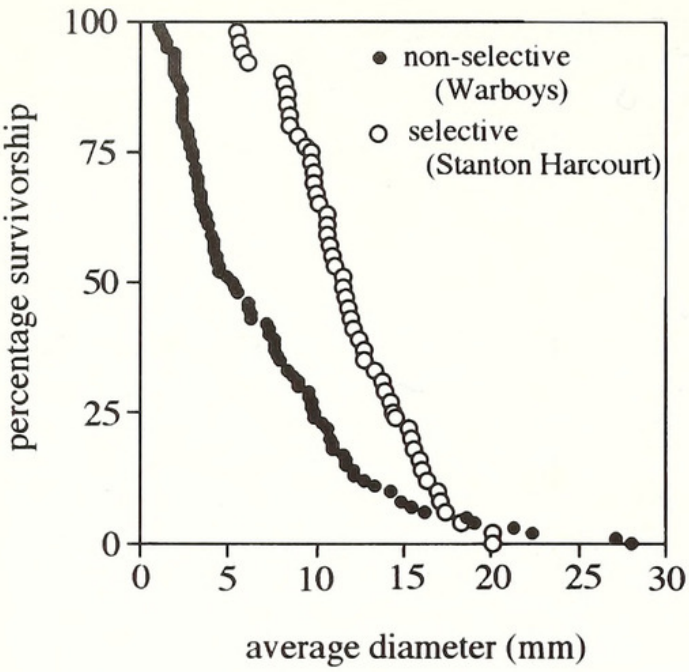
Potential collection bias

In order to estimate the degree of bias introduced by using museum collections for characterization of the life history attributes of the species used in this study, we duplicated measurements on two collections of the Jurassic species *Hyporosopora dilatata* and *Plagioecia* sp. 2. One suite of specimens for each of the two species was collected from Stanton Harcourt prior to this study, with strong field and laboratory selection for 'well-preserved', conspicuous specimens. The other was collected from the Warboys Clay Pit in Cambridgeshire by keeping all *Gryphaea* and other oysters encountered in the field, cleaning them in the laboratory, and then searching for all encrusting cyclostome colonies using hand lens and microscope. In addition, data on several colonies of *Plagioecia* sp. 2 found on a single museum specimen of *Gryphaea dilatata* from St Ives, Cambridgeshire, were combined with data on specimens from Warboys.

Numerical evaluation of the suites of *Hyporosopora dilatata* specimens from Stanton Harcourt and Warboys yielded some similar and some different results, as can be seen in Tables 2 and 3 (pp. 518–519). The greatest difference is that the more intensive search for and retention of specimens from Warboys yielded a greater number of small colonies, which is reflected in smaller average diameters and area for Warboys *H. dilatata* and *Plagioecia* sp. 2, in comparison with those from Stanton Harcourt (Table 2). Distributions of colony size parameters are strongly different for the two suites of specimens, with near-normal distributions for the Stanton Harcourt *H. dilatata* sample (average diameter skewness 0·1997, kurtosis −1·0133; area skewness 0·781, kurtosis −0·5219) and strongly right-skewed distributions for the Warboys sample (average diameter skewness 1·516, kurtosis 2·3755; area skewness 3·745, kurtosis 19·7818). These distributions differ significantly from one another (Kolgomorov Smirnov test, $p < 0{\cdot}001$ for both measures). Because of the small sample size, statistical tests for differences between the two suites of *Plagioecia* sp. 2 were not made; the patterns of differences, however, appear to be similar to those for *H. dilatata*. Although we infer that collecting bias was entirely or largely the cause of the differences in size distributions of colonies of *H. dilatata* and *Plagioecia* sp. 2 between Stanton Harcourt and Warboys, we cannot rule out the possibility that somewhat different environments may have prevailed during deposition at the two sites that may have contributed to the differences.

The different distributions of colony sizes resulted in strikingly different survivorship curves for *Hyporosopora dilatata* based on average colony diameter. Colonies that had been chosen while at Stanton Harcourt were all about 5 mm or more in diameter and produce a linear distribution of colony sizes (Text-fig. 10); in contrast, about half the specimens from Warboys were less than 5 mm in diameter. In addition, larger specimens were included in the Warboys collection than were in the Stanton Harcourt collection, possibly due to the largest colonies commonly being less pristine than smaller colonies and therefore being left behind at Stanton Harcourt. Consequently, the survivorship curve for Warboys *H. dilatata* is concave as plotted on arithmetic axes, in contrast to the linear, more steeply sloped curve for the Stanton Harcourt specimens. However, data on colony reproductive attributes are virtually identical for the two suites of specimens of *H. dilatata*, whereas it appears that fertile colonies of *Plagioecia* sp. 2 were collected preferentially at Stanton Harcourt (Table 3).

We suspect that a lesser degree of selectivity, certainly no more than for specimens from Stanton Harcourt, was exercised by the collectors of the Cretaceous species used in this study. Consequently, the patterns determined here for all species are accepted by us as in general highly similar to the patterns that would characterize suites of specimens made without collector bias. The greatest differences would be in the range of colony sizes and the pattern of the survivorship curve; in



TEXT-FIG. 10. Comparison of percentage survivorship curves for *Hyporosopora dilatata* (d'Orbigny, 1850) based on size (average diameters), for a non-selective, thorough collection from Warboys and field- and laboratory-selected specimens from Stanton Harcourt.

addition, there may be a consistent slight overestimation of average colony size. Within-colony reproductive patterns as determined from the skeleton appear to be affected little if at all.

