The palaeobiology and systematics of some Jurassic bryozoa

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THE PALAEOBIOLOGY AND SYSTEMATICS OF SOME JURASSIC BRYOZOA

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A thesis presented for the degree of Doctor of Philosophy in the University of Durham

Volume 2 - Figures, plates and appendices

Department of Geological Sciences,
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September, 1977

Figure 1. Autozooid structure in the Cyclostomata (from Ryland 1970).

A, tubuloporinid zooid with tentacles retracted.

B, an adjacent zooid (middle region omitted) with tentacles expanded.

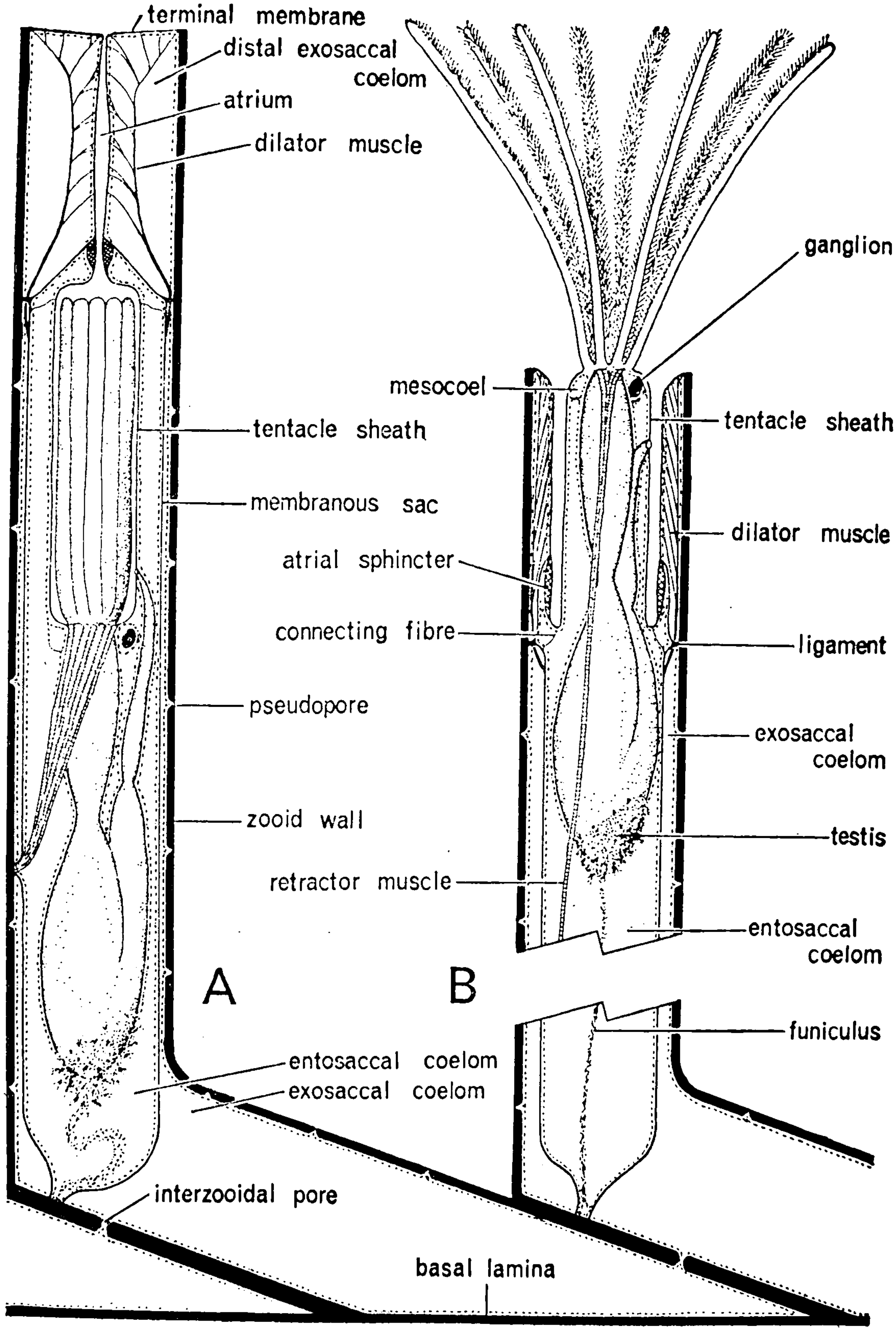

terminal membrane
distal exosaccal coelom
atrium
dilator muscle
tentacle sheath
membranous sac
pseudopore
zooid wall
A
entosaccal coelom
exosaccal coelom
interzooidal pore
basal lamina
B
ganglion
mesocoel
tentacle sheath
dilator muscle
atrial sphincter
connecting fibre
ligament
exosaccal coelom
testis
retractor muscle
entosaccal coelom
funiculus

Figure 2 The common bud of a cyclostome colony (after Borg 1926; Brood 1972). Arrows indicate direction of migration of epithelial cells (shown as rectangles with black nuclei) relative to growing edges. Black, cuticle; stipple, primary skeletal layer; unshaded, secondary skeletal layer; bl, basal lamina; gz, generative zone; ip, interzooidal pore; pb, polypide buds; pp, pseudopore; tm, terminal membrane. The older, more proximal of the two polypide buds possesses a hoop of ectodermal and mesodermal cells, supported by the ectodermal cord, containing a central lumen. Elongate cells of the rudimentary membranous sac surround the bud.

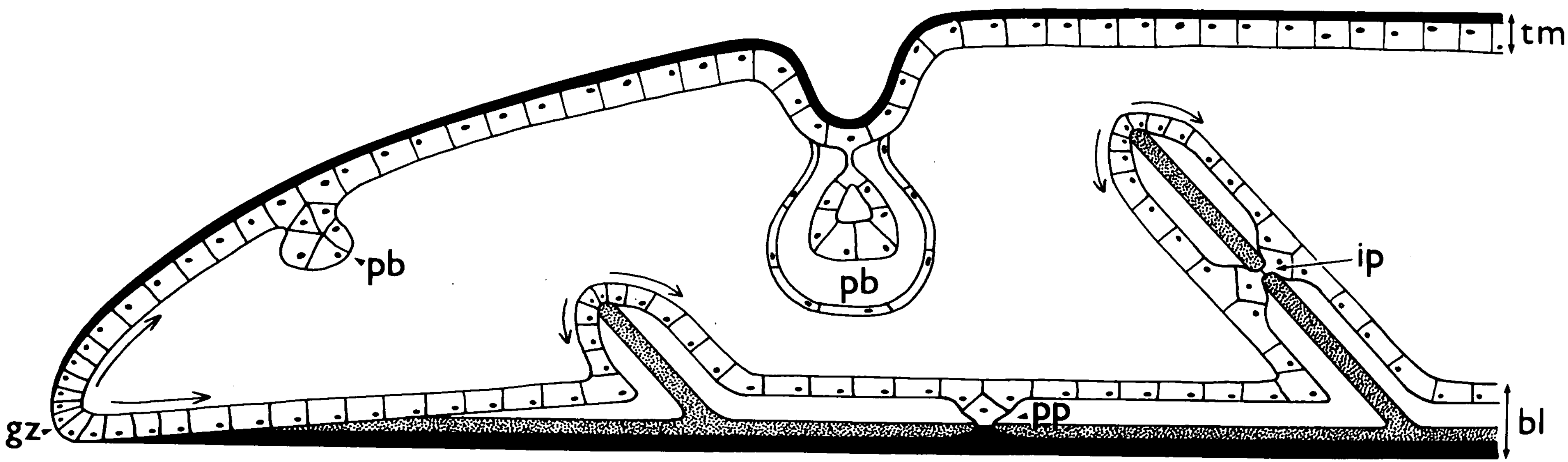
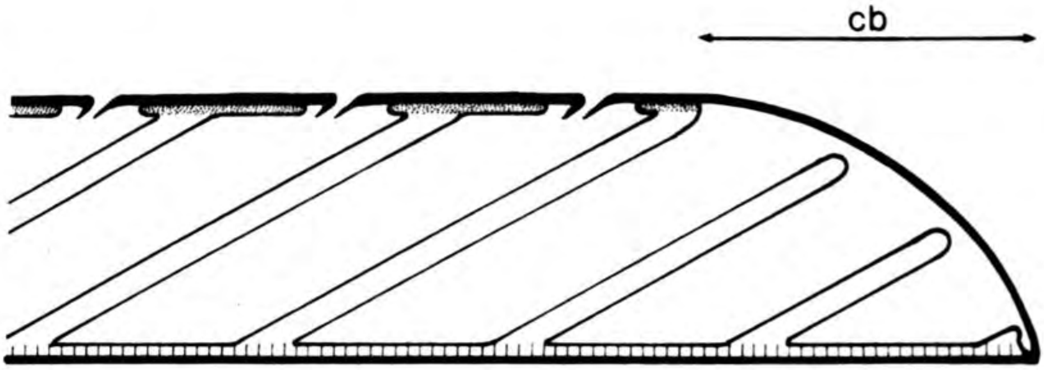
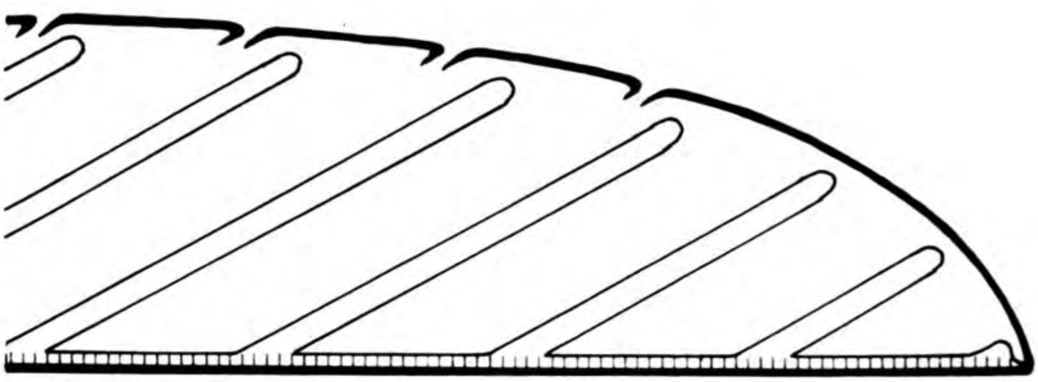

tm
pb
pb
ip
gz
pp
bl

Figure 3 Comparison between single-walled and double-walled cyclostomes.
Longitudinal sections through the distal parts of adnate colonies. Zooidal epithelia and polypides are omitted. Black, cuticle; stipple, zooecial frontal walls; hatching, basal lamina; cb, common bud. The common bud of the double-walled form covers the whole colony frontal surface.



SINGLE-WALLED



DOUBLE-WALLED

Fig.4. *Idmonea triquetra* Lamouroux PT C13. Upper Bathonian, Bradford Clay, Bradford-on-Avon, Wiltshire. Occluded growth margin including some zooecia with apertures. Bar represents 1 mm.

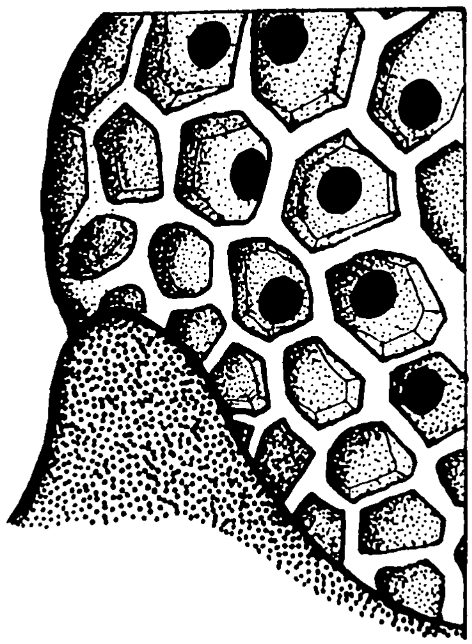


Figure 5. Camera lucida drawing of *Terebellaria* exozonal zooecia displaying ontogenetic zonation. Zone 1 (the growth margin) is the region of partly formed zooecia. Zone 2 contains zooecia with open apertures and peristomes. In zone 3 zooecia are occluded by terminal diaphragms. The distal fringe of the budding lamina belonging to the growth margin next nearest the branch apex overgrows zone 3. BMNH 1151d, 'Great Oolite ?locality'. X50.

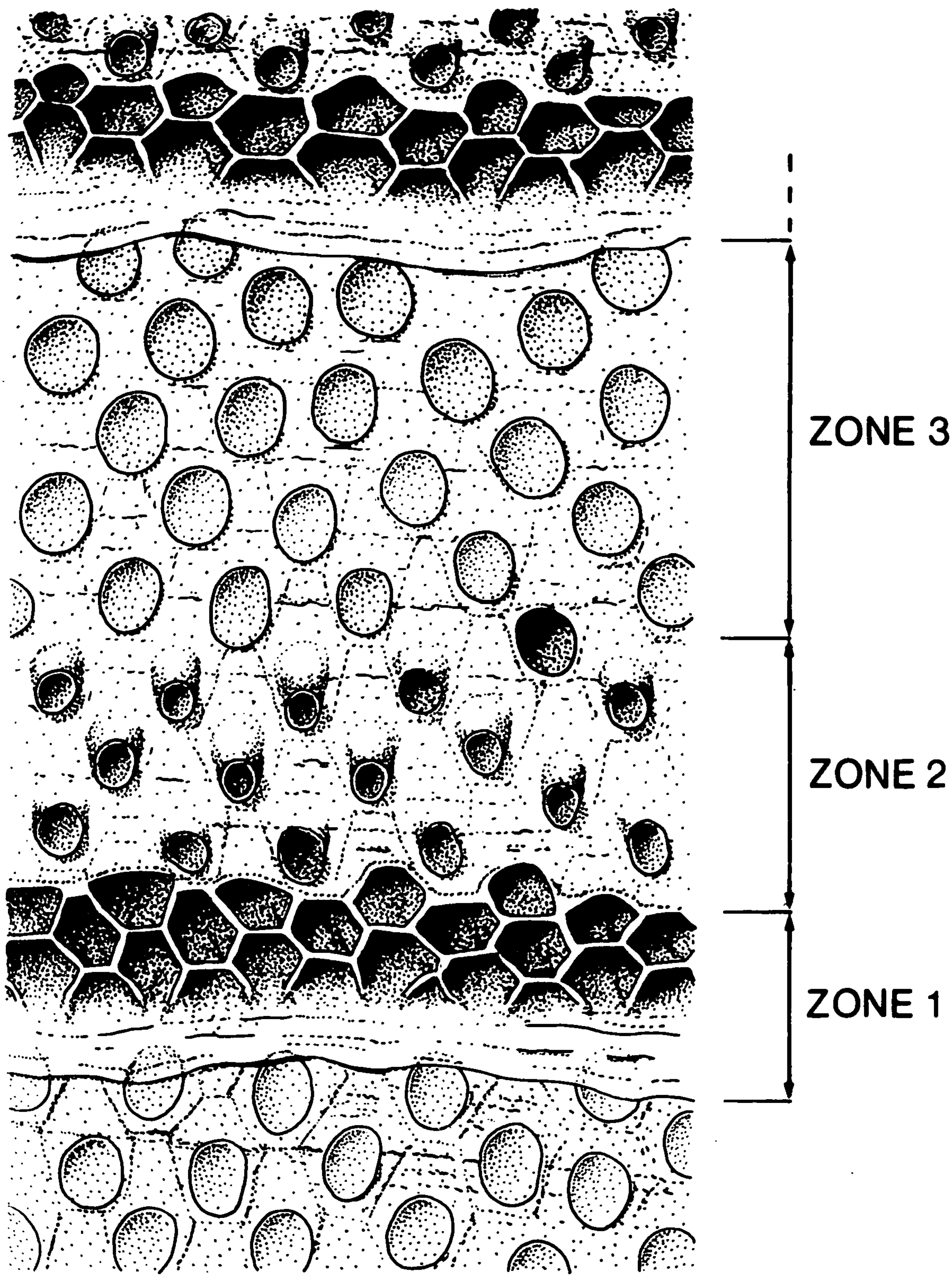
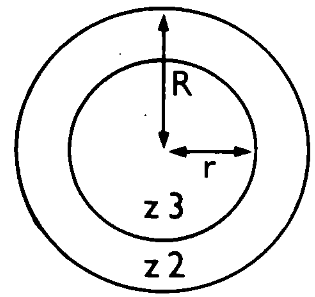

ZONE 3
ZONE 2
ZONE 1

Figure 6. The relationship between colony size and ontogenetic zones in a discoidal tubuloporinid of the *Berenicea*-type. The upper figure is a diagram of the colony from which the growth margin (zone 1) has been omitted. R, colony radius; r, radius of zone 3 (occluded zooids); z3, zone 3; z2, zone 2 (feeding zooids). The graph is a plot of R^2-r^2 against r^2 in a colony in which zone 2 (R-r) remains a constant width (2 units) throughout growth. R^2-r^2 is proportional to the area of zone 2; r^2 is proportional to the area of zone 3. Increase in zone 3 area: zone 2 area during growth is evident from the graph. Full explanation given in the text (p.68).


R
r
z 3
z 2

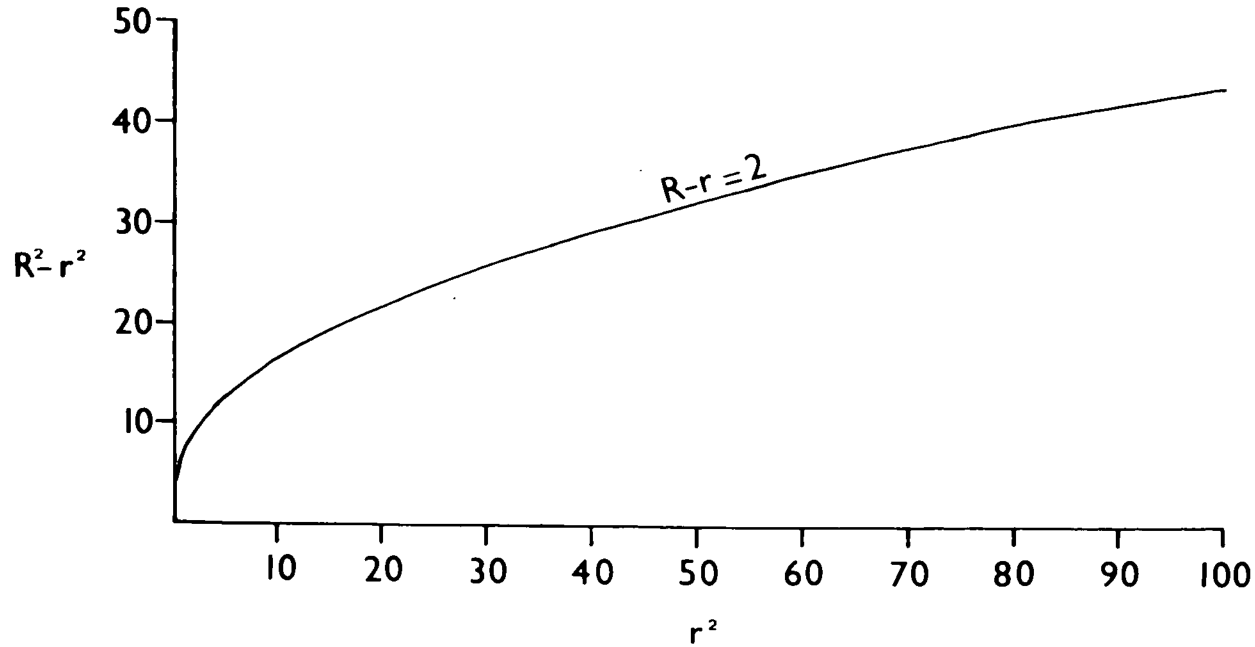

50
40
30
20
10
$R^2 - r^2$
R-r = 2
10
20
30
40
50
60
70
80
90
100
r^2

Figure 7. Ontogenetic model 1. A time-distance graph explaining the variations in ontogenetic zonation (zones 1 to 3) of tubuloporinidean bryozoan colonies. Colony growth rate (zooidal budding rate) has been made to decrease at time C. Full explanation given in the text (p. 70) W_1, width of zone 1 at time C; W_2, width of zone 2 at time C; W_3, width of zone 3 at time C. Short dashes, distal edge of the common bud; long dashes, distal edge of zooecial frontal walls; solid line, line of occlusion.

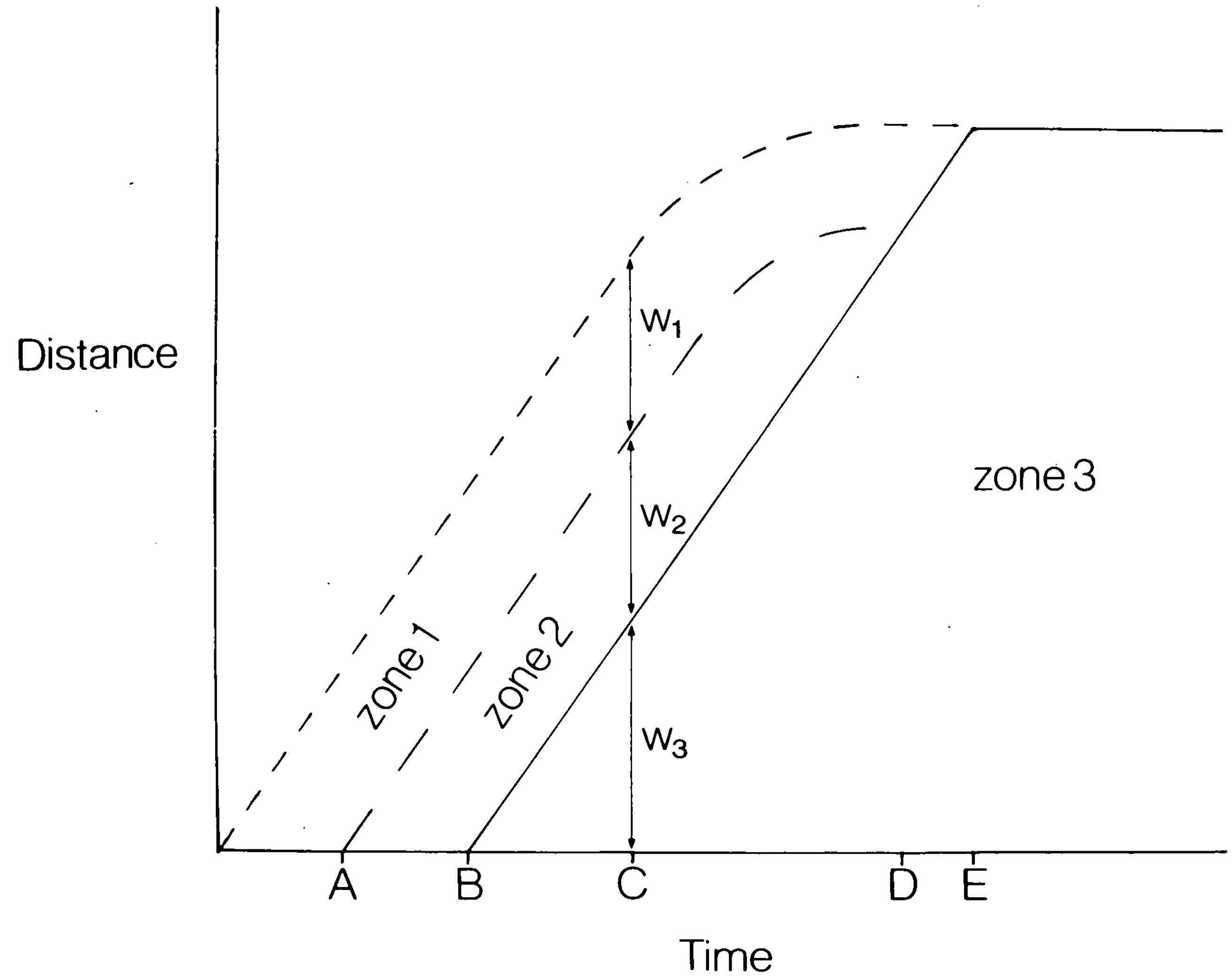

Distance
zone 1
zone 2
zone 3
w_1
w_2
w_3
A
B
C
D
E
Time

Figure 8. Idealized tubuloporinidean colony exhibiting the ontogenetic rate:colony growth rate variations shown in ontogenetic model 1. O, origin of colony; A-E, successive intervals of time shown on the horizontal axis of ontogenetic model 1 (fig. 7). Open autozooecial apertures are shown in black; terminal diaphragms covering apertures and the common bud are stippled.

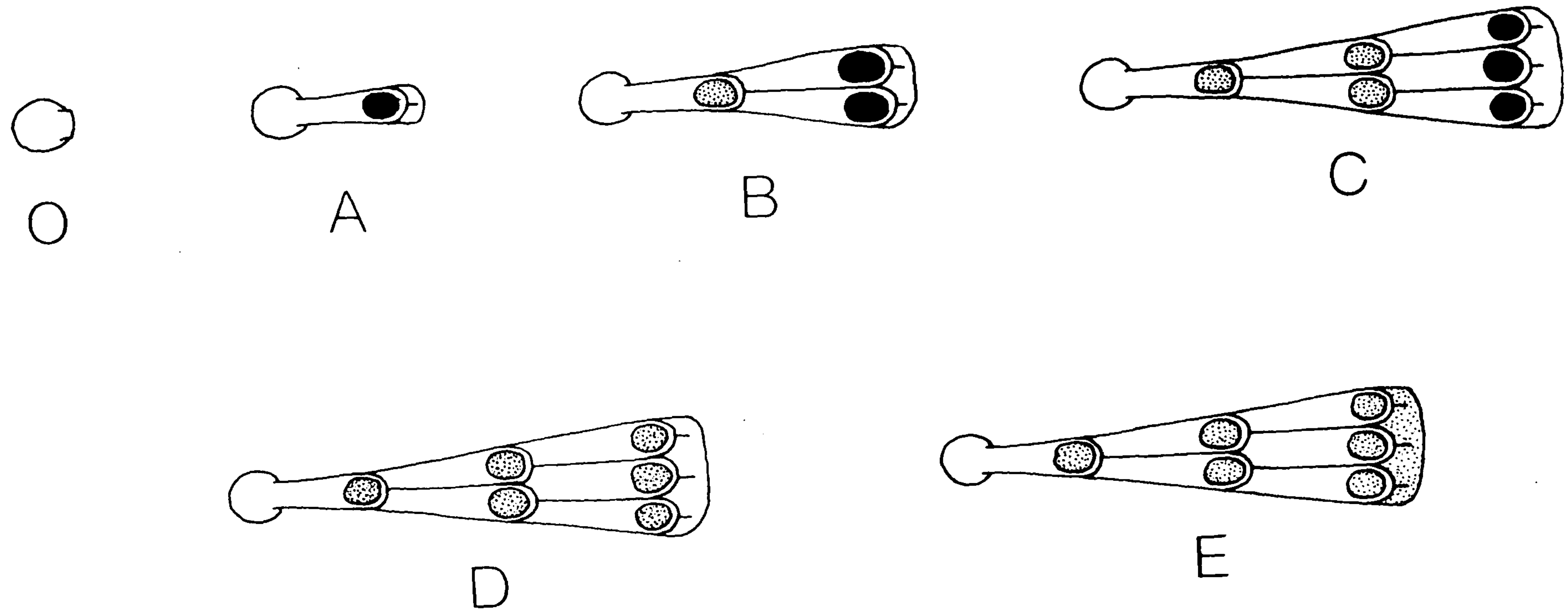

O
A
B
C
D
E

Figure 9. Ontogenetic model 2. A time-distance graph explaining the variations in ontogenetic zonation of tubuloporinidean bryozoan colonies. Ontogenetic rate (rate at which zooids reach skeletal maturity) has been made to increase at time C. Full explanation given in the text (p. 71). Legend as in figure 7 .

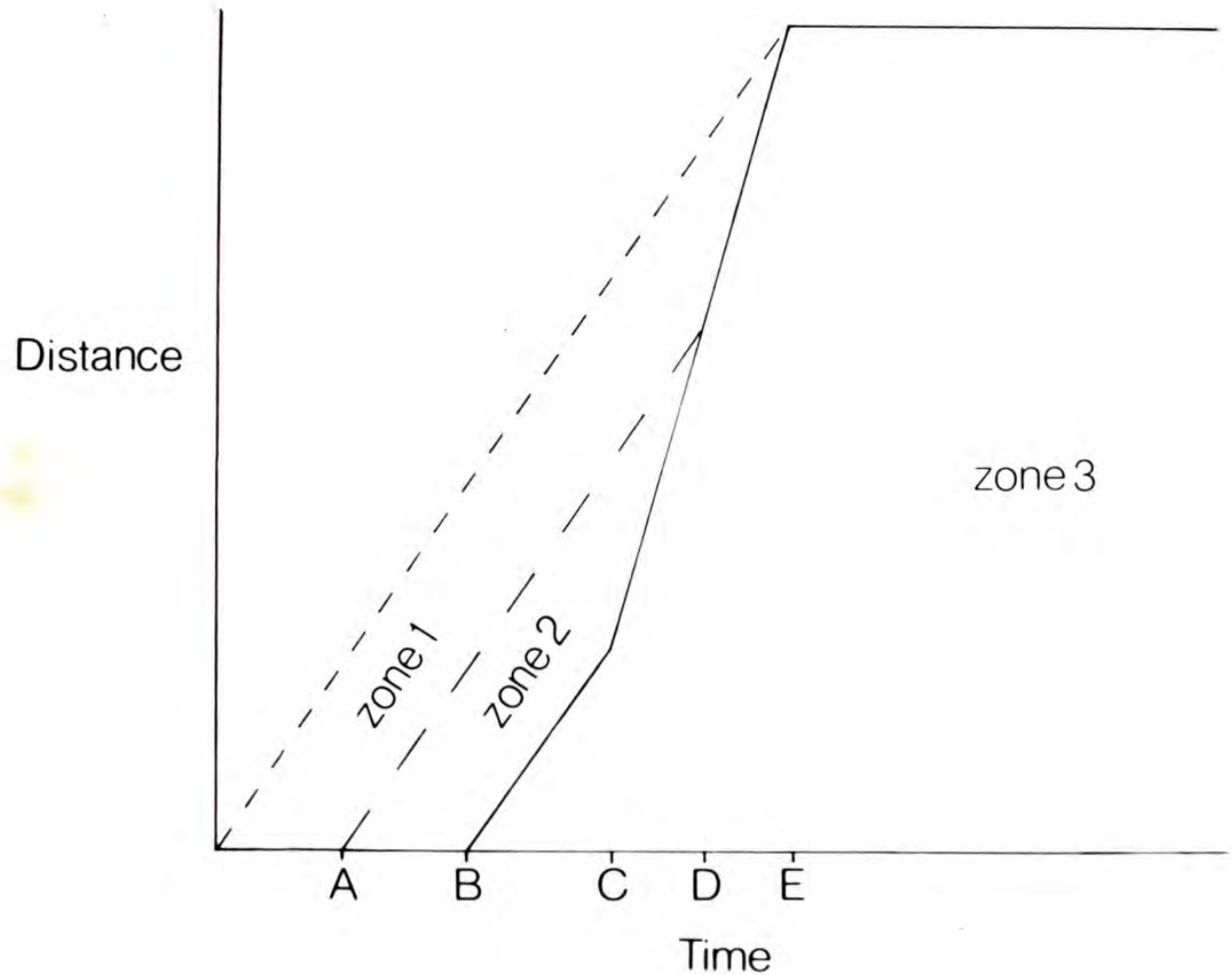

Distance
zone 1
zone 2
zone 3
A
B
C
D
E
Time

Figure 10. Idealized tubuloporinidean colony exhibiting the ontogenetic rate:colony growth rate variations shown in ontogenetic model 2. Legend as in fig. 8 .

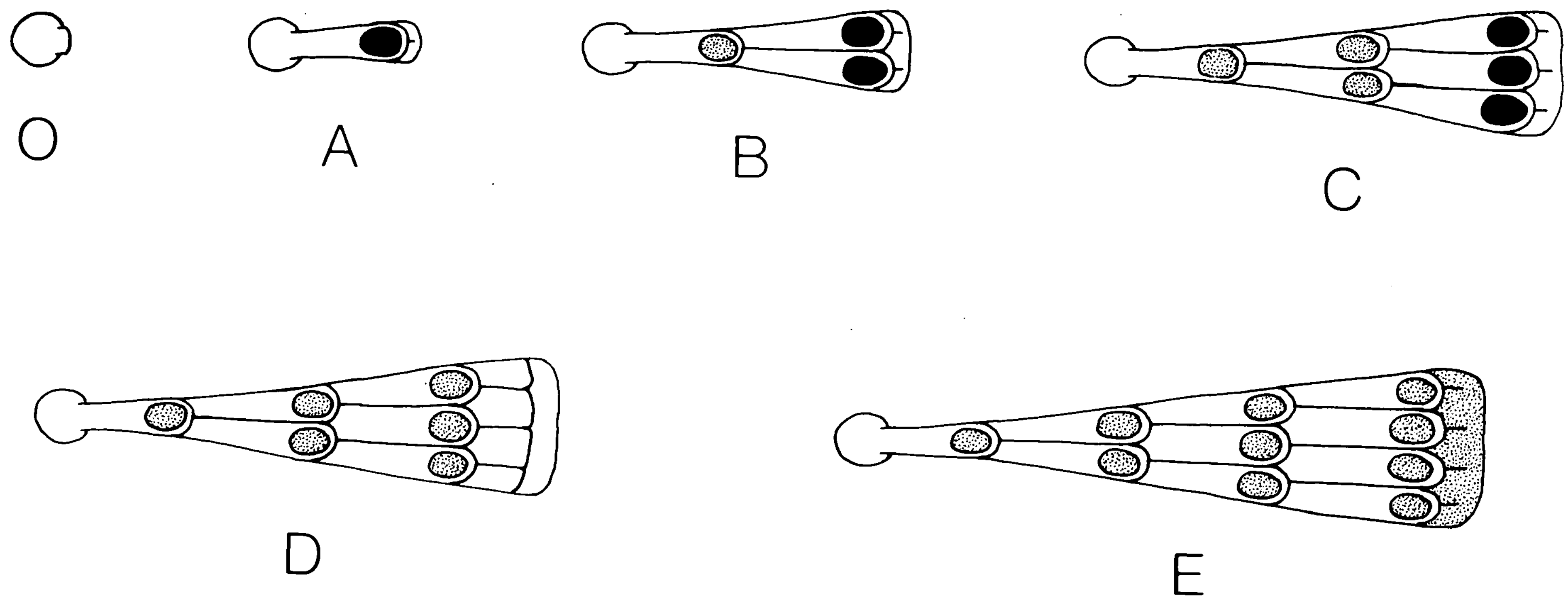

O
A
B
C
D
E

Figure 11. Model of astogenetic zooidal size variation in simple tubuloporinid colonies. A phase of increasing zooid size forms the primary zone of astogenetic change and is followed by a phase of constant zooid size which forms the primary zone of astogenetic repetition.

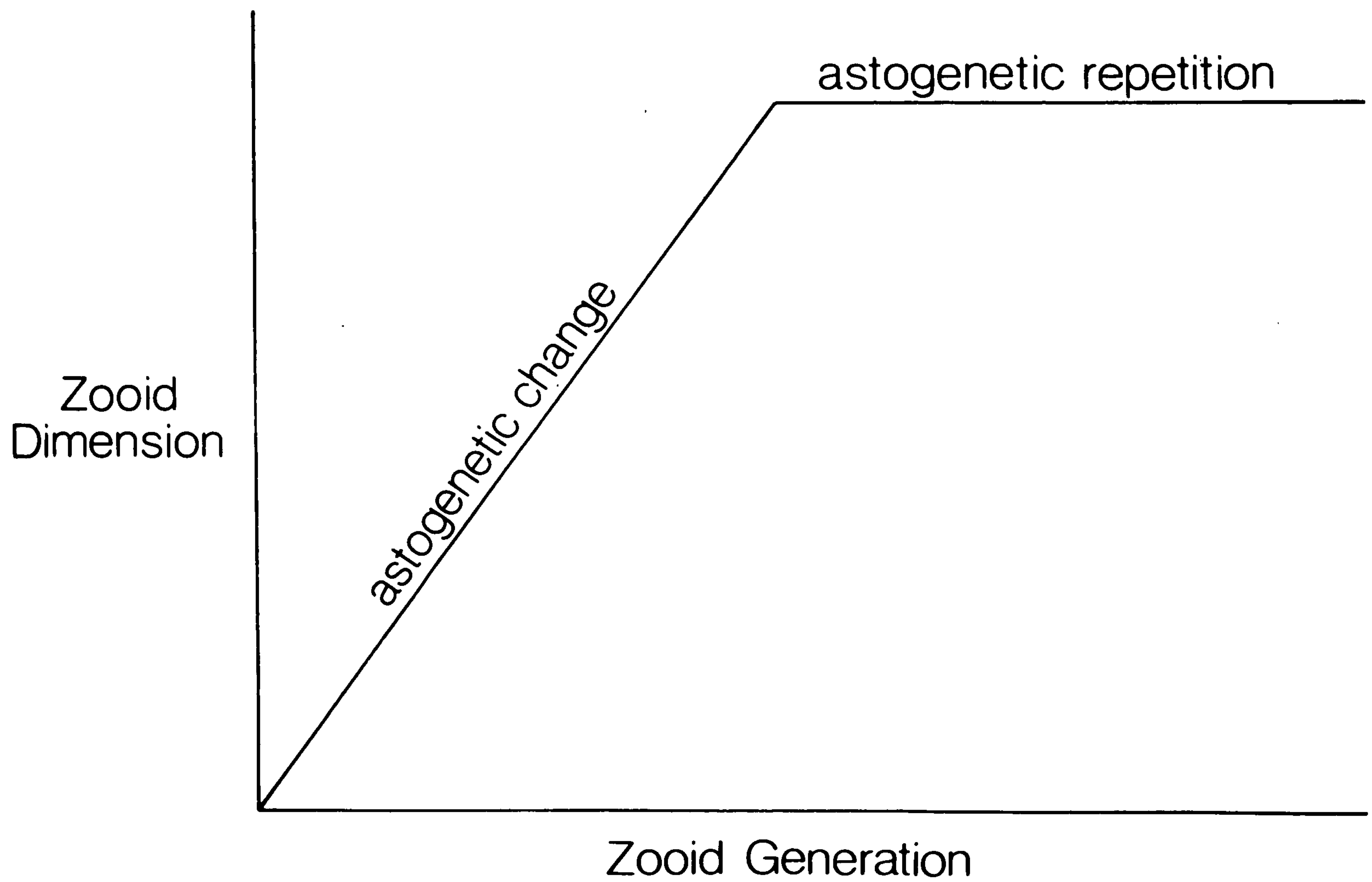

astogenetic repetition
astogenetic change
Zooid
Dimension
Zooid Generation

Figure 12. *Stomatopora* zooecia.