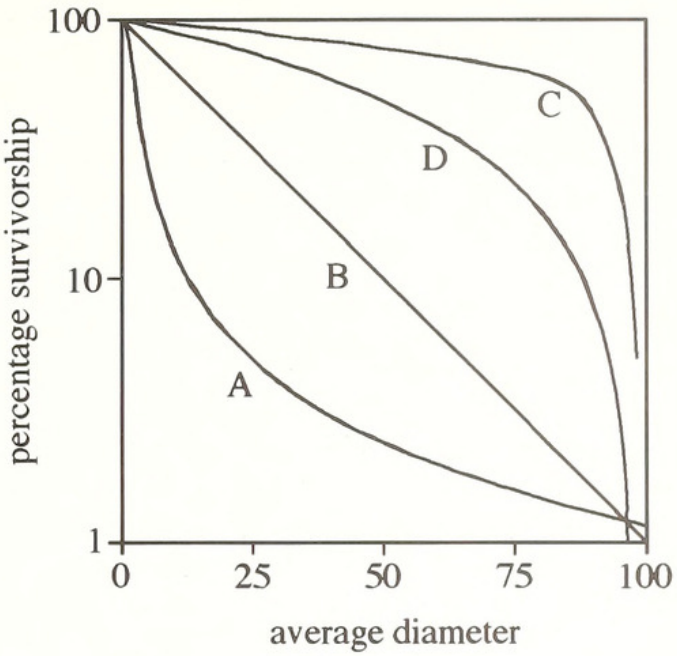
Patterns of life history characteristics

Survivorship curves. 'Survivorship' as used in this paper is based entirely on the pattern of size-frequency distributions of available colonies within a species. Size-frequency distributions of population samples are influenced by several intrinsic attributes of a species, including number of recruits per class, seasonality of recruitment, rate of growth of individuals, coefficient of variation of growth rate, mortality rate, and seasonal interruptions in growth that are due either to adverse conditions or to reproduction (Craig and Oertel 1966). Fossil assemblages are almost always time-averaged, and they are necessarily time-averaged where specimens are taken from multiple beds as in this study. Therefore recruits per class, seasonality of recruitment, and seasonal interruptions in growth cannot be analysed for the assemblages reported here, although growth interruptions can be recognized in individual specimens of some species such as '*Mesonopora*' *laguncula* and *Plagioecia*? *reniformis* (Pl. 5, fig. 1).

Setting aside possible taphonomic and collector biases to size distributions (see discussions above), the size-frequency distributions of the fossil assemblages and the size-based survivorship curves derived from these distributions are primarily influenced by growth rate and by mortality rate. Other than uncommon partial overgrowth, none of the encrusting cyclostome species in this study show any indication of negative growth (shrinkage), which may be caused by partial overgrowth, partial predation, or fission. Several studies have shown that growth rate, onset of reproduction, reproductive output, and mortality are influenced by size rather than by age in clonal organisms (e.g. Hughes and Jackson 1980). Although within each species in this study size is presumed to correlate closely with age, size is not used as a proxy for age but rather as a measure of colony development against which mortality rate and other aspects of life history are compared.

Whether based on age units or size units, mortality rate patterns (Text-fig. 11) generally fall into three groups: (1) high mortality in infancy, decreasing to low death rate; (2) constant mortality, in which the same proportion of the population dies per unit time/size; and (3) low initial mortality followed by an increase to high mortality rate (Craig and Oertel 1966). A special case of the latter is a constant number of deaths per unit time/size.

Each of the three species in which unselective collections were analysed shows a somewhat different survivorship curve. The overall curve for *Reptomultisparsa hybensis* (Text-fig. 1C) is



TEXT-FIG. 11. Survivorship curves. A, high initial mortality followed by decreased mortality rate. B, constant mortality rate. C, low initial mortality followed by abruptly increased mortality rate. D, low initial mortality with constantly increased mortality rate due to constant number dying for each size unit.

somewhat irregular but is overall essentially linear or slightly convex, indicating a constant or slightly increasing mortality rate with colony size. The first portion of the curve, up to about 5 mm, is distinctly convex if plotted with survivorship on a logarithmic scale; plotted on a linear scale, this portion of the curve is straight, indicating that deaths were constant per unit size. The survivorship of *Hyporosopora dilatata* (Text-fig. 2C) is linear and indicates a constant probability of death per unit size. In contrast with the first two species, the survivorship curve for *Plagioecia* sp. 2 (Text-fig. 3C) is convex up to 4 mm average diameter, indicating increased mortality rate, and linear above 4 mm average diameter, indicating constant mortality rate for such larger colonies.

Although the survivorship curves of the other species are potentially influenced by collecting bias, the range of shapes found roughly corresponds with the range of shapes of curves for the three unselectively sampled species described above. *Actinopora disticha* (Text-fig. 4C), '*Mesonopora*' *laguncula* (Text-fig. 7C), and *Plagioecia*? *reniformis* (Text-fig. 9C) show constantly increasing mortality rates for most of the population samples, reflecting a constant number of deaths per unit size, until a certain size threshold was reached, at which point mortality rate declined for the few large colonies that exceeded this size. *Discocavea irregularis* (Text-fig. 5C) and '*Mesonopora*' sp. (Text-fig. 8C) have survivorship curves essentially similar to that of *Reptomultisparsa hybensis* (Text-fig. 1C). The survivorship curve for *Liripora complanata* (Text-fig. 6C) is more complex but overall nearly straight or slightly convex. About 60 per cent. of the *L. complanata* colonies died between diameters of 3 mm and 5 mm, but those that passed the 5 mm threshold could reach much larger sizes.

None of the species studied shows any evidence of reaching a maximum size beyond which growth could not occur. Even species such as *Actinopora disticha* and '*Mesonopora*' *laguncula*, and *Plagioecia*? *reniformis*, for which pronounced convex survivorship curves show that mortality rate increased for the majority of the size distribution of colonies, include several specimens that 'escaped' to grow into substantially larger colonies. These larger, 'Methusalah' colonies may have grown anomolously rapidly during the normal life span of colonies of the species, or they may represent colonies that survived beyond the normal life span, perhaps to continue living into or through the following growth season.

The survivorship curves for Mesozoic cyclostomes, including those potentially influenced by collecting bias, are similar to curves found in some Eocene and Recent encrusting cyclostomes (McKinney *et al.* 1996; G. M. Galloway, pers comm.). Some of these post-Mesozoic encrusting cyclostomes exhibit increasing mortality rate generated by a constant number of deaths per unit size, while others are characterized by constant mortality rate. The post-Mesozoic species reached,

on average, smaller colony diameters than did the Mesozoic species, but also include a small number of relatively large, 'Methusalah' colonies.

These mortality patterns contrast with Håkansson's (1976) findings in a study of two free-living Cretaceous cheilostome bryozoans, *Stichopora pentasticha* (von Hagenow) and *Lunulites mitra* von Hagenow. Both species evidently suffered high juvenile mortality rates and probably decreasing growth rates, resulting in population structures similar to those seen in non-clonal benthic marine invertebrates.