A. External view showing measurements taken. zl, zooecial length (frontal wall length); zw, zooecial width. Apertures are shown in black.

B. Longitudinal section. a, aperture; p, peristome; stipple, frontal wall; hatching, basal lamina; unshaded interzooecial wall.

A

B

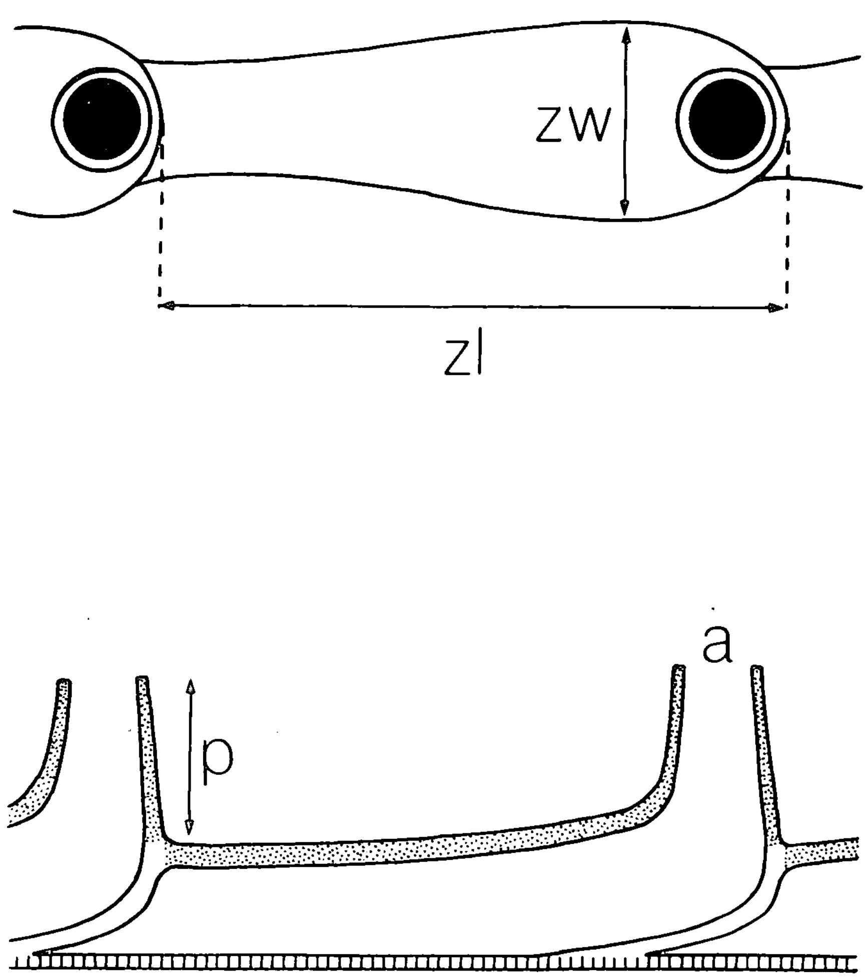


Figure 13. Mean zooecial dimensions for each generation in *Stomatopora bajocensis* (A-D) and *S. dichotomoides* (E-G). In every case the upper curve represents zooecial length, the lower curve zooecial width. Stars are placed at the boundary between zones of astogenetic change and repetition found by the linear regression method. Their position on the vertical axis is the mean value in the zone of astogenetic repetition. A-G, D52638-D52644 respectively.

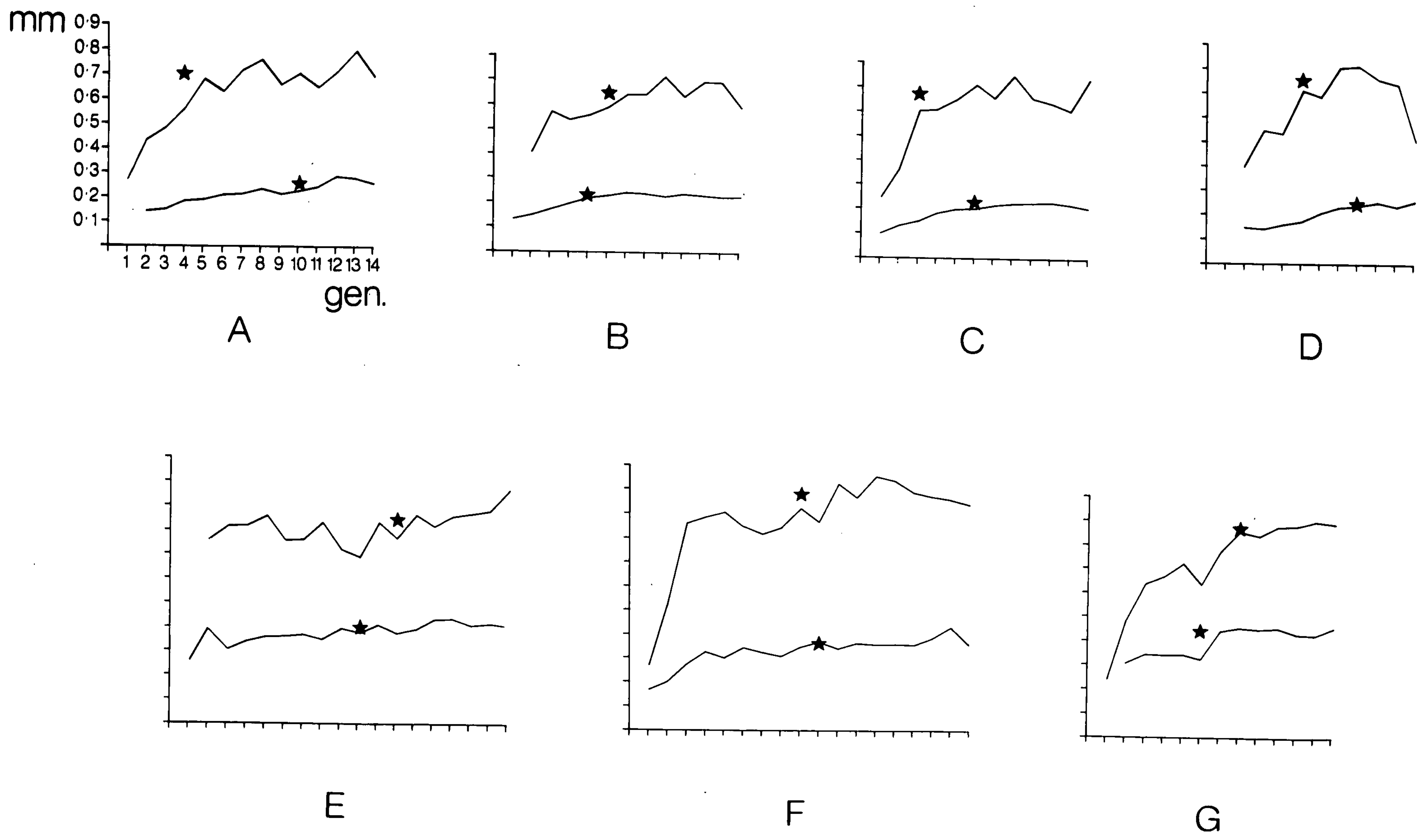

mm
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
1 2 3 4 5 6 7 8 9 10 11 12 13 14
gen.
A
B
C
D
E
F
G

Fig. 14. '*Proboscina*' *sp*. PT 102. ?Lower Callovian, Upper Cornbrash, Thrapston, Northamptonshire. Autozooecia and inflated gonozooecium. The zoarial lateral wall above and right of the gonozooecium is formed of kenozooecia. Inflation of the gonozooecium has caused the two zooecia at either side of the gonozooecium to be terminated and to form kenozooecia. Bar represents 1 mm.

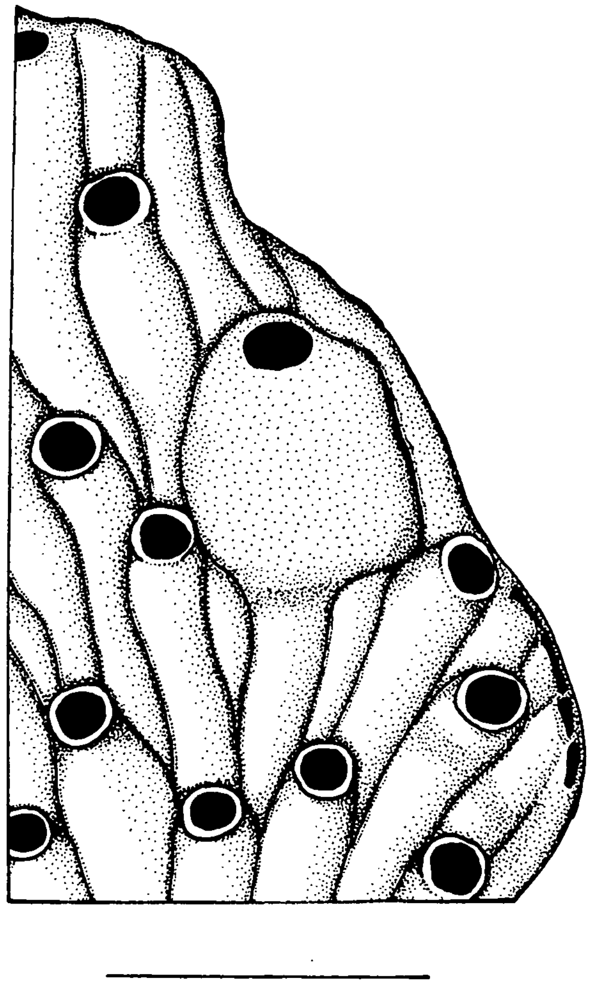


Fig. 15. '<u>Idmonea</u>' sp. PT 765-2. Bajocian, Microzoa Bed, Shipton Gorge, Dorset. Erect branch with large autozooecia on the front surface (left), small autozooecia on the lateral surface (centre), and kenozooecia on the back surface. Bar represents 1 mm.

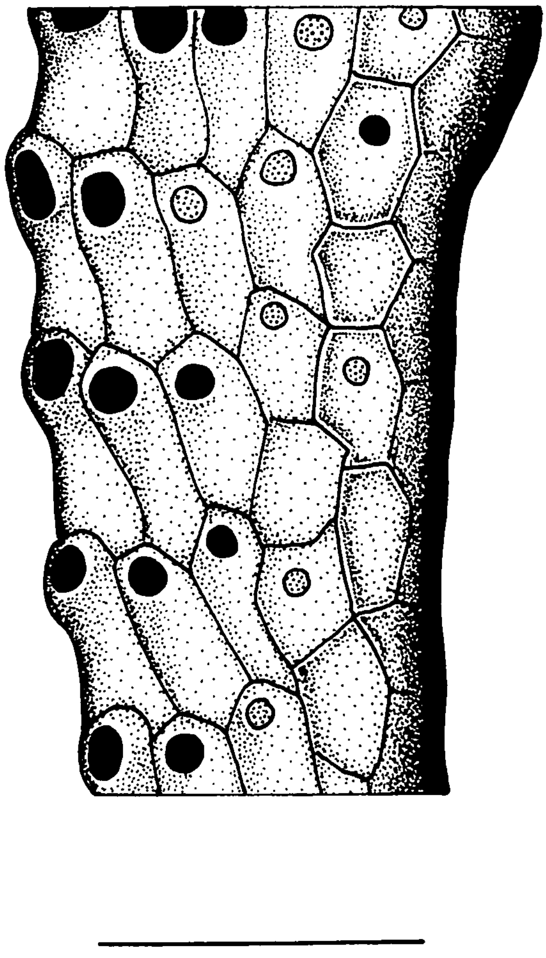


Fig.16. <u>Reptoclausa</u> <u>porcata</u> sp. nov. BMNH D8724. Upper Aalenian, Pea Grit, Birdlip, Gloucestershire. A ridge of autozooecia and a depression with kenozooecia (right). Autozooecial size decreases towards the depression. Bar represents 1 mm.

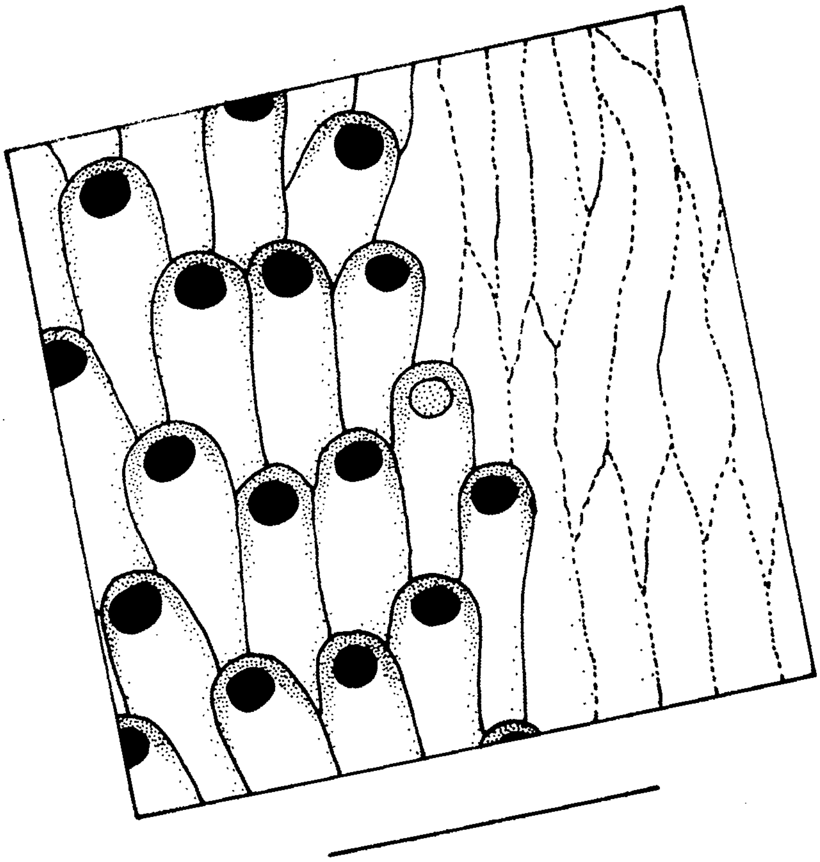
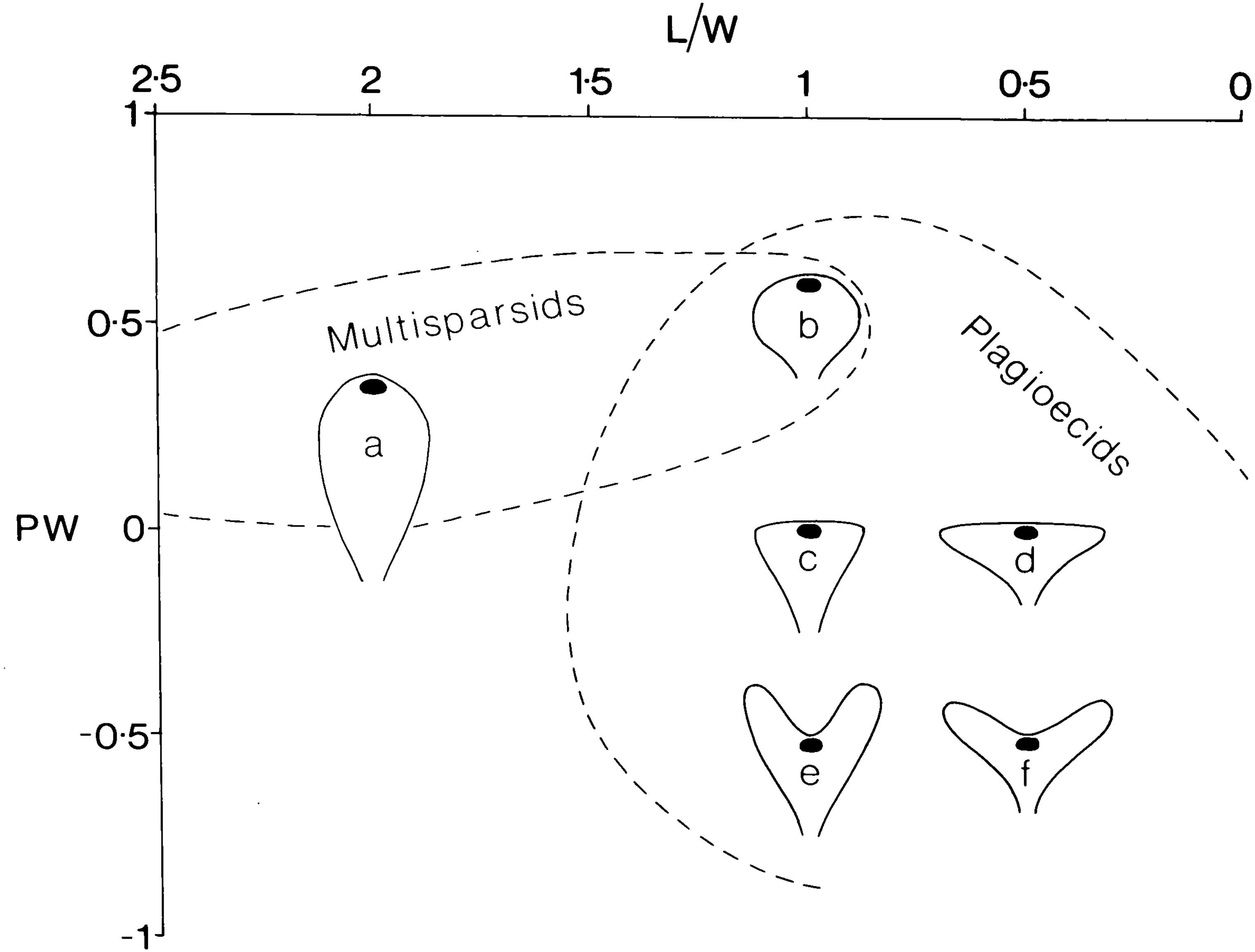


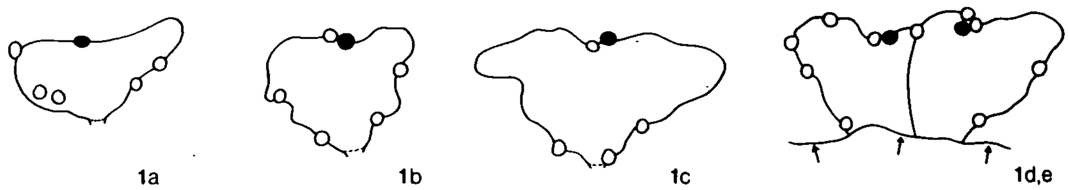
Figure 17. Variation of gonozooecial form in Jurassic tubuloporinids. The diagram is a 2 dimensional morphoseries on which is indicated the fields of occurrence of plagioecids and multisparsids. The vertical axis labelled PW indicates the position of maximum gonozooecium width. Gonozooecia with a positive value of PW have their maximum width proximal of the ooeciopore, gonozooecia with a negative value of PW have their maximum width distal of the ooeciopore. For example, a PW value of +0.5 indicates that the maximum gonozooecium width occurs midway between its ooeciopore and its proximal extremity. The horizontal axis labelled L/W is the ratio between gonozooecium length and width. Ooeciopores are shown in black and placed in a subterminal position throughout. Multisparsid gonozooecia are typically pyriform (gonozooecium a). Globular gonozooecia (b) occur in both multisparsids and plagioecids. Subtriangular gonozooecia (c and d) and boomerang-shaped gonozooecia (e and f), characterise plagioecids.



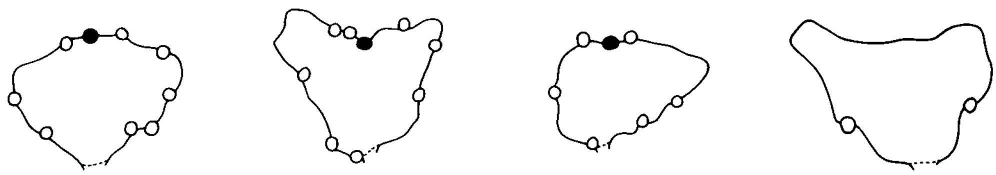
L/W
2·5
2
1·5
1
0·5
0
PW
1
0·5
0
-0·5
-1
Multisparsids
Plagioecids
a
b
c
d
e
f

Figure 18. Variation in gonozooecium shape in *Mesenteripora undulata* from the caillasse of the Upper Bathonian Langrune Member at Luc-sur-mer, Normandy. Numbers indicate separate colonies, letters indicate gonozooecia within a colony. Ooeciopores and probable ooeciopores are shown in black, autozooecial apertures are unshaded. Dashed lines indicate the boundary between proximal uninflated and distal inflated portions of the gonozooecia. In gonozooecium 6a, the probable outline of an incomplete lobe is dashed. An intrazoarial overgrowth partly covers the juxtaposed gonozooecia 1d and 1e. Gonozooecium 2c is involved in a growth margin anastomosis. Ooeciopores could not be identified in gonozooecia 2a, 2b and 2e which were probably aborted.

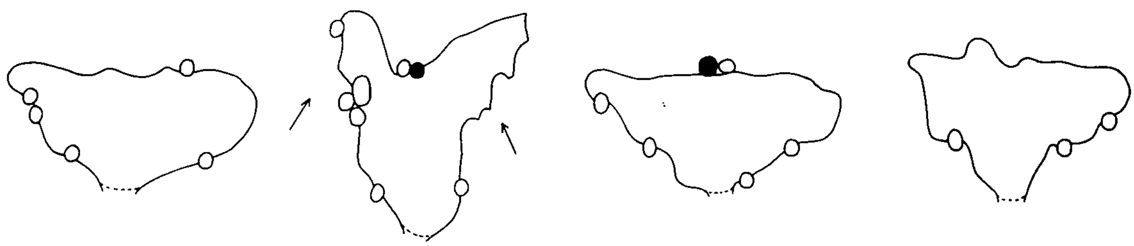
Colony 1 = PT 641-1; colony 2 = PT 641-2; colony 3 = PT 642-23; colony 4 = PT 641-25; colony 5 = PT 642-42; colony 6 = PT 642-46.



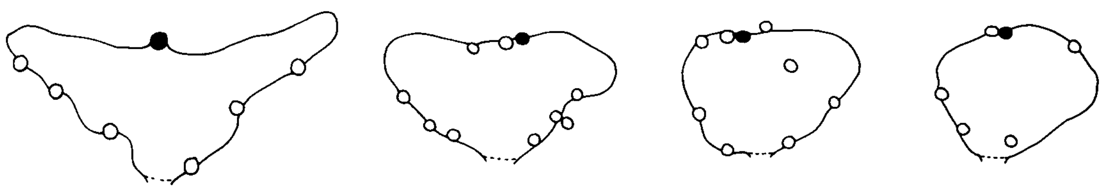
1a 1b 1c 1d,e



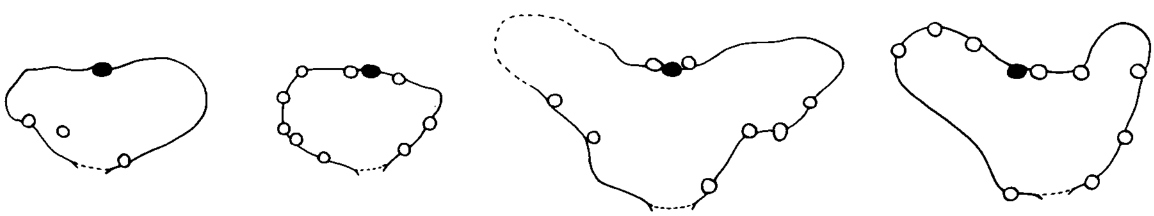
1f 1g 1h 2a



2b 2c 2d 2e



2f 3a 3b 3c



4 5 6a 6b

Figure 19. Histograms showing the frequency distributions of the within colony coefficient of variation (CV) for 5 gonozooecial characters in 13 Jurassic tubuloporinid species. Class intervals are of 2 units. N, number of colonies analysed; $\bar{x}$, mean value of within colony CV for the colonies analysed; tgl, total gonozooecial frontal wall length; igl, length of inflated portion of gonozooecial frontal wall; gw maximum gonozooecial width; low, longitudinal ooeciopore width; tow, transverse ooeciopore width.

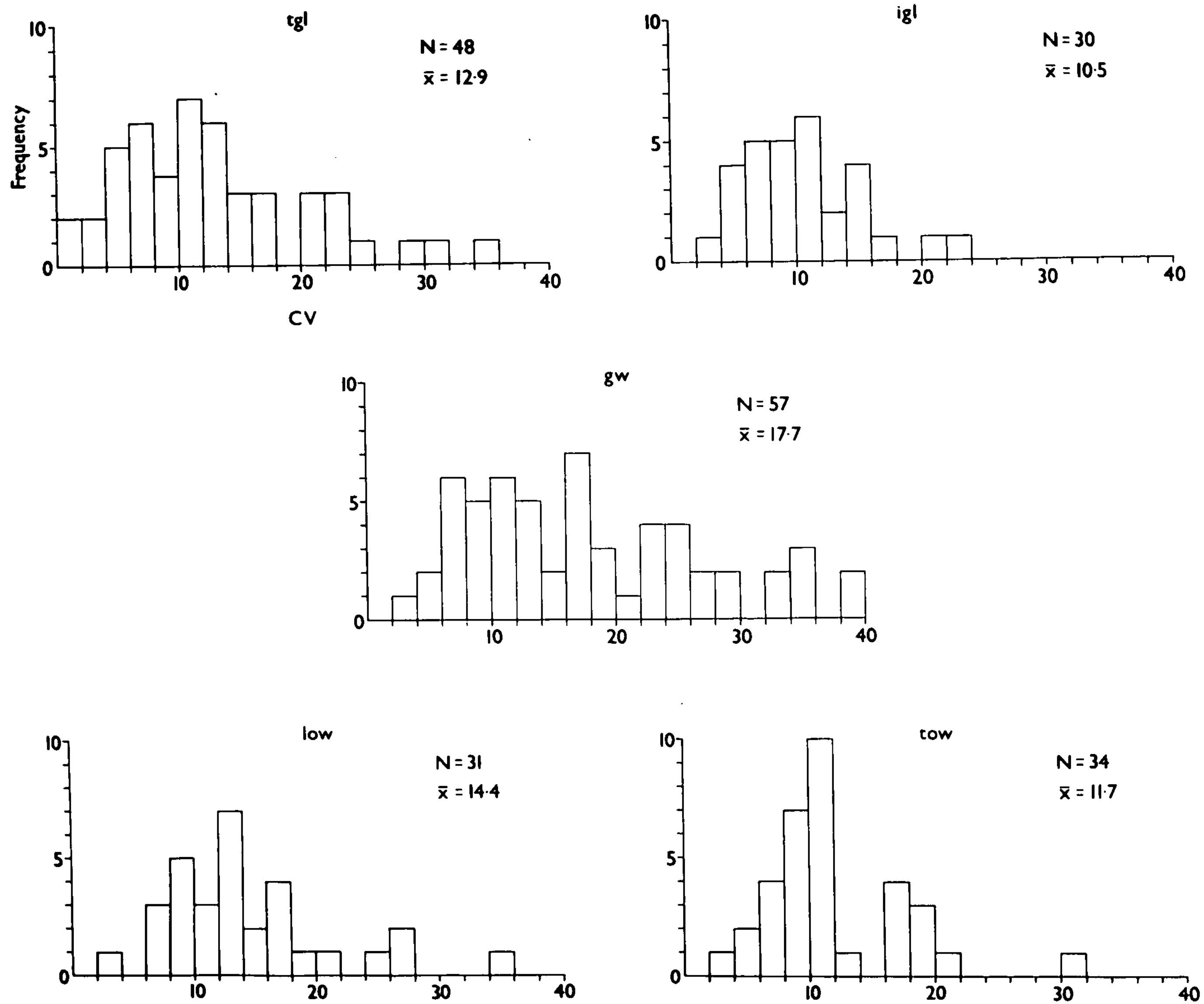
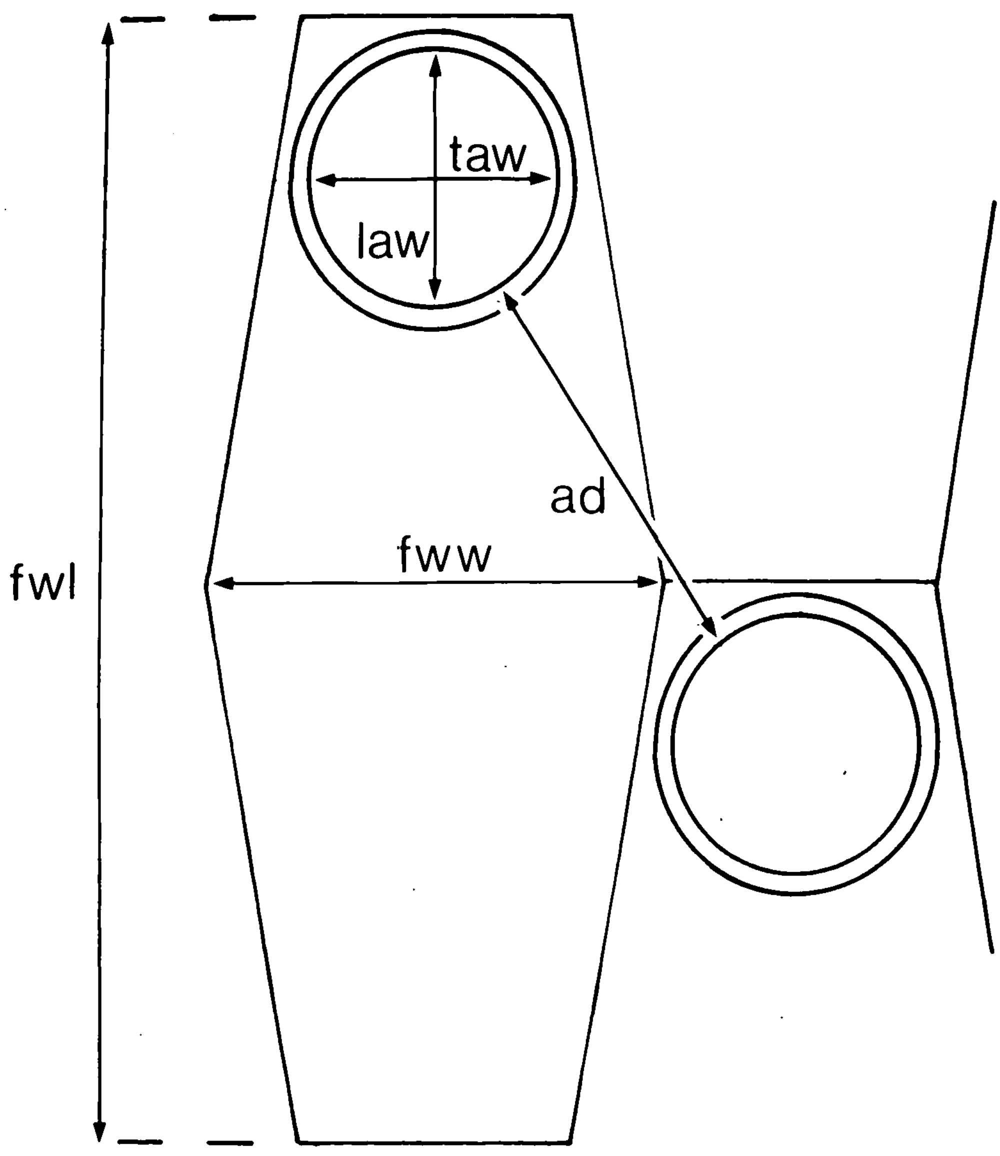

tgl
N = 48
x̄ = 12·9
Frequency
CV
igl
N = 30
x̄ = 10·5
gw
N = 57
x̄ = 17·7
low
N = 31
x̄ = 14·4
tow
N = 34
x̄ = 11·7

Figure 20. Diagram to show the autozooecial morphological characters measured during biometrical studies. taw, transverse apertural width; law, longitudinal apertural width; ad, apertural distance (distance from the aperture to its nearest neighbour); fwl, frontal wall length; fww, frontal wall width.



taw
law
ad
fww
fwl

Figure 21. Histogram showing the frequency distribution (F) of the coefficient of variation (CV) for longitudinal apertural width (law) in 153 colonies of the 15 species studied systematically.

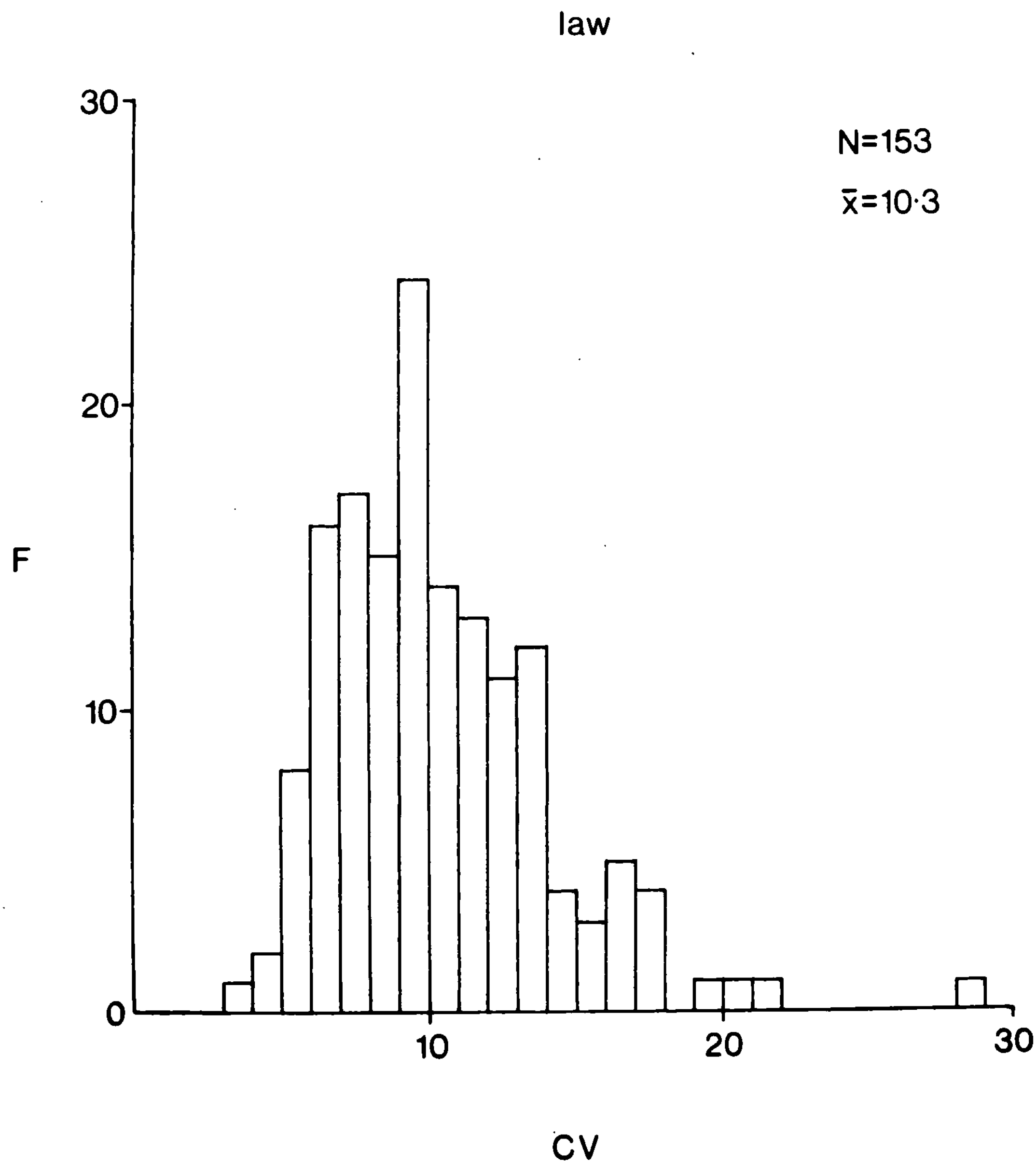

law
N=153
$\bar{x}$=10·3
F
30
20
10
0
10
20
30
CV

Figure 22. Histogram showing the frequency distribution (F) of the coefficient of variation (CV) for transverse apertural width (taw) in 150 colonies of the 15 species studied systematically.