Colony sizes and shapes. Equidimensionality of colonies, as expressed by the ratio of minimum to maximum colony diameters, was predicted to decrease with increasing colony size and to be positively correlated with the width to length ratio of brood chambers. In other words, we expected that in species that usually grew to larger sizes the colonies would be more irregular in shape than those that usually grew to smaller sizes, and that those species in which brood chambers are very broad, essentially parallel with colony margins, would have grown to more circular shapes than those with equidimensional or longitudinally elongated brood chambers. However, although the ratio of minimum to maximum colony diameters is negatively correlated with all measures of colony size (minimum diameter, maximum diameter, area), none are significant (Table 4). Also contrary to prediction, ratio of mean values for minimum and maximum diameters for each species was not correlated with shape of brood chambers (Table 4).

Table 4 lists correlation values based on the ratios of mean values of minimum and maximum diameter for each species; the same patterns of non-significance were obtained when ratios based on median values were used. If characterized by median values rather than mean values, 12 of the 15 species have more nearly equidimensional colonies, indicated by higher ratios in Table 2. This is statistically different from the null hypothesis of neither being preferentially larger ($X^2 = 5{\cdot}40$, $p = 0{\cdot}020$, $df = 1$, $N = 15$) and suggests that extreme values for individual colonies within most species have a measureable effect on the ratios, because the degree of asymmetry of individual colonies would affect the mean values more than the median values. Twelve of the species do indeed have larger mean colony diameters than median colony diameters (Table 2). However, a test for correspondence of low ratio of mean values for colony diameters with larger values for colony means rather than medians fails ($X^2 = 1{\cdot}67$, $p = 0{\cdot}194$. $df = 1$, $N = 15$). Apparently some other source of difference in colony equidimensionality is also involved, perhaps the high asymmetry of very young colonies (e.g. Pl. 1, fig. 2; Pl. 2, fig. 5) before they attain a disc-shape with a circumferential growing edge.

Zooid sizes. We used two measures to characterize size of zooids for each species, aperture diameter and centre-to-centre spacing between neighbouring zooidal apertures. Both of these measures are correlated with zooidal tentacle length, diameter of lophophores when in the feeding position, and with diameter of mouth (Winston 1981*a*; McKinney and Jackson 1989) in living cyclostomes. They are therefore related to strength of feeding currents and to potential rate of nutrient intake and growth rate (Winston 1977; McKinney 1993).

Aperture diameter is significantly correlated with zooidal spacing but is not correlated at $p < 0{\cdot}05$ with any other characteristics (Table 4). Zooidal spacing correlates significantly with all measures of colony size and with presence of subcolonies, and correlates at $p < 0{\cdot}001$ with distance between protoecium and ooeciopore, ooeciopore to adjacent colony margin, and minimum size at reproduction. These latter three characteristics are all related to colony size measures and so part of their correlation with zooidal spacing derives from that. However, each of them is much more highly correlated with zooidal spacing than are measures of colony size, so that zooidal size itself must have a close relationship to size at reproduction and survival after reproduction in cyclostomes.

Subcolonies. Subcolonies are absent in most Triassic and Jurassic species included in this study, although irregular, lobate extensions from the colony perimeter do occur in *Reptomultisparsa*

TABLE 4. Kendall's rank order correlations for life history characteristics of Mesozoic encrusting Cyclostomata. The correlation coefficients are followed by p values, which are enclosed in brackets. Coefficients for which $p > 0.05$ are printed in boldface. $N = 14$ for all correlations involving brood chamber shape and placement of the ooeciopore; for other correlations, $N = 15$.

	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)	(i)	(j)	(k)
Maximum diameter (a)	**0·905** (0·0000)										
Min. diameter to max. diam. (b)	−0·298 0·121	−0·202 0·294									
Area (c)	**0·943** (0·0000)	**0·943** (0·0000)	−0·260 0·177								
Ancestrula to 1st ooeciopore (d)	**0·773** (0·0001)	**0·778** (0·0001)	−0·156 0·436	**0·796** (0·0001)							
$\bar{x}$ ancestrula to ooeciopore (e)	**0·758** (0·0002)	**0·758** (0·0002)	−0·277 (0·166)	**0·780** (0·0001)	**0·818** (0·0000)						
Ooeciopore to colony edge (f)	**0·715** (0·0004)	**0·671** (0·0008)	−0·239 (0·234)	**0·692** (0·0006)	**0·753** (0·0002)	**0·686** (0·0006)					
% area as brood chamber (g)	−0·287 (0·152)	−0·376 (0·061)	0·291 (0·148)	−0·354 (0·076)	−0·278 (0·167)	−0·265 (0·186)	−0·079 (0·695)				
% fertile colonies (h)	0·298 (0·121)	0·240 (0·212)	0·049 (0·801)	0·240 (0·212)	0·000 (1·000)	−0·100 (0·618)	0·113 (0·573)	0·112 (0·578)			
Brood chamber shape (i)	−0·287 (0·152)	−0·199 (0·217)	−0·078 (0·698)	−0·221 (0·271)	−0·322 (0·108)	0·319 (0·112)	−0·281 (0·162)	0·221 (0·293)	−0·179 (0·373)		
Aperture diameter (j)	0·278 (0·186)	0·344 (0·086)	−0·316 (0·115)	0·322 (0·108)	0·301 (0·153)	0·379 (0·071)	0·278 (0·186)	−0·379 (0·071)	−0·056 (0·780)	−0·052 (0·805)	
Zooidal spacing (k)	**0·516** (0·010)	**0·495** (0·013)	−0·291 (0·148)	**0·516** (0·010)	**0·813** (0·0001)	**0·735** (0·0004)	**0·719** (0·0006)	−0·219 (0·297)	−0·033 (0·868)	−0·282 (0·180)	**0·478** (0·017)

hybensis (Pl. 1, fig. 3) and *Hyporosopora dilatata* (Pl. 1, fig. 6). We do not consider such lobate outgrowths to be subcolonies because they originate from variably broad portions of the colony perimeter and there is no conspicuous and consistent differentiation between them and the original part of the colony from which they extend (e.g. no secondary zone of astogenetic change).