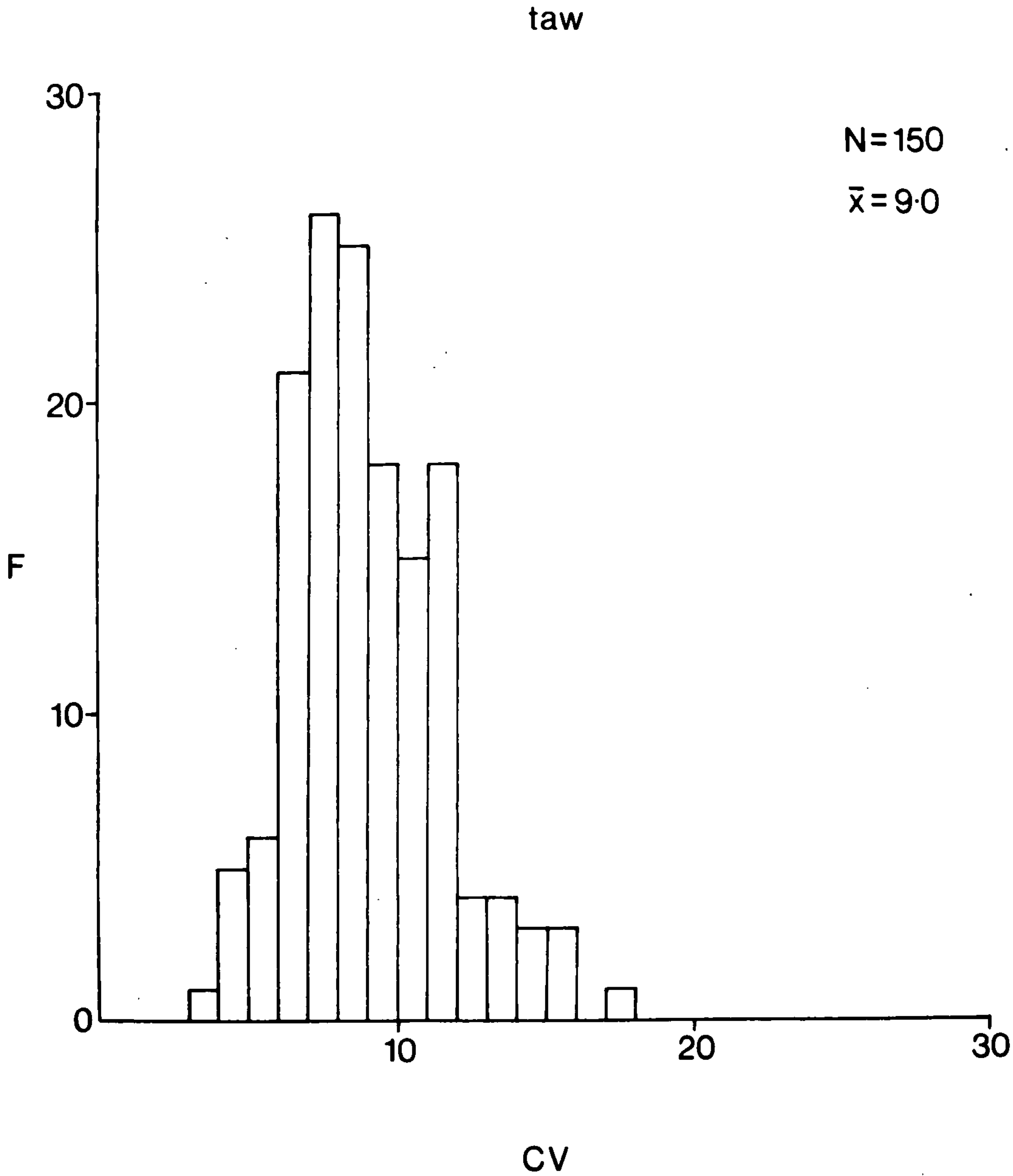
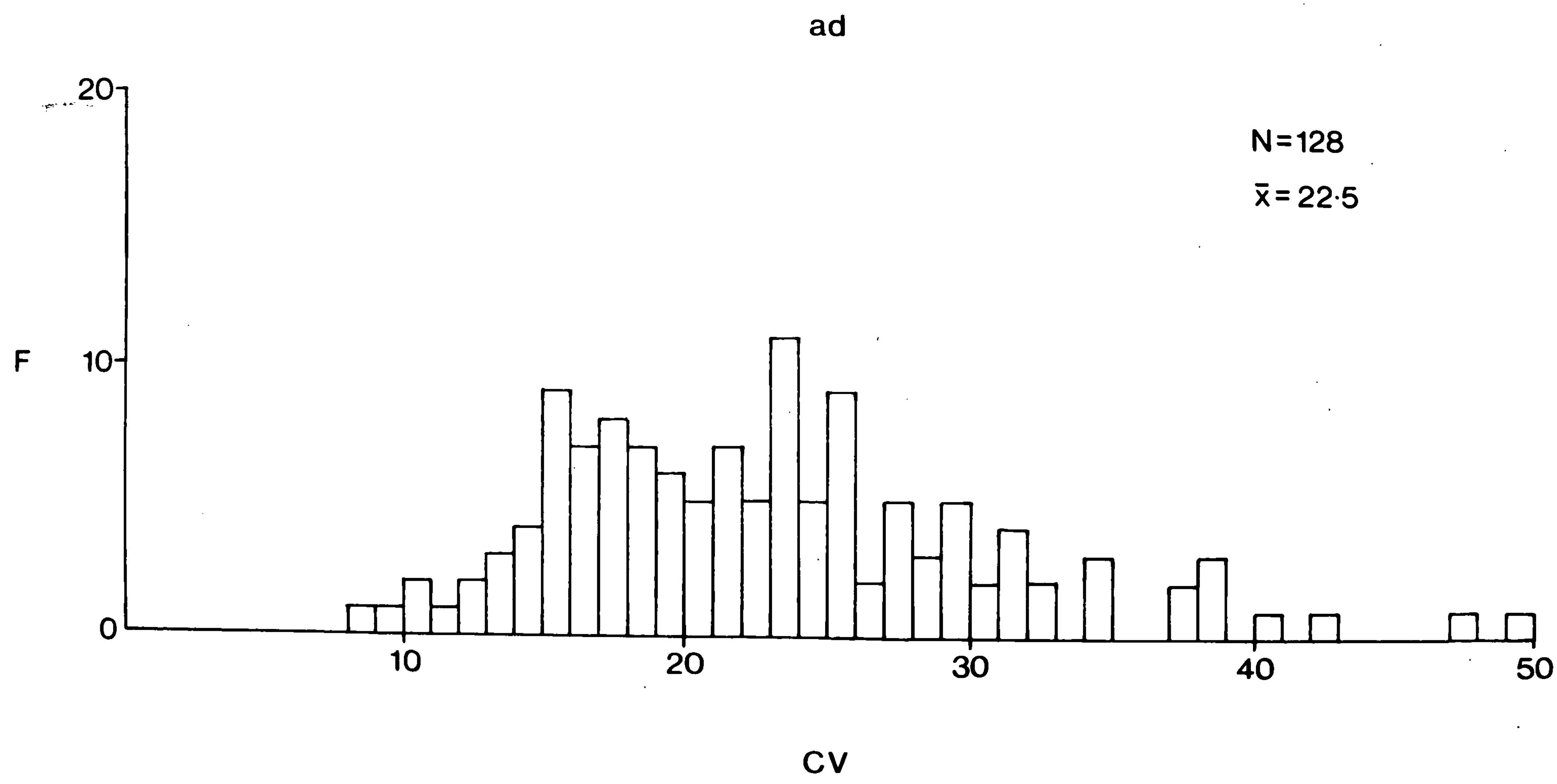
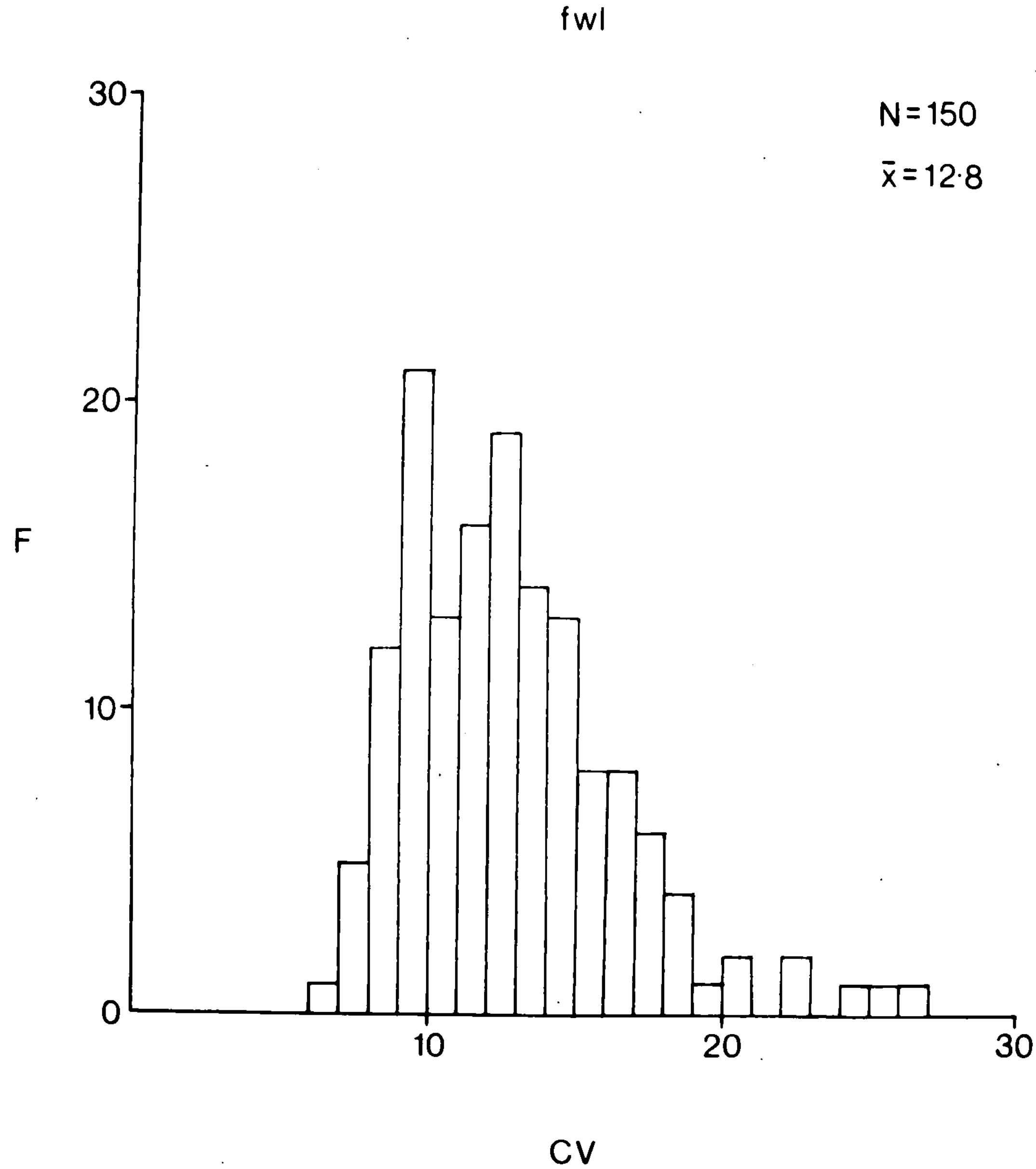

taw
N = 150
x̄ = 9·0
F
CV
0
10
20
30
10
20
30

Figure 23. Histogram showing the frequency distribution (F) of the coefficient of variation (CV) for minimum apertural distance (ad) in 128 colonies of the 15 species studied systematically.



ad
F
20
10
0
N=128
$\bar{x}$ = 22·5
10
20
30
40
50
CV

Figure 24. Histogram showing the frequency distribution (F) of the coefficient of variation (CV) for frontal wall length (fwl) in 15 colonies of the 15 species studied systematically.



fwl
30
20
10
0
F
N = 150
x̄ = 12·8
10
20
30
CV

Figure 25. Histogram showing the frequency distribution (F) of the coefficient of variation (CV) for frontal wall width (fww) in 152 colonies of the 15 species studied systematically.

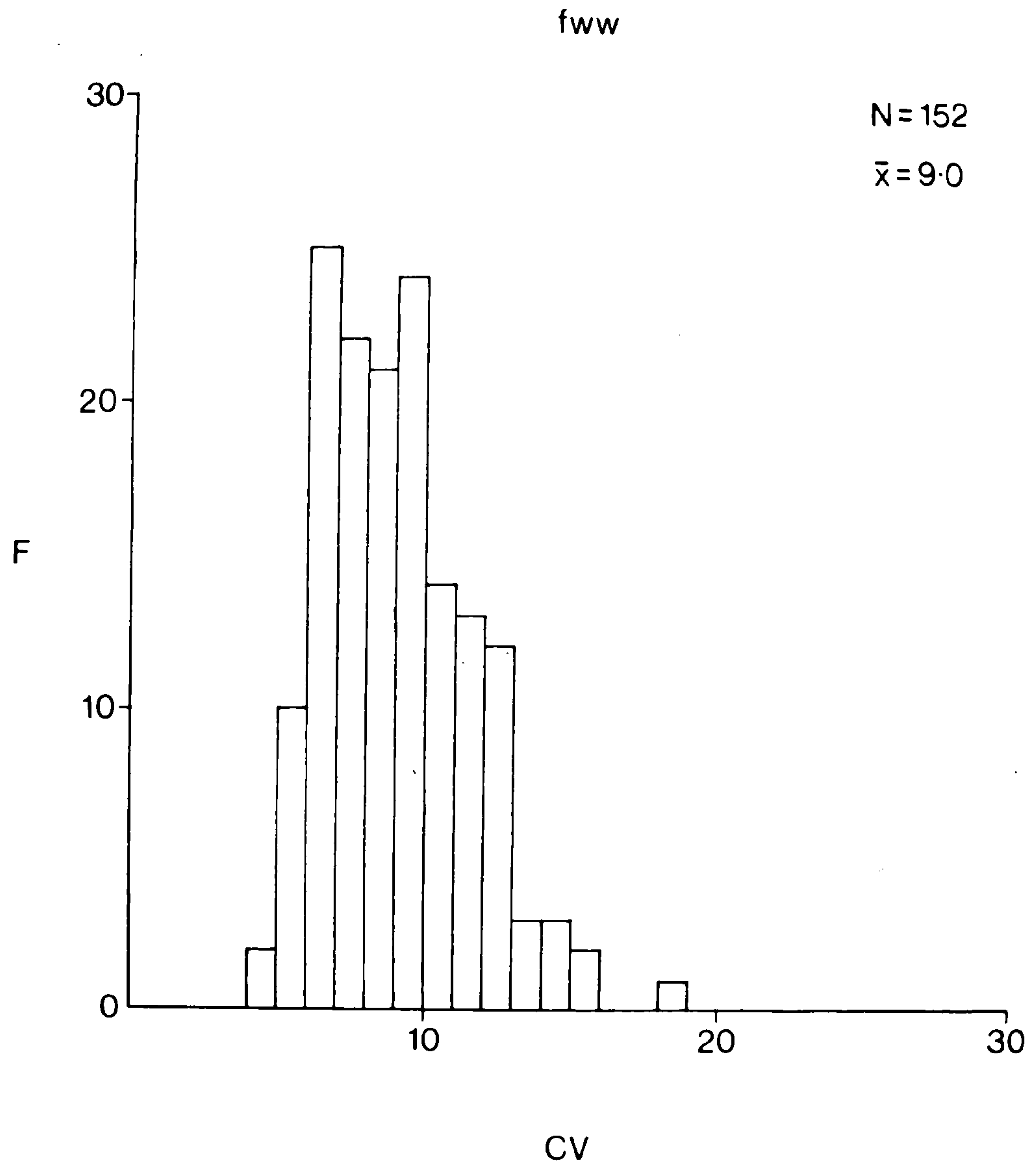

fww
N = 152
$\bar{x}$ = 9·0
F
CV
0
10
20
30
10
20
30

Figure 26. Analysis of spatial heterogeneity of zooecial length in colony D52642, _Stomatopora dichotomoides_. The correlation coefficient (r) is plotted against the distances (d) between pairs of zooecia (9 units of d = 1mm). Bars show 95% confidence intervals and sample sizes are given below each bar. The correlation is not significant for cases where the 95% confidence interval overlaps r = 0.

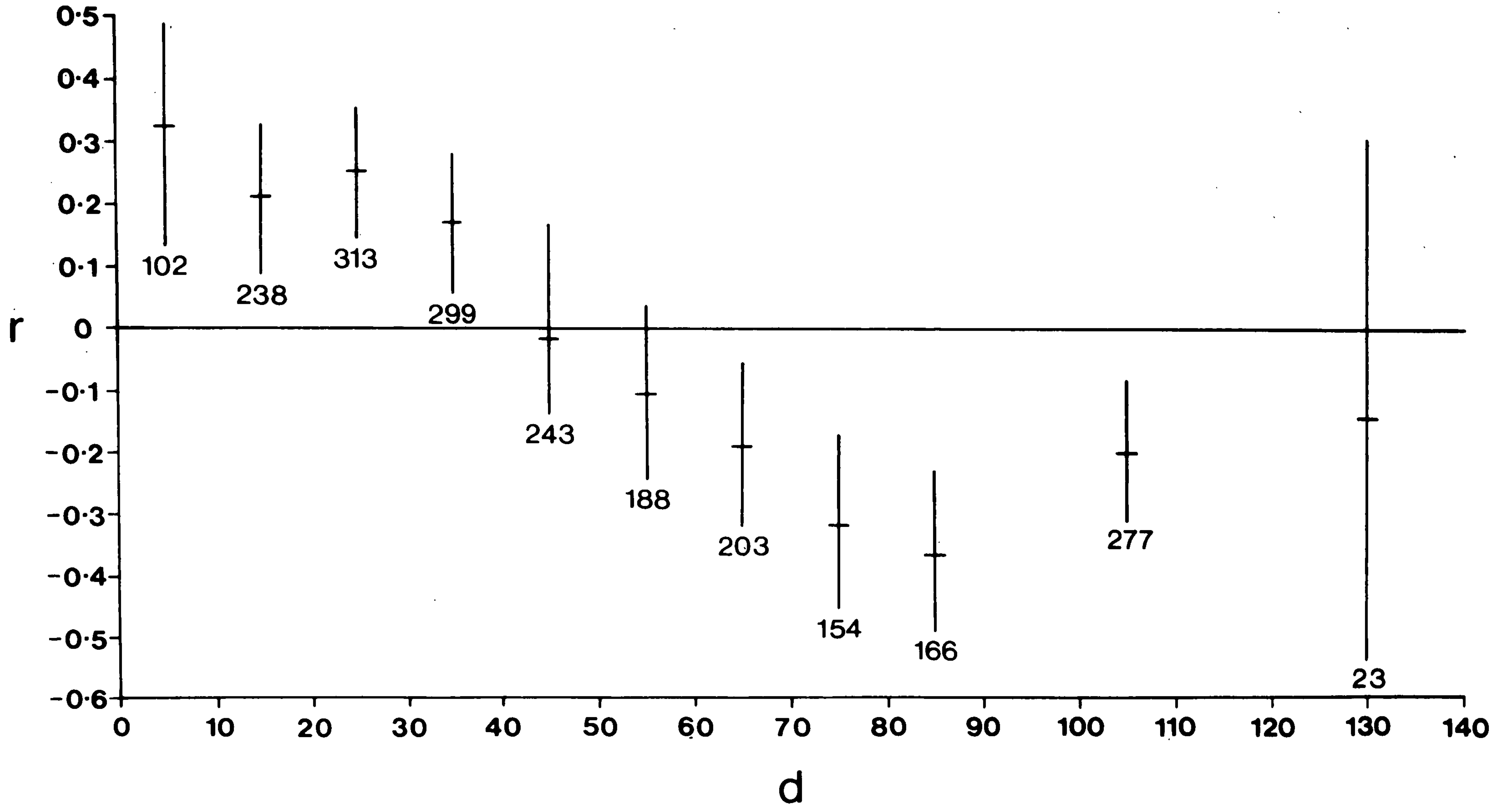

0·5
0·4
0·3
0·2
0·1
0
-0·1
-0·2
-0·3
-0·4
-0·5
-0·6
r
102
238
313
299
243
188
203
154
166
277
23
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
d

Figure 27. Growth-forms of adnate unilamellar tubuloporinideans. A, stomatoporiform; B, probosciniiform; C, fan-shaped bereniciform; D, discoidal bereniciform. a, ancestrula; gm, growth margin; p, protoecium.

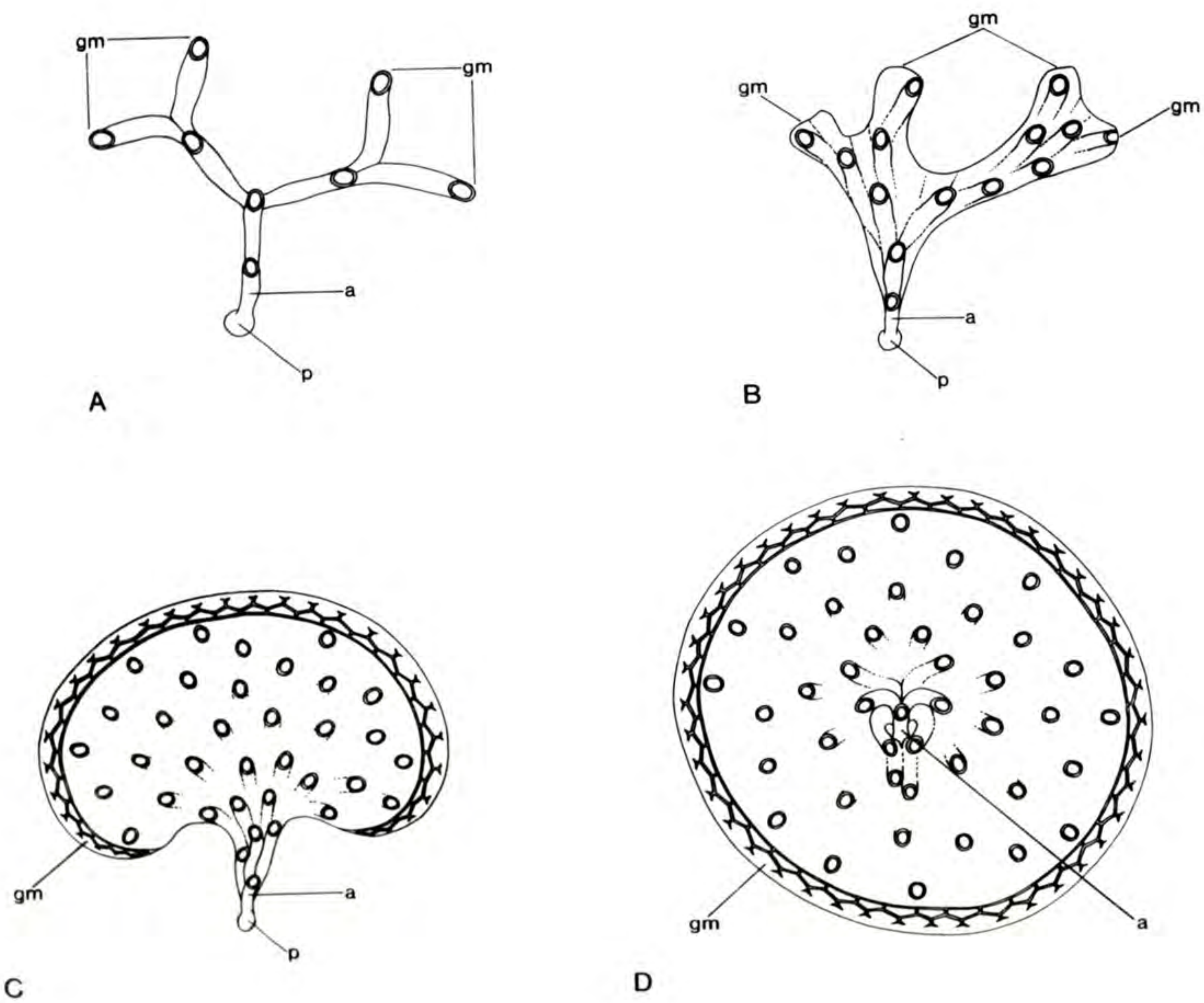

gm
gm
a
p
A
gm
gm
gm
a
p
B
gm
a
p
C
gm
a
D

Figure 28. Diastoporidiform frond arising from an adnate base (ab). Arrows indicate direction of growth and numbers show 3 growth stages. The growth margin (gm) is evenly stippled.

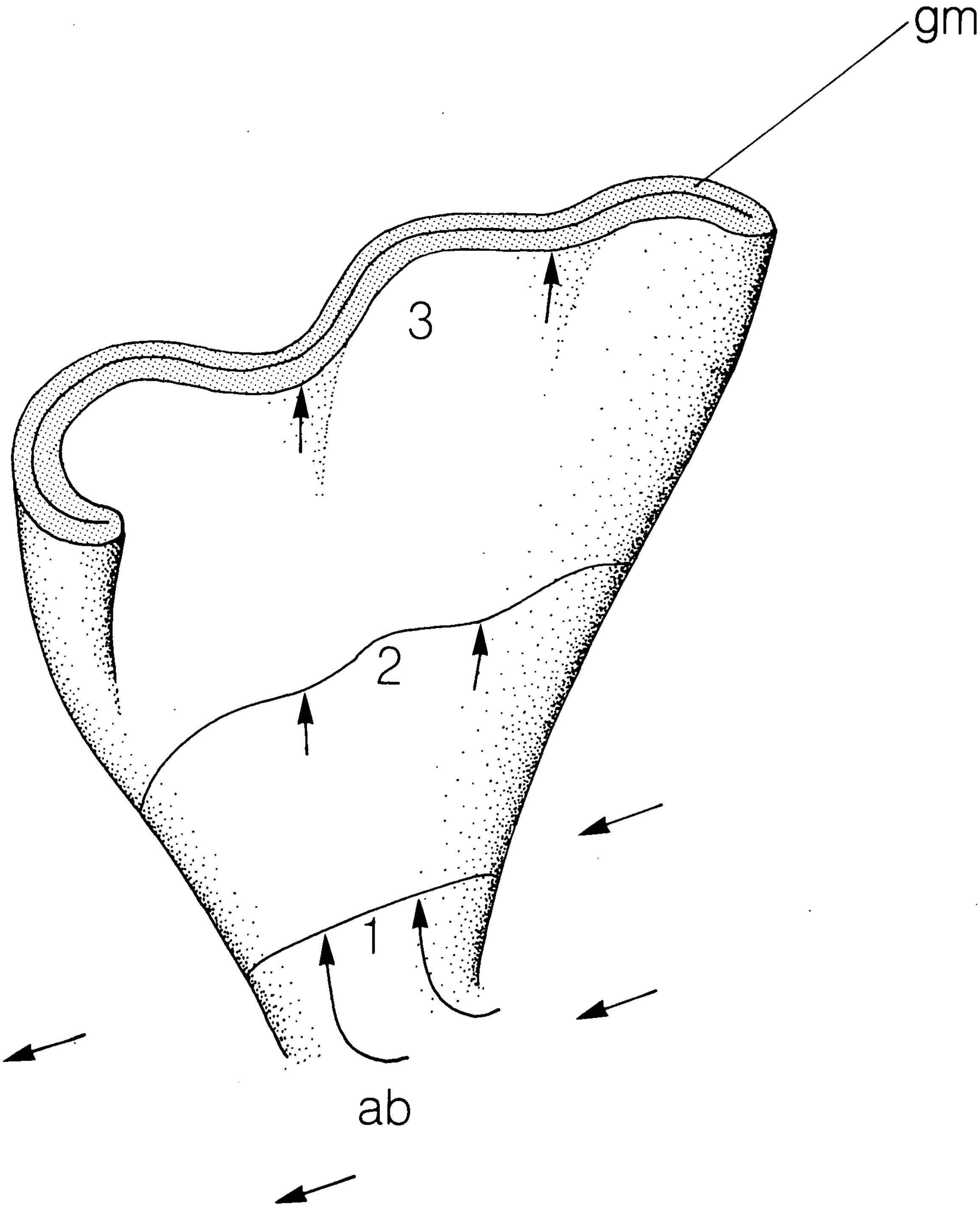
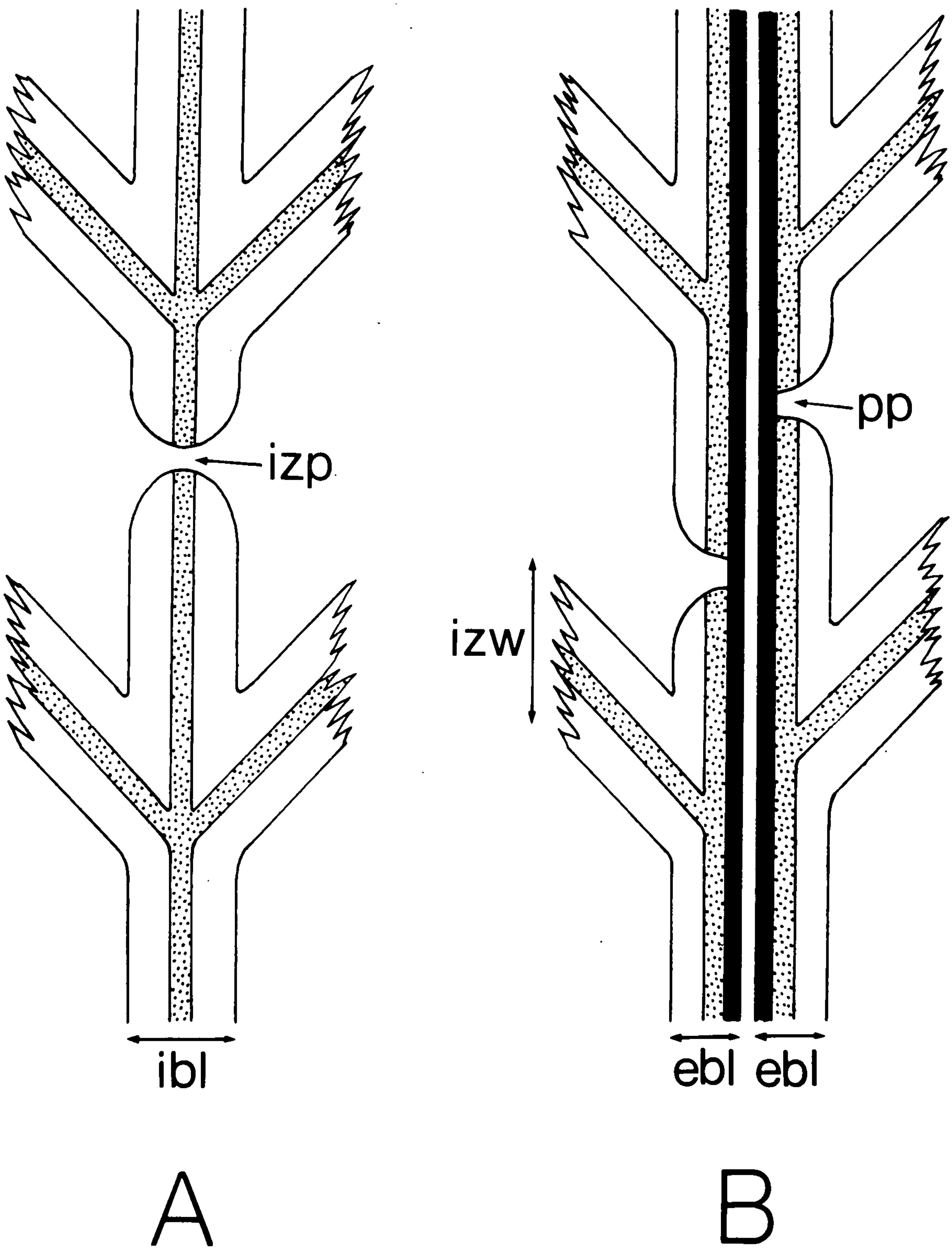

gm
3
2
1
ab

Figure 29. Bilamellar budding laminae in longitudinal section. A, interior body wall budding laminae (ibl) with an interzooecial pore (izp). B, juxtaposed exterior body wall laminae (ebl) with pseudopores (pp). The gap between the two exterior body wall laminae is exaggerated. Black, cuticle; stipple, primary skeletal layer; izw, interzooecial wall.



izp
ibl
A
pp
izw
ebl
ebl
B

Figure 30. Dichotomies of tubuloporinidean interzooidal walls (interior body wall) to form two exterior body walls.

A, normal type of dichotomy (after Brood 1972, fig. 7D; Hinds 1975, text-fig.1). The interzooidal wall (iw) is composed of a primary skeletal layer (stippled) flanked by secondary skeletal layers (white) bordered by secretory epithelia (dotted line). It divides to form two zooecial frontal walls (fw) composed of a surficial cuticle (black) underlain by a primary skeletal layer which overlies a secondary skeletal layer and secretory epithelia. Arbitrary boundary between the interzooidal wall and the frontal walls is a dashed line.

B, dichotomy of an interzooidal wall (iw) to form a zooecial frontal wall (fw) and a basal budding lamina (bl) which subsequently covers the frontal wall.

C, dichotomy of an interzooidal wall (iw) to form two basal budding laminae (bl) juxtaposed with a substrate (indicated by small crosses).

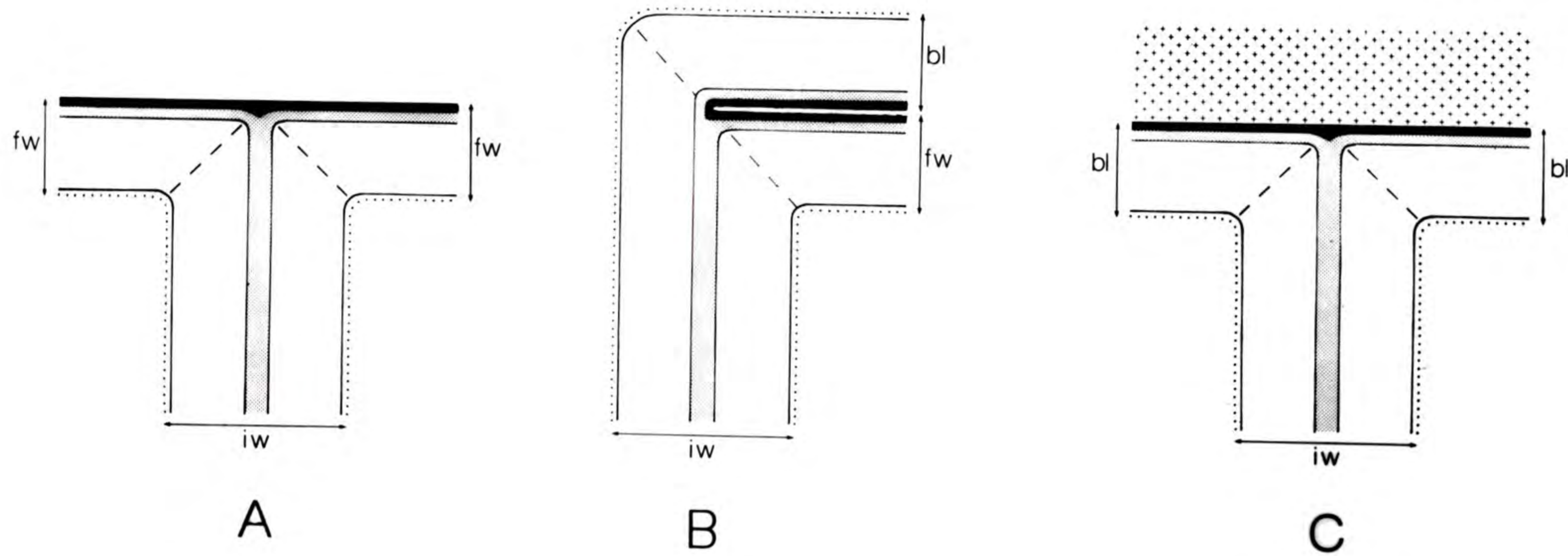

fw
fw
iw
A
bl
fw
iw
B
bl
bl
iw
C

Figure 31. Lamellar zooecial budding styles. Three budding styles (A,B and C) are shown in three growth stages (1,2 and 3). Diagrams are views of portions of the colony growth margin with the budding lamina at the bottom and the zoarial frontal surface at the top. Zooecia are shown with a regular hexagonal cross-section and a single zooecium in each growth series is indicated with a star. In budding style A new zooecia arise at divisions (ds) of septa perpendicular to the budding lamina. In budding style B new zooecia are partitioned off by the formation of a transverse septum (ts). Budding style C is an intermediate between styles A and B.