One Oxfordian species, *Plagioecia* sp. 2, gave rise to peripheral subcolonies from single zooids that functioned as pseudoancestrulae from which a well-defined fan of zooids formed a radially expanding, secondary growth centre readily recognizable as a subcolony (Pl. 2, fig. 4). A similar pattern of subcolony origination (Pl. 3, fig. 2) is seen in the Late Cretaceous species *Actinopora disticha*. Alternative patterns of subcolony formation were present in other Late Cretaceous species. *Discocavea irrgeularis* had both local proliferation of budding from a small group of peripheral zooids that gave rise to satellite daughter subcolonies with central maculae resembling those in the parent colony, and also eruptive budding from within the central portion of the colony to form one or more basal wall-bounded, 'stacked' frontal subcolonies above the parent colony (Pl. 3, fig. 5).

Discocavea irregularis developed raised colony margins (Pl. 3, fig. 5) much more commonly than did other species included in this study. Some modern cyclostomes also elevate the colony margin upon approach or contact with competitiors, which serves to defer overgrowth by encroaching encrusters (Stebbing 1973; McKinney 1992). Among eight species of northern Adriatic encrusting cyclostomes, several species occasionally develop raised colony margins, but *Plagioecia patina* does so commonly (McKinney 1992). In addition, *P. patina* often develops frontally budded daughter subcolonies (McKinney 1992, fig. 2A–C). The correspondence between propensity to elevate the growing margin of the parent colony and frontal budding of daughter subcolonies may be a general pattern in cyclostomes. For those species with the capacity to initiate daughter colonies above the parent colony surface, elevation of the growing margin may stop or delay overgrowth by an approaching competitor long enough for the elevated daughter colony to become established. An analogous situation exists in some Recent cheilostome bryozoans: *Antropora tincta* is able to overgrow the cheilostome *Onychocella alula* because, although *A. tincta* has smaller zooids than *O. alula*, *A. tincta* can frontally bud new layers whereas *O. alula* cannot. Where *A. tincta* can block lateral growth of *O. alula*, it then buds frontally and spreads laterally over the top of *O. alula* (Buss 1981). This is but one example of how topographical advantage can influence the outcome of overgrowth competition (Walters and Wethey 1986). The topographically higher position of the daughter subcolonies in *D. irregularis*, *P. patina* and other cyclostomes with the same potential for frontal budding of daughter subcolonies may enable them to survive after overgrowth of the parent colony and may even serve as a position from which to spread over a competitor that has covered the lower, parent colony. Therefore, elevated margins of parent colonies and production of frontally budded daughter subcolonies probably extend the life span of the colony as a whole, and the two characteristics together constitute an important life history trait.

Subcolonies provide new regions of growth and therefore increase the area of those colonies in which they are developed. However, formation of subcolonies occurred predominantly in species with relatively small colony sizes among the species included in the study; generally, species that produced colonies characterized by a non-subdivided encrusting sheet grew to larger sizes (Mann-Whitney $U = 7{\cdot}00$, $p = 0{\cdot}027$, $N = 15$; identical results based on minimum diameter, maximum diameter, and colony area). The only other life history attributes listed in Table 4 to which presence of subcolonies is related, are the distance from the point of origin of the colony to the closest ooeciopore (Mann-Whitney $U = 2{\cdot}00$, $p = 0{\cdot}011$, $N = 14$) and the mean distance from the point of origin of the colony to all ooeciopores in the colony (Mann-Whitney $U = 3{\cdot}00$, $p = 0{\cdot}016$, $N = 14$), both of which are highly correlated with colony size (Table 4).

Fission of encrusting bryozoan colonies, typically caused by local abrasive grazing or by overgrowth separating two or more parts of a colony, is common for some species that live on hard substrata at the present day (Jackson and Winston 1981; Vail and Wass 1981*a*, 1981*b*; Winston and Jackson 1984). None of the species studied here was seen to reproduce asexually by fission, even those in which the existence of peripheral subcolonies derived from single-zooid 'pseudoancestrulae' would seem to offer potential for fragmentation. The absence of fragmentation among the

specimens studied was possibly due to some combination of relatively small colony size and perhaps less pervasive grazing damage in the Mesozoic than at the present day (Vermeij 1987).

Size at sexual reproduction. Sexually reproductive male zooids are skeletally indistinguishable from non-reproductive autozooids (feeding zooids) in cyclostome bryozoans (Harmer 1896; Borg 1926; Ryland 1970; Silén 1972, 1977), and in a large proportion of bryozoan species the normal feeding zooids produce sperm from early in their individual life cycles (Mawatari 1975). Therefore, the onset of sperm production and release cannot be determined from fossils or the skeletal remains of Recent cyclostomes. In contrast, brood chambers produced by female zooids in cyclostomes have characteristic skeletal morphologies (e.g. Silén 1977; Ström 1977; Schäfer 1991) which are readily recognizable in fossil and Recent skeletal remains. In most of the studied species brood chambers comprise gonozooids that are broader and more bulbous than the autozooids in the same colony (e.g. Pl. 2, figs 3, 6; Pl. 3, fig. 4; Pl. 4, fig. 6; Pl. 5, fig. 2). Such brood chambers usually have a roof of densely pseudoporous exterior wall. However, in *Discocavea irregularis* the brood chambers are roofed by interior walls and are much less conspicuous (Pl. 3, fig. 6). Throughout this paper, the terms 'fertile colony' and 'reproduction' refer to colonies in which are present brood chambers, complete with the ooeciopore through which the larvae were released.

There is a strong, positive correlation between the colony size typically attained by species included in this study and the size at which they first reproduced and at which the major reproductive effort was made (Table 4; see 'Ancestrula to 1st ooeciopore' and '$\bar{x}$ ancestrula to ooeciopore'). Both of these are reasonable outcomes: colonies in species that reached larger sizes had a greater range of distances from the point of colony origin at which to form gonozooids. Similar results in correlation of average colony size and average size of reproductive colonies have recently been documented for three co-occurring species of the encrusting cheilostome genus *Stylopoma* (Herrera *et al.* 1996).