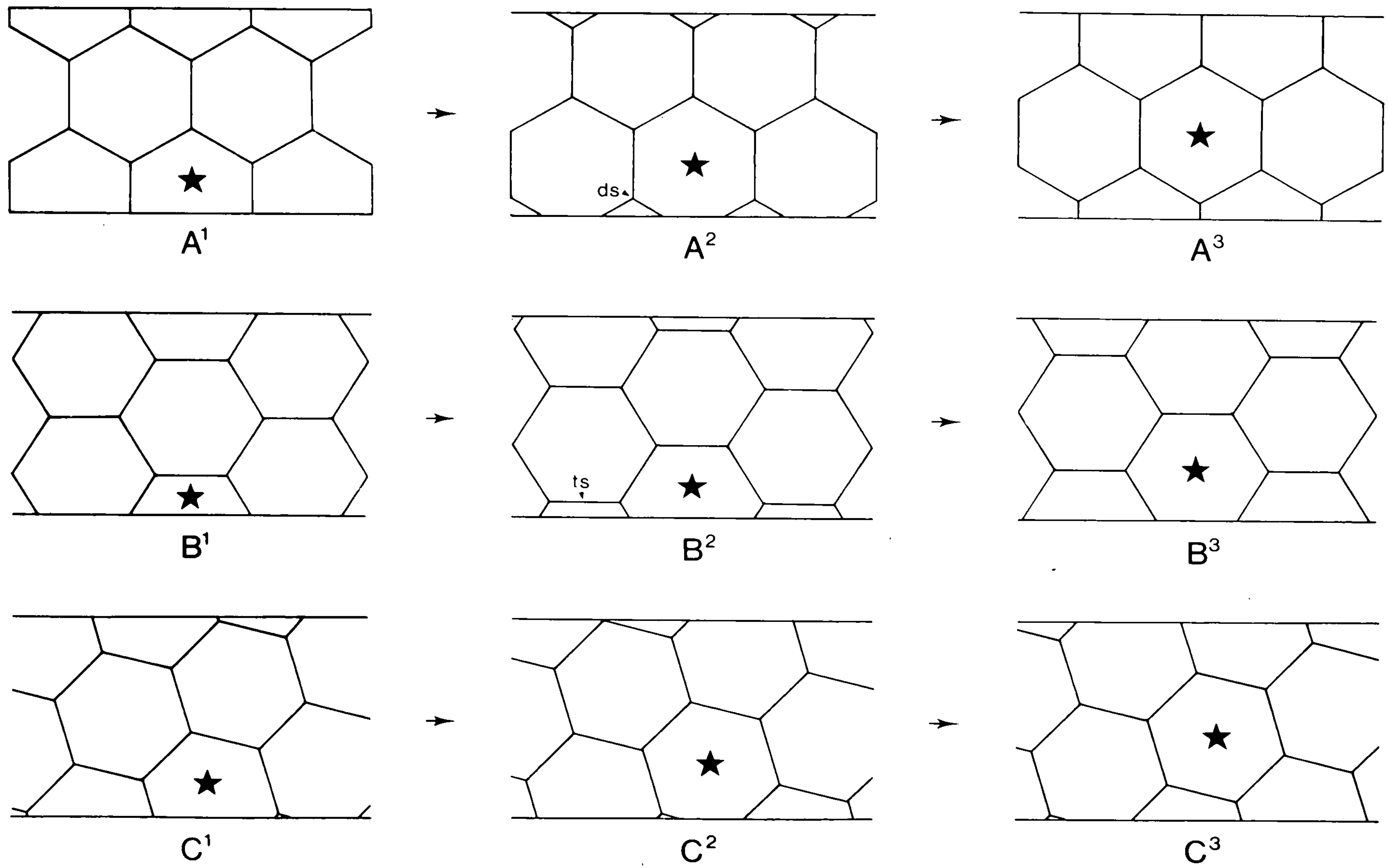
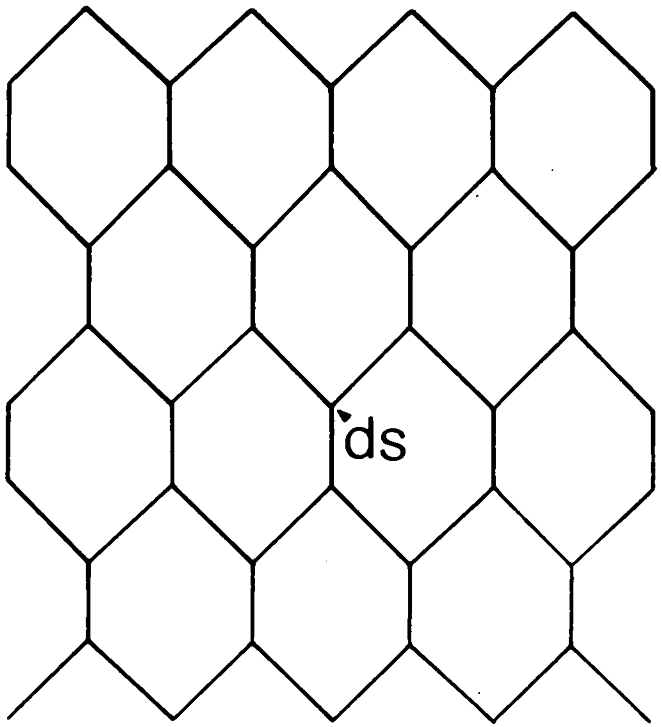
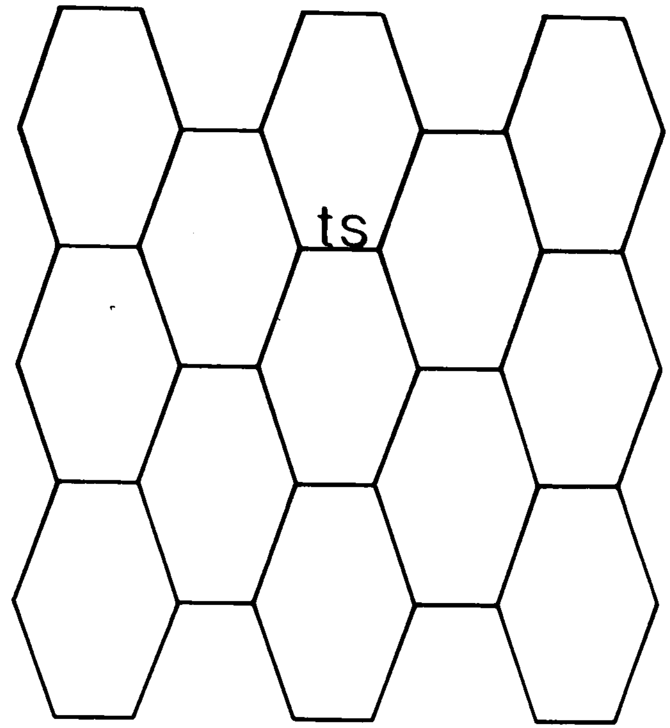

ds
A1
A2
A3
ts
B1
B2
B3
C1
C2
C3

Figure 32. Tubuliporinidean septal trace patterns formed by budding zooecia in lamellar styles. Growth direction is from top to bottom. A, pattern formed when zooecia are budded by the division of an existing interzooecial wall or septum (ds). B, pattern formed when zooecia are budded by the formation of obliquely inclined transverse septa (ts).

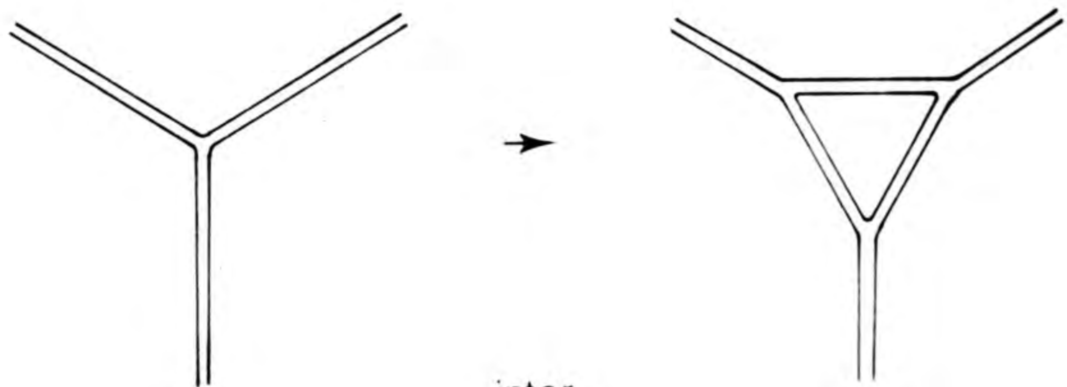


A

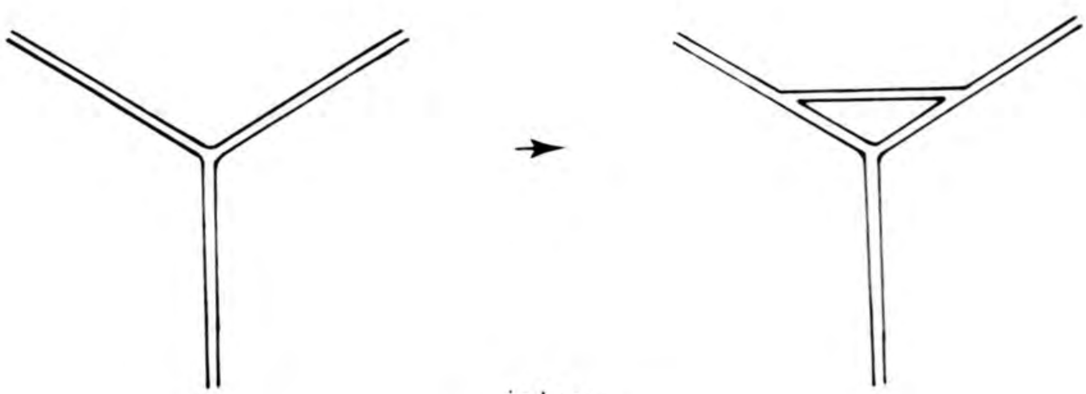


B

Figure 33. Non-lamellar zooecial budding styles. The two budding styles recognised by McKinney (1975) are interzooecial and intrazooecial. An interzooecial bud occupies space partitioned off from more than one existing zooecium. An intrazooecial bud occupies space partitioned off from one existing zooecium only.

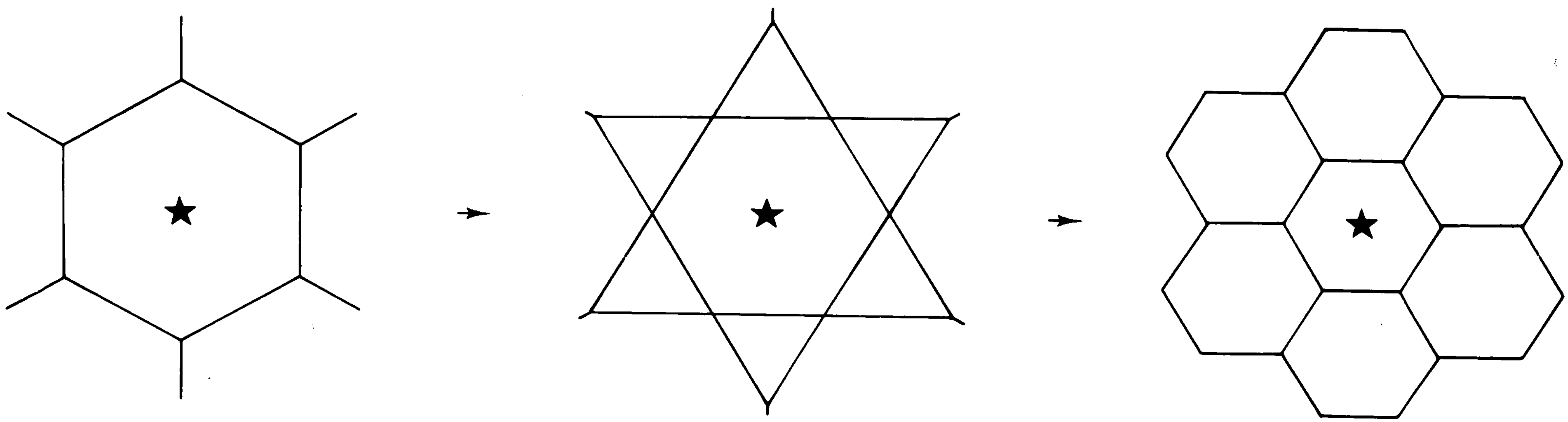


inter-



intra-

Figure 34. Idealized pattern of interzooecial budding around a hexagonal zooecium (marked with a star). The triangular zooecial buds shown in growth stage 2 increase in size and become hexagonal shaped when walls of adjacent buds contact one another. By growth stage 3 all zooecia are equivalent in size and each is half the size of the starred zooecium at growth stage 1.



1 2 3

Figure 35. Four growth stages in the division of a zooecial budding locus.

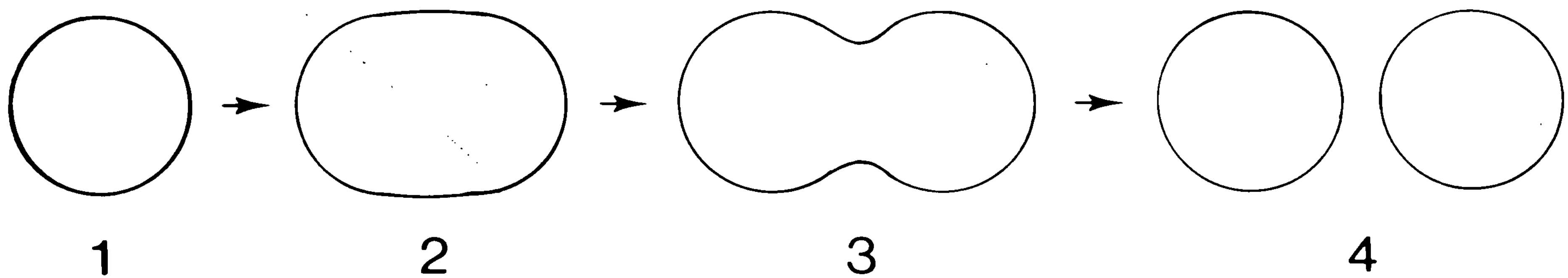

1
2
3
4

Figure 36. Plot of angle of branch dichotomy against zooecial generation number at which the dichotomy occurred in 7 zoaria of Stomatopora. Black dots indicate the mean value; bars indicate the observed range. The graph is based on 120 measurements of dichotomy angle from 4 zoaria of S.bajocensis (BMNH D52638 - D52641) and 3 zoaria of S.dichotomoides (BMNH D52642 - D52644).

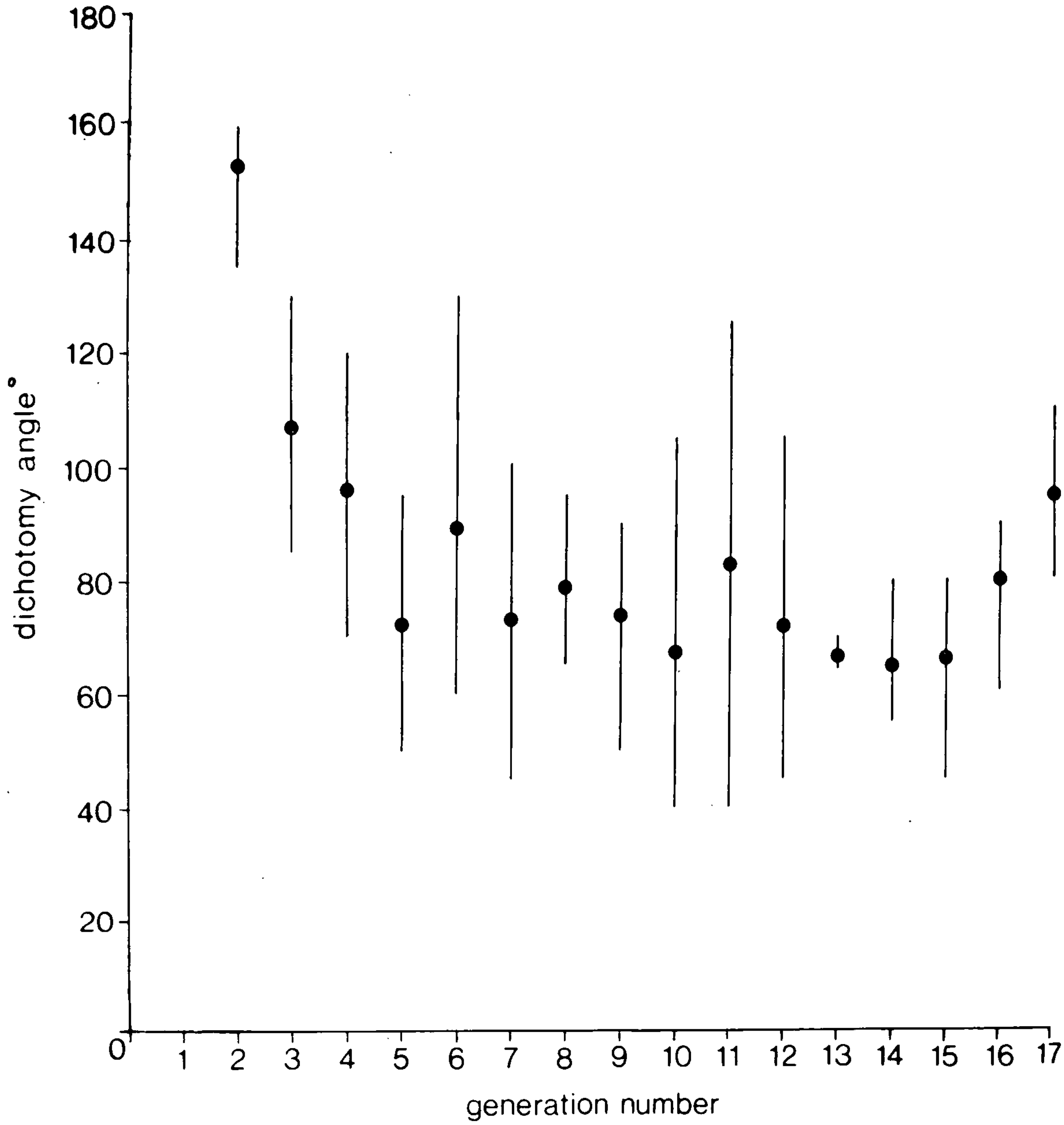
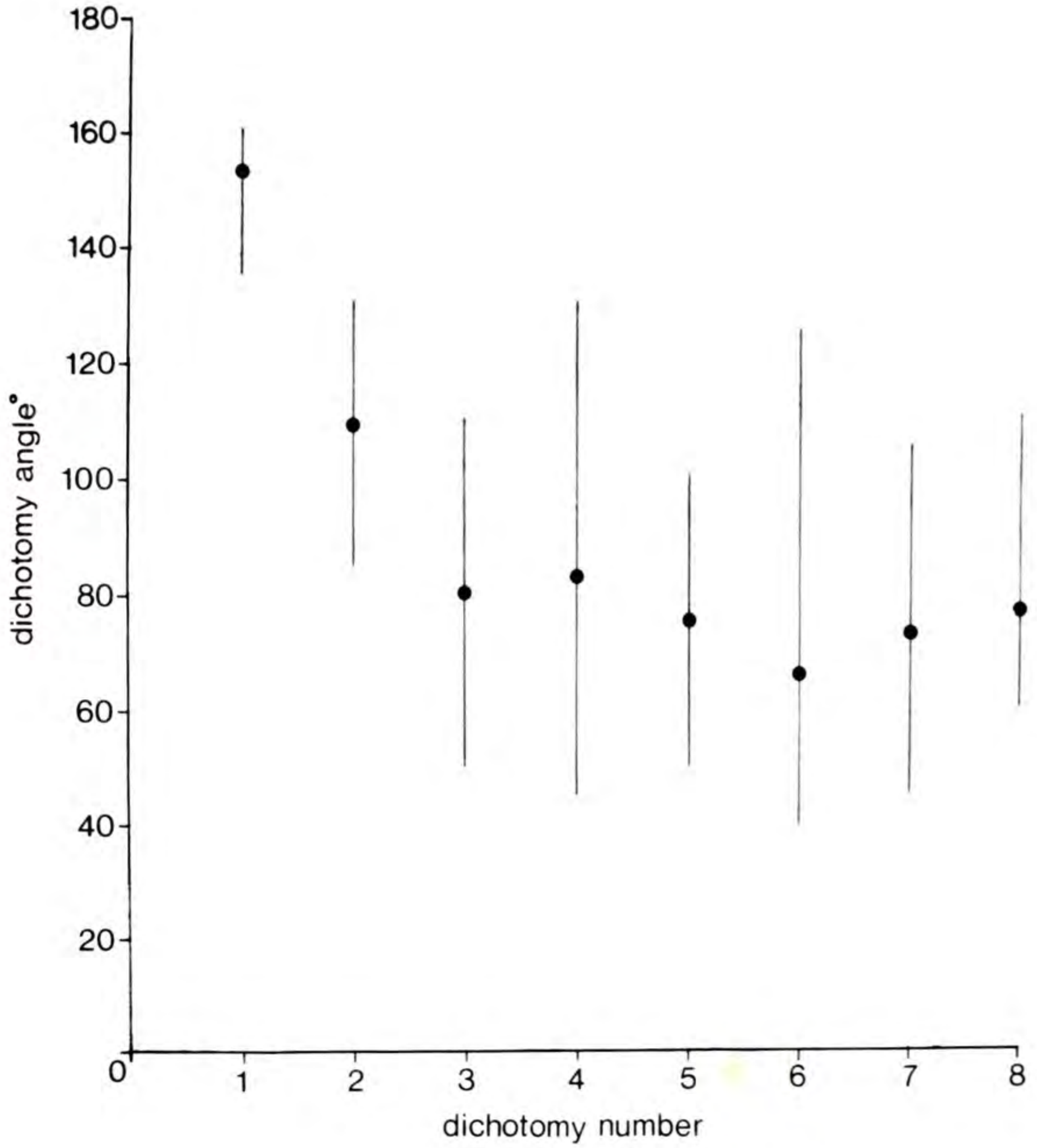
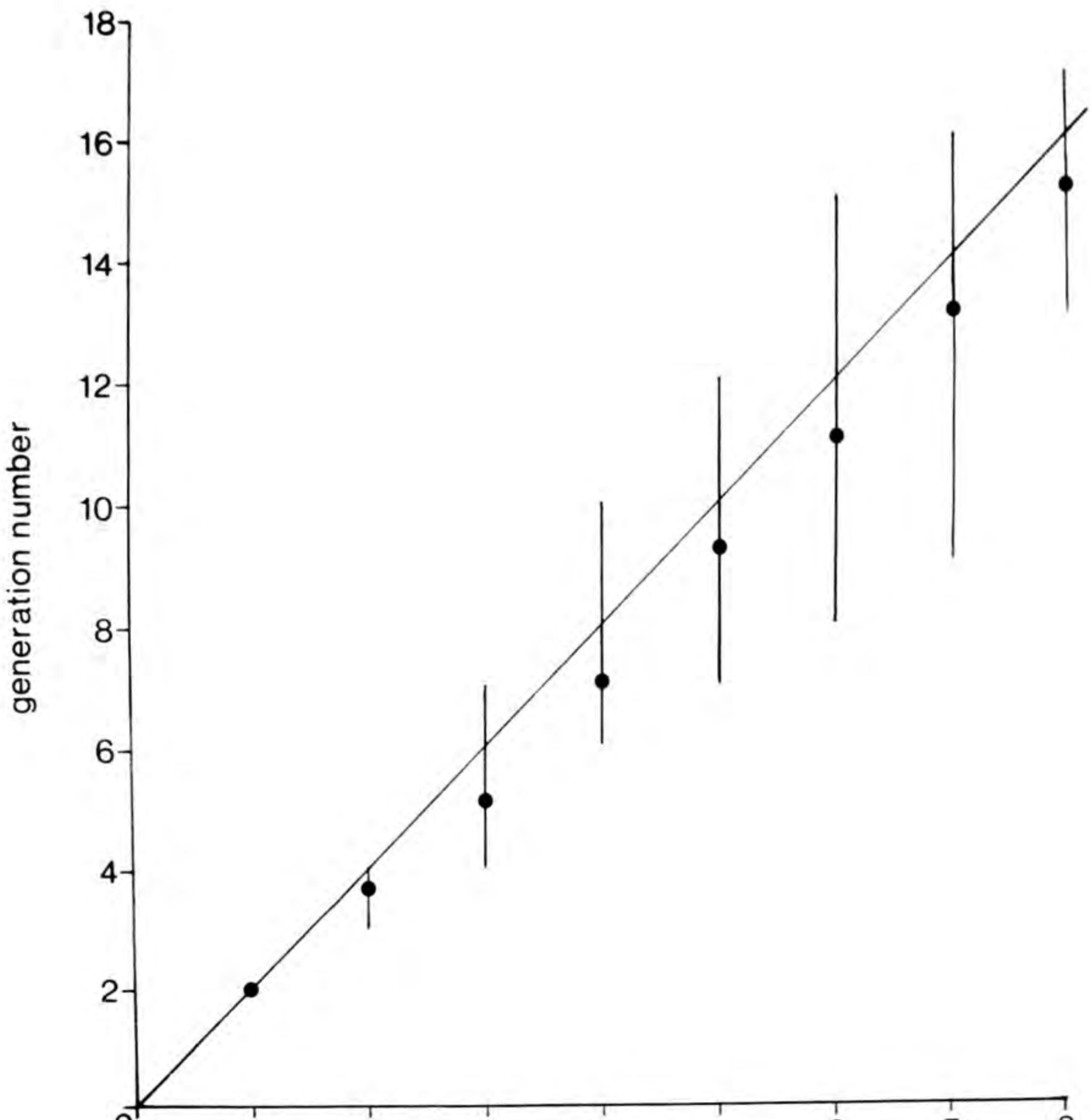

dichotomy angle°
180
160
140
120
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
generation number

Figure 37. Plot of angle of branch dichotomy against dichotomy number (number of dichotomies from the ancestula) in 7 zoaria of *Stomatopora*. Black dots indicate the mean value; bars indicate the observed range. The graph is based on 120 measurements of dichotomy angle from 4 zoaria of *S.bajocensis* (BMNH D52638 - D52641) and 3 zoaria of *S.dichotomoides* (BMNH D52642 - D52644).



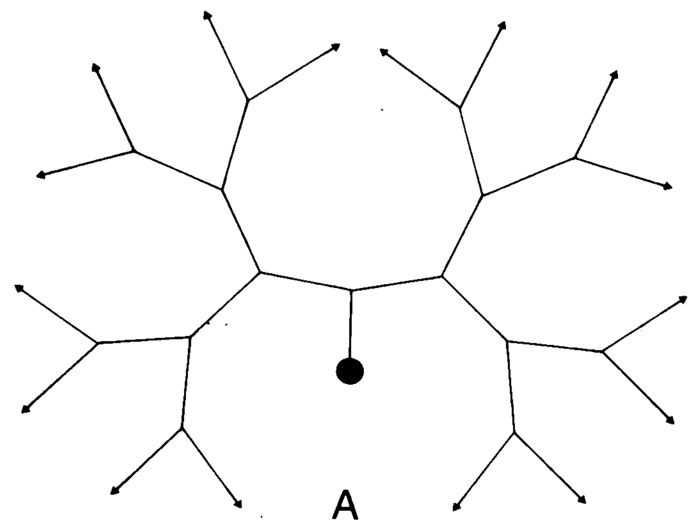
180
160
140
120
100
80
60
40
20
0
dichotomy angle°
1
2
3
4
5
6
7
8
dichotomy number

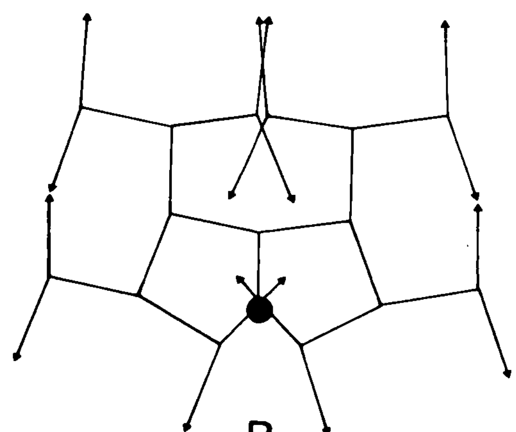
Figure 38. Plot of zooecial generation number at which a dichotomy occurred against dichotomy number (number of dichotomies from the ancestrula) in 7 zoaria of *Stomatopora*. Black dots indicate the mean value; bars indicate the observed range. Values tend to fall slightly beneath the regression line which is $x = 2y$. Based on 120 determinations from 4 zoaria of *S. bajocensis* (BMNH D52638 - D52641) and 3 zoaria of *S. dichotomoides* (BMNH D52642 - D52644).



18
16
14
12
10
8
6
4
2
0
generation number
1
2
3
4
5
6
7
8
dichotomy number

Figure 39. Branching patterns in model uniserial zoaria. Colony origins are represented by solid black circles and branch growth tips are indicated by arrowheads orientated in the direction of growth. Colony A was constructed using the mean angles of dichotomy found in Jurassic *Stomatopora*, successive dichotomies having angles of 160°, 120°, 80° and 80°. Colony B was constructed with all angles of dichotomy equal to 160°. Colony C was constructed with all angles equal to 80°.


A


B

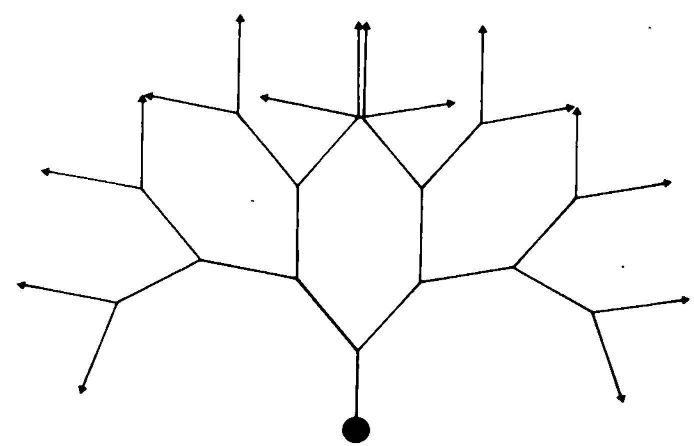
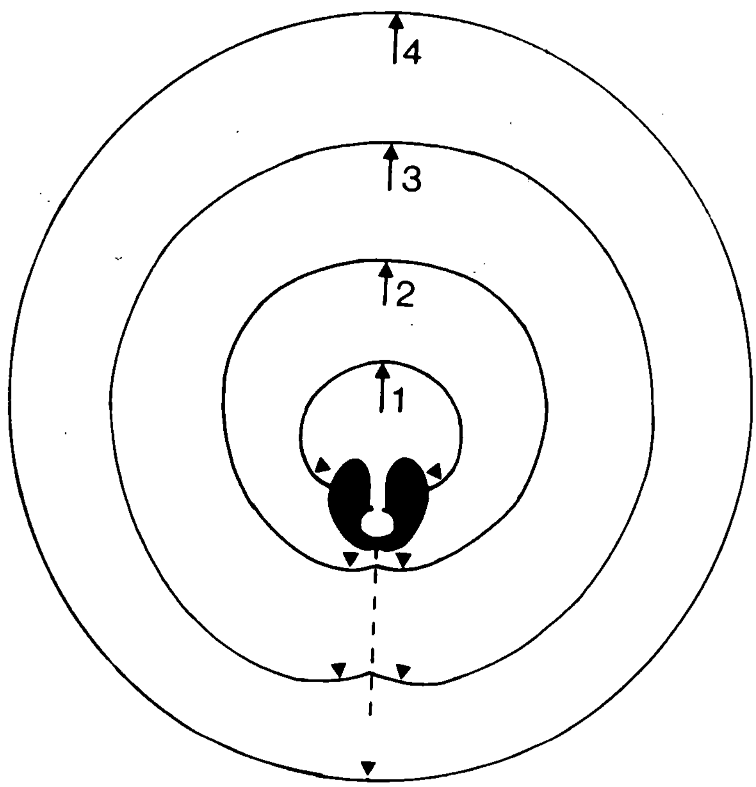

C

Figure 40. Stages in the growth of an idealized discoidal bereniciform tubuloporinid. Arrows indicate the direction of growth and 4 growth stages are numbered. The colony is initially fan-shaped (growth stage 1) but the lateral edges of the fan anastomose proximal to the protoecium (circular) during later growth. The line of anastomosis is dashed.



4
3
2
1

Figure 41. Camera lucida drawings of zooecial lateral wall traces on the zoarial surfaces of bereniciform tubuloporinids. These traces are usually identical to the septal trace patterns formed on basal laminae by zooecial budding. Arrowheads indicate zooecial growth directions, scale bars are 1 mm long, and the black area within colony C is a region of vacant substrate. Colony A, PT 497-12b *Hyporosopora? dilatata*; Colony B, PT 497-50b, *Hyporosopora? dilatata*; Colony C, PT C53 indeterminate discoidal bereniciform tubuloporinid; Colony D, BMNH D47331 *Hyporosopora? sp.*

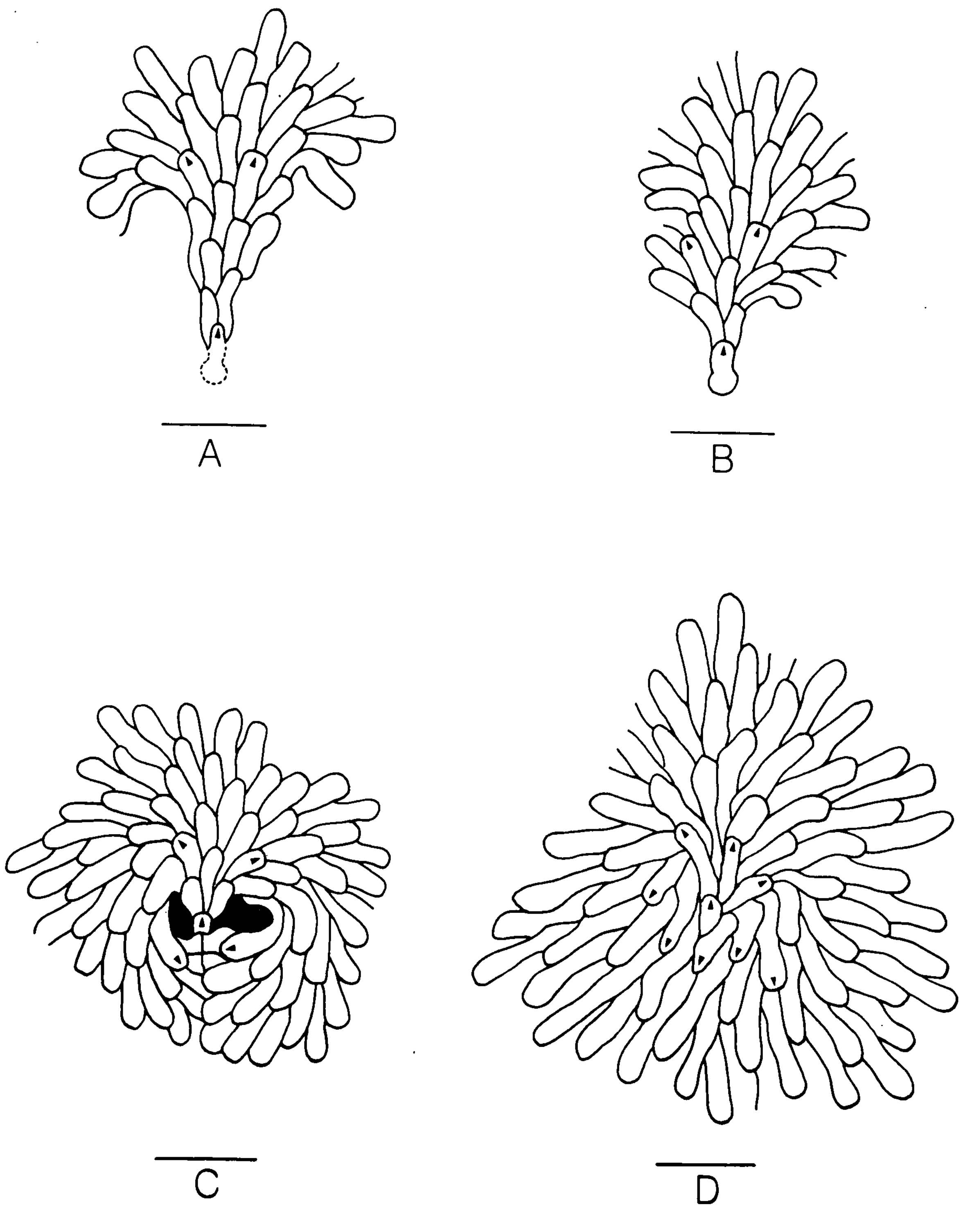

A
B
C
D

Figure 42. The septal trace pattern in the early parts of a theoretical tubuloporinid colony in which zooecia are budded by simple cycles of interzooecial wall division. The generation number of each zooecium is indicated and the protoecium is labelled 'P'. After Borg 1926, fig.36.

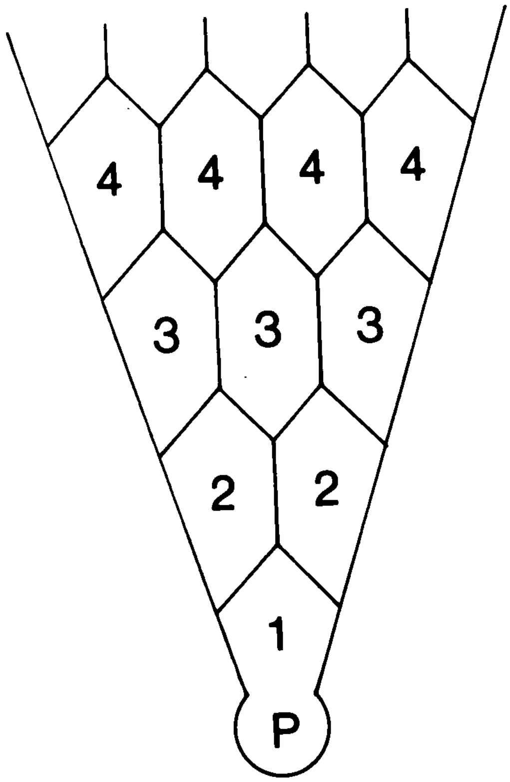