It is conceivable that colonies in some species, even though commonly reaching large sizes, may be genetically programmed consistently to initiate reproduction at small colony size. Histograms of distances from ancestrulae to ooeciopores show a variety of distribution patterns. The most tightly constrained pattern is seen in *Actinopora disticha*, in which almost all brood chambers developed close to the point of origin of the colonies, with the ooeciopores closely grouped approximately 1 mm away (Text-fig. 4H). *Plagioecia*? *reniformis* also tended to reproduce at a fairly uniform distance from the colony origin, with most brood chambers having been completed between 2 mm and 4 mm from the origin. These patterns of limited range in size of colonies at time of reproduction seem to indicate that reproductive maturity for *A. disticha* and *P.*? *reniformis* was a constrained part of the astogenetic developmental programme characteristic of the species, even though only a small proportion of colonies in each of the species reproduced. However, none of the Mesozoic cyclostome species has such a highly regulated onset of female reproduction as seen in the living cheilostome *Celleporella hyalina*, in which reproduction begins at about the 57-zooid stage, regardless of the rate at which the colony grew to that stage (Cancino and Hughes 1987).

In contrast with the patterns of distribution of gonozooids found in *Actinopora disticha* and *Plagioecia*? *reniformis*, ooeciopores of the highly elongate brood chambers (Pl. 1, fig. 4) of *Reptomultisparsa hybensis* are relatively uniformly scattered across a wide range of distances (2 mm to 6 mm) from the point of colony origin (Text-fig. 1D). Distribution patterns of distances between colony origins and ooeciopores in other species in this study tend to be closer to that of *R. hybensis* than to the other end-member patterns.

The highly deterministic pattern of small range in distribution of colony origin to ooeciopore distances in *Actinopora disticha* is consistent with a 'determinate' growth pattern in which reproduction occurs at small colony size, after a short period of growth, largely controlled by an intrinsic, relatively rigid programme of growth. The broad range of distances between the point of colony origin and ooeciopores in *Reptomultisparsa hybensis* suggests that in this species reproduction is largely stimulated by some environmental signal. For some colonies in several species (*Hyporosopora dilatata*, *Liripora complanata*, '*Mesonopora*' *laguncula*, '*Mesonopora*' sp., *Plagioecia*

sp. 2) the probable environmental stimulus can be identified: approach to or contact with an obstruction, commonly another skeletized organism, either a conspecific colony or a representative of a different species.

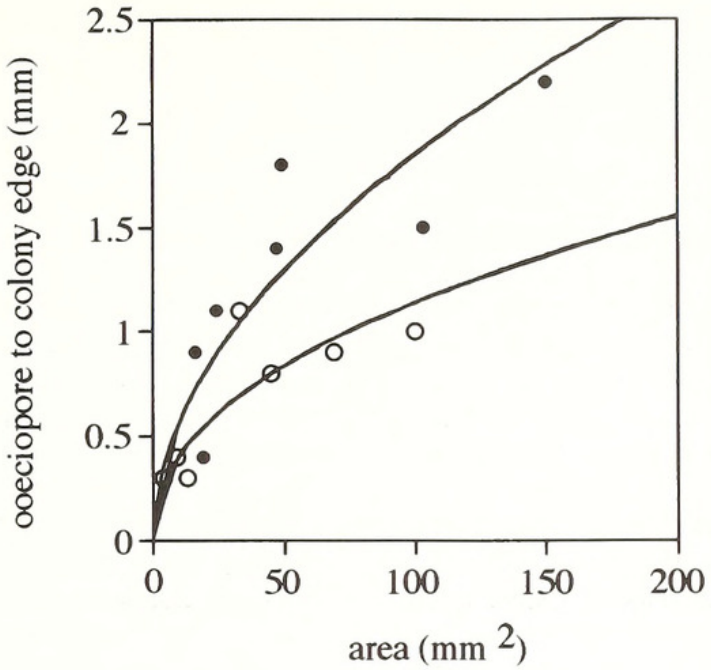
For most species, there was no statistical difference in size of fertile colonies and size of non-fertile colonies that had reached or passed the size of the smallest fertile colony. For three species (*Actinopora disticha*, *Liripora complanata*, *Plagioecia*? *reniformis*), however, fertile colonies were on average significantly larger than non-fertile colonies that had reached or passed the size of the smallest fertile colony. Therefore, although reproduction was followed by only slightly more growth before death of the colony, reproduction did not result in colonies of smaller-than-average size. On the contrary for the three species cited above, reproduction was more characteristic of larger colonies.

Most of the species in this study, therefore, have a reproductive pattern that to some degree resembles that previously documented for several cheilostome bryozoans, especially *Electra posidoniae* (see Silén 1966) and species of *Membranipora* (Harvell and Grosberg 1988; Cancino *et al.* 1991; Karande and Udhayakumar 1992). Crowding of *M. membranacea* by conspecifics triggers the onset of reproduction across a broad range of colony sizes (3–30 mm diameter; Harvell and Grosberg 1988). In *Membranipora isabelleana* (see Cancino *et al.* 1991), onset of both male and female reproduction is highly flexible in size and age, with early reproduction induced by conspecific crowding and characterized by sexual reproduction at the crowded edge. Where uncrowded, *M. isabelleana* eventually reproduced sexually in centres of colonies. Apparently in the three cyclostome species (*Actinopora disticha*, *Liripora complanata*, *Plagioecia*? *reniformis*) in which fertile colonies were on average larger than infertile colonies, larger colonies tended to become reproductive more readily than younger colonies even in the absence of contact or crowding, as seen by Cancino *et al.* (1991) in *M. isabelleana*. The lack of statistical difference in size of fertile and nonfertile colonies for other Mesozoic cyclostomes implies that they had not reached a size at which reproduction is increasingly likely.

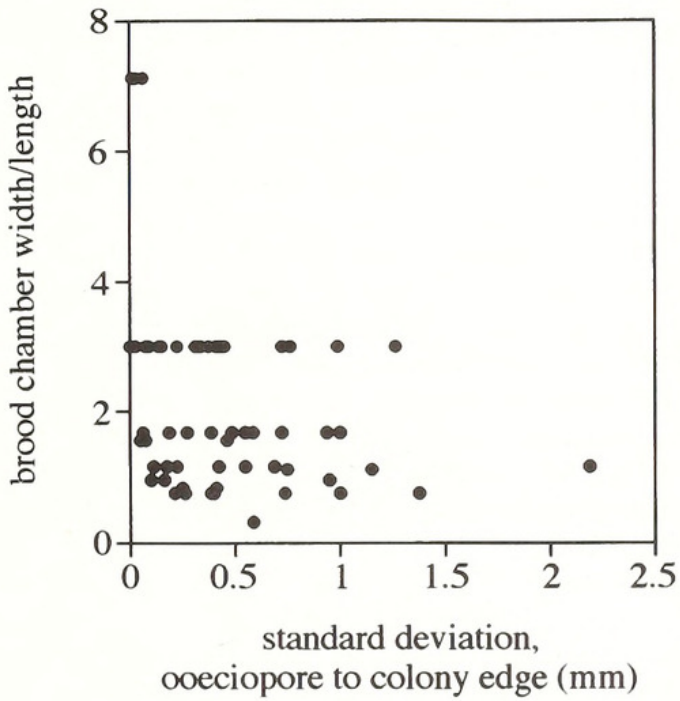
Where there is no skeletal evidence of crowding, the stimulus (if extrinsic) for onset of reproduction cannot be determined. Among the possibilities are contact or imminent contact with a non-preserved neighbour, change in temperature (Dudley 1973), plankton bloom (Gordon 1970), grazing (Harvell and Grosberg 1988), and fine-scale variation in the physical environment (Keough 1989). Recent evidence has shown that turbulent diffusion can reduce sperm availability and influence female reproductive success in free-spawning marine animals (Levitan and Petersen 1995). Therefore, sperm availability is another factor that could potentially determine the occurrence of female reproduction in cyclostomes (Ryland 1996) assuming that brood chambers develop only after eggs have been successfully fertilized, an idea that requires testing using living colonies.

Colony survival after reproduction. With the exception of *Discocavea irregularis*, all of the species included in this study have brood chambers that developed at or very close to the distal growing edge of the colony (e.g. Pl. 1, fig. 5; Pl. 3, fig. 3; Pl. 4, figs 1, 5). Continued growth of the colony generated an ever increasing growth increment beyond the completed brood chambers.

In most species, where multiple brood chambers occurred within a single colony, they were formed almost simultaneously, as indicated by a relatively uniform distance between each of the brood chambers within the colony and the adjacent margin to which the colony had grown at death (e.g. Pl. 1, fig. 5; Pl. 2, fig. 1; Pl. 3, fig. 3; Pl. 4, figs 1, 5; Pl. 5, fig. 1). In all species apart from *D. irregularis*, regardless of how large a colony had grown before formation of brood chambers, growth in most instances continued for only a short distance beyond the completed brood chambers (Table 3). Species characterized by larger colonies tended to grow for greater distances following completion of brood chambers (Text-fig. 12; Table 4). In addition, for *Actinopora disticha*, *Hyporosopora dilatata*, '*Mesonopora*' sp., *Plagioecia* sp. 1 and *Plagioecia* sp. 2, there is significant ($p < 0{\cdot}01$) positive correlation between size of colonies within the species and distance beyond ooeciopores to which the colonies continued to grow.



TEXT-FIG. 12. Plot of species averages (means) of distance between ooeciopores and adjacent colony edges, versus species averages (means) of colony areas. Filled circles represent species with narrow brood chambers (width:length ratios < 1·5; regression, $Y = 0{\cdot}171X^{0{\cdot}516}$), and open circles represent species with broad brood chambers (width:length ratios > 1·5; regression, $Y = 0{\cdot}143X^{0{\cdot}450}$).



TEXT-FIG. 13. Plot of standard deviations of distance between ooeciopores and adjacent colony edges, versus species averages (means) of brood chamber width:length ratios. Each point on the graph represents a value from a single colony in which there are three or more gonozooids.

In species with broad brood chambers, especially where the brood chambers followed the curvature of the colony margin as in *Actinopora disticha*, a conspicuous ring of brood chambers developed that in some instances extended the full 360° around the colony perimeter (Pl. 3, fig. 3). Colonies of such species appear to have been semelparous, reproducing over a short period and dying soon after this time of high expenditure of energy. Semelparous reproduction followed by death of the colony is common for cyclostome species living at the present day and has been documented for *Crisidia cornuta* (see Eggleston 1972), *Disporella ovoidea* (see Winston 1985), *D. plumosa* Winston and Håkansson, 1986, and *Lichenopora verrucaria* (see Harmer 1896).

Colonies in Mesozoic species with equidimensional or elongate brood chambers (e.g. Pl. 1, fig. 4) commonly do not have such conspicuous alignment of brood chambers and give the appearance of having reproduced over a longer period and to have survived longer following production of the brood chambers. Less precise alignment of equidimensional or elongate brood chambers around the

periphery of colonies is not supported by significant correlation of each species' standard deviation for mean distance from ooeciopores to colony edge, compared with the species' brood chamber width:length ratio (Kendall's rank order correlation, tau = −0·015, p = 0·094, N = 12). However, if within-colony means of the distance between ooeciopores and the adjacent colony edge are compared with the species' brood chamber width: length ratios, there is a highly significant negative correlation (Text-fig. 13; Kendall's rank order correlation, tau = −0·254, p = 0·0035, N = 62, using individual colonies with three or more brood chambers from all species in the study). That is, the broader the brood chambers with respect to their length, the more precisely they are arranged around the colony perimeter where three or more occur within a colony.

Species with small colonies grew only slightly more after completion of brood chambers, regardless of the shape of the brood chambers. However, species with larger colonies do fall into two groups; those with equidimensional or elongate brood chambers continued to grow further than did those with broad brood chambers (Text-fig. 12; Table 4). No species with broad brood chambers averaged more than 1·1 mm growth beyond the positions at which brood chambers formed, even those with colony areas averaging up to 100 mm^2, whereas for species with equidimensional or elongate brood chambers, there is a uniform correspondence between average colony area and average distance between ooeciopores and colony edge (Text-fig. 12).

The proximity of brood chambers to the colony margin at time of death, and their occurrence in a single near-marginal ring where multiple brood chambers occur, indicate that in almost all instances in these exterior-walled species there was a single period of reproduction, followed shortly by death. Formation of a completed brood chamber was probably the less energetically costly part of reproduction, exceeded by the subsequent nourishment of the embryos which are rich in protein- and lipid yolk (Dyrynda and King 1983). This period of nourishment of the developing embryos would have corresponded with the time during which a colony continued to grow the short distance between brood chamber completion and the final colony margin.

It is unusual to find colonies that have brood chambers in two distinctly different positions, one inner and the other outer, but this occurred in single colonies of some species (e.g. '*Mesonopora*' sp., *Hyporosopora* sp., *Reptomultisparsa hybensis*, *Plagioecia* sp. 2: Pl. 2, fig. 1), indicating two distinct periods of reproduction (iteroparity). This occasional occurrence of two distinct reproductive periods in otherwise semelparous cyclostome species is known in some living species. *Lichenopora verrucaria* and *Disporella ovoidea* are small, encrusting cyclostomes with overall colony morphology much like that of *Discocavea irregularis* in this study. In colonies of *L. verrucaria* that live into a second year, it is common for subsequent broods of embryos again to be produced, occupying the original centrally located brood chamber (Harmer 1896). *D. ovoidea* colonies in Jamaica have a 'pseudo-solitary' ecology, with rapid growth to finite adult size, a single central excurrent outlet for filtered water, and one colony brood chamber; most die after a single period of sexual reproduction, but a few colonies survive and reproduce again after a few months (Winston 1985).

It is impossible to determine the relationship between sexual reproduction and death of the colony for *Discocavea irregularis* because the potential for brood chambers to develop proximally of the growing edge in this free-walled cyclostome does not allow determination from skeletal evidence of how much further a colony grew after reaching sexual maturity. Only three out of 146 specimens (2 per cent.) showed clear brood chambers. This contrasts strongly with Harmer's (1896) observations for the morphologically similar *Lichenopora verrucaria* in which all colonies became reproductive upon reaching approximately 1 mm diameter, after which growth continued for a few more millimetres.

Reproductive effort. The proportion of colonies that became fertile upon reaching or exceeding the minimum observed size for female reproduction appears to have been essentially species-specific, perhaps related to some unknown environmental factor(s). The proportion of fertile colonies does not correlate with any of the other characteristics measured or scored in this study (Table 4). This lack of correlation is most notable for brood chamber shape, mean colony size, and proportion of

the colony surface area devoted to brooding, because one would expect that there would be a discernible pattern relating each of these with the proportion of fertile colonies. The observed lack of pattern may be due more to collector bias than to reality if there was a difference in preference for fertile versus non-fertile colonies among the various collectors who provided the bulk of the material for each of the species (other than the three species for which it is known that all specimens were kept when encountered).

In particular, one would predict a general pattern of higher reproductive effort for smaller-growing, more 'opportunistic' species than for larger-growing species in which colonies might have been longer-lived. Neither of the two skeletal measures of reproductive effort – proportion of fertile colonies, and proportion of the colony surface area devoted to brooding – correlates significantly with any of the measures of colony size (Table 4). There is the possibility that with a larger sample of species, the significance ($p < 0{\cdot}10$) of the negative correlation determined in this study between proportion of the colony surface area devoted to brooding and colony size (maximum diameter, area) might improve to acceptable significance.

Life histories of small clones: constrained, plastic or both?

There are several facets of life history theory pertinent to small clones. The theories can be broadly separated into two groups: those that seek to explain the organism's response to prevalent environmental conditions, and those that seek to explain the effect on life history of the organism's clonal growth.

The concept of 'spot colonies' was introduced for colonies of encrusting 'species settling in small spatially predictable refuges and growing to small, early maturing colonies of determinate or semi-determinate size' (Bishop 1989, p. 214). Spot colonies are essentially equidimensional. Their attributes are well demonstrated by two cheilostome species: *Cribrilina puncturata* that grew preferentially on the concave surfaces of bivalve shells in the Plio-Pleistocene Red Crag of England, and which became reproductive when the colony had grown to about ten zooids (Bishop 1994); and *Celleporella hyalina*, most commonly growing on the alga *Laminaria saccharina*, which becomes reproductive when the colony reaches about 57 zooids (Cancino and Hughes 1987).

Reproduction at small size and overall small total body size are characteristic of '*r*-selection', which forms an end member of the highly debated, and currently less favoured than previously, conceptual system of life history strategies varying from long-lived, successful competitors in stable environments (*K*-selection) to early-reproducing, poor competitors in uncertain environments (*r*-selection) (see MacArthur and Wilson 1967; Pianka 1970; Stearns 1992). In the system of *r*- versus *K*-selection, small clones on substrata such as shell debris that may be intermittently disturbed are expected to have other attributes of *r*-selection, including rapid development, early reproduction, and semelparity, but during their single period of reproduction the capacity for production of a large number of offspring compared with more long-lived relatives that produce fewer offspring at any given period of reproduction.

Another way to conceive of life history attributes of clonal animals is to examine the trade-off between early and late sexual maturity in the context of clonal growth. Timing of sexual maturity in clonal animals has the potential for extreme flexibility because the germ line is not sequestered during early growth of the organism but can be developed from one or more groups of somatic cells as the clone grows (reviewed in Buss 1987). While the modules (e.g. zooids in bryozoans) within clones eventually senesce, the clones themselves are theoretically immortal (Jackson 1985; Orive 1995), and often reach great ages (Cook 1983; Jackson 1983). For many clonal species, the larger an individual clone becomes, the higher its chance of surviving (Jackson 1985; Jackson and Coates 1986; Harvell and Grosberg 1988). Therefore, if fitness can be increased by delaying reproduction, selection may favour indefinite delay.

Sexual reproduction consumes energy that in clones could otherwise go into clonal growth, i.e. asexual increase in the number of modules. Therefore, sexual reproduction at any stage in the growth of a clone should temporarily decrease or arrest growth, so that at some later stage the clone

will be smaller than it would have been if sexual reproduction had not occurred. An intriguing exception was noted for the arborescent cheilostome bryozoan *Bugula neritina*, with an unexplained increase in growth rate occurring simultaneously with reproduction (Keough 1989).

Where reproductive output scales linearly or geometrically with size, as it does in many clonal animals (e.g. Gordon 1970; Hayward and Ryland 1975; Dyrynda and King 1982; Bishop 1994), it would benefit the clone to reach a maximum possible size before reproducing sexually. Such delay can be indexed to a specific size (or age) of the clone at which point reproduction occurs; the extent of the delay in reproduction would be a trade-off between probability of survival to that size-stage, versus the rate of increase in reproductive potential with increased size. Mortality of non-senescent clones is due to extrinsic, environmental factors. Therefore, for potentially immortal clones of a species living in stable environments, reproduction may be delayed until a very large size has been reached, at which point reproduction occurs for some proportion of the clones (Winston and Jackson 1984; Jackson and Wertheimer 1985).

Alternatively, clones may defer sexual reproduction until some external cue is received that stimulates reproduction. The most obvious cues would be those that signal imminent total or partial mortality of the clone, such as proximity of predators or of powerful competitors, crowding by conspecifics, some temperature threshold, or physical disturbance. Such flexibility in timing of reproduction, while rare in aclonal animals, should be favoured in clonal animals 'in which (1) the size-dependent fecundity benefits of postponing reproduction can increase without intrinsic limit and (2) the cumulative risk of reproductive failure through genet mortality increases very slowly with genet size' (Harvell and Grosberg 1988, p. 1859). Consequently, in many species of clonal animals, once the minimum size (or age) threshold is passed, reproduction should be initiated over a broad range of sizes and should correlate neither with size nor age but instead should reflect a 'complex interaction between intrinsic factors such as size, age, and physiological condition, as well as extrinsic factors such as density, food availability, physical disturbance, and predation' (Harvell and Grosberg 1988, p. 1862).

Individual life histories and patterns of life histories of Mesozoic encrusting cyclostomes described above are in general more consistent with hypotheses of flexibility in life history attributes, especially in flexibility in timing of reproduction, than with the concepts of *r*- and *K*-selection. Among the attributes of *r*-selection seen in the Mesozoic encrusting cyclostomes are (1) small body size, although there is a relatively broad range in mean size from species-to-species and even in the smallest species some colonies extended over an order of magnitude larger than the average area; (2) semelparity; and (3) a potentially large number of sexual offspring. Although there are few gonozooids per colony in each of the species studied, polyembryony is characteristic of cyclostomes, with up to at least 11 primary embryos per brood chamber (Harmer 1896) and the capacity for a primary embryo to divide into over 100 secondary embryos (Borg 1926, p. 425). In addition, a minority of the species (e.g. *Actinopora disticha*) tended to reproduce at a small size rather than across a broad range of sizes.

The prevalence of semelparity in most of the Mesozoic encrusting species was not associated with reproduction at some specific small colony size. Most colonies that reached the size at which reproduction could occur within their species failed to produce brood chambers. Instead, the first (and usually only) reproductive period was initiated across a range of colony sizes. In some instances, crowding with conspecifics or contact with another species or some obstruction can be seen to have been accompanied by production of brood chambers, and colonies typically grew only a short distance beyond the point at which brood chambers were completed. All of these observations are consistent with a high degree of flexibility in timing of reproduction, with reproduction stimulated by some extrinsic factor in the environment.

Interaction between colony size and extrinsic factors appears to have triggered the onset of reproduction in *Actinopora disticha*, *Liripora complanata* and *Plagioecia*? *reniformis*. In these species, the average sizes of fertile colonies are significantly greater than the average sizes of nonfertile colonies, indicating that as the colony increased in size (or age) some intrinsic factor interacted with extrinsic factors to increase the probability of the onset of reproduction. For other

species, for which there is no statistical difference in size of fertile and non-fertile colonies (Table 4), nor a strongly left-skewed distribution of distances from the point of colony origin to ooeciopores, increased colony size apparently did not increase the probability of extrinsic factors stimulating onset of reproduction. Production of brood chambers upon contact with other organisms is evidence that variation in size of colonies at time of reproduction is due largely to environmental factors rather than to large variations in growth rate of colonies with reproduction set to occur after a certain time has elapsed.

CONCLUSIONS

1. Mesozoic encrusting cyclostomes show variable patterns of size-related survivorship; some species exhibit approximately constant mortality rates per unit size, whereas others have increasing mortality rates with size. In none of the species is there evidence for a fixed maximum size beyond which colonies did not grow. Even in species in which mortality rate increased with size, a few 'Methusalah' colonies avoided death and achieved a large size.
2. Several species were capable of producing subcolonies, usually originating at the growing edge of the parent colony but occasionally through frontal budding on to the upper colony surface. There may be a correlation between the ability to produce frontal subcolonies and to elevate the colony margin; both are traits that prevent or retard overgrowth by competitors. Species in this study lacking subcolonies achieved larger colony sizes than those with subcolonies.
3. Colony size at the onset of female sexual reproduction (as indicated by the development of brood chambers) was relatively constant in some species (e.g. *Actinopora disticha*) but very variable in others (e.g. *Reptomultisparsa hybensis*). It seems likely that environmental stimuli, such as contact with a neighbouring encruster, triggered sexual reproduction and were responsible for the observed flexibility in the timing of reproduction.
4. Colony growth typically continued for only a short time after female sexual reproduction, as indicated by the close proximity of brood chambers to colony growing edges. However, species characterized by large colony size or with longitudinally elongate brood chambers typically grew further than those with small colony size or transversely elongate brood chambers. Most colonies appear to have been semelparous with one female reproductive period, although some colonies of a few species were iteroparous with two periods.
5. Between-species comparisons of reproductive effort show no correlation between colony size and the proportion of colonies having brood chambers, or between colony size and the proportion of the colony surface occupied by brood chambers. Species with relatively large zooids reproduced at larger colony sizes and survived for longer after reproducing.
6. Mesozoic multiserial encrusting cyclostomes exhibit considerable flexibility in timing of reproduction and other life history attributes. Although having some attributes of *r*-selection, they do not conform to the rigid concepts of either *r*- or *K*-selection. This supports Winston's (1981*b*) view that life history patterns in clonal organisms cannot be explained in any single or simple way.

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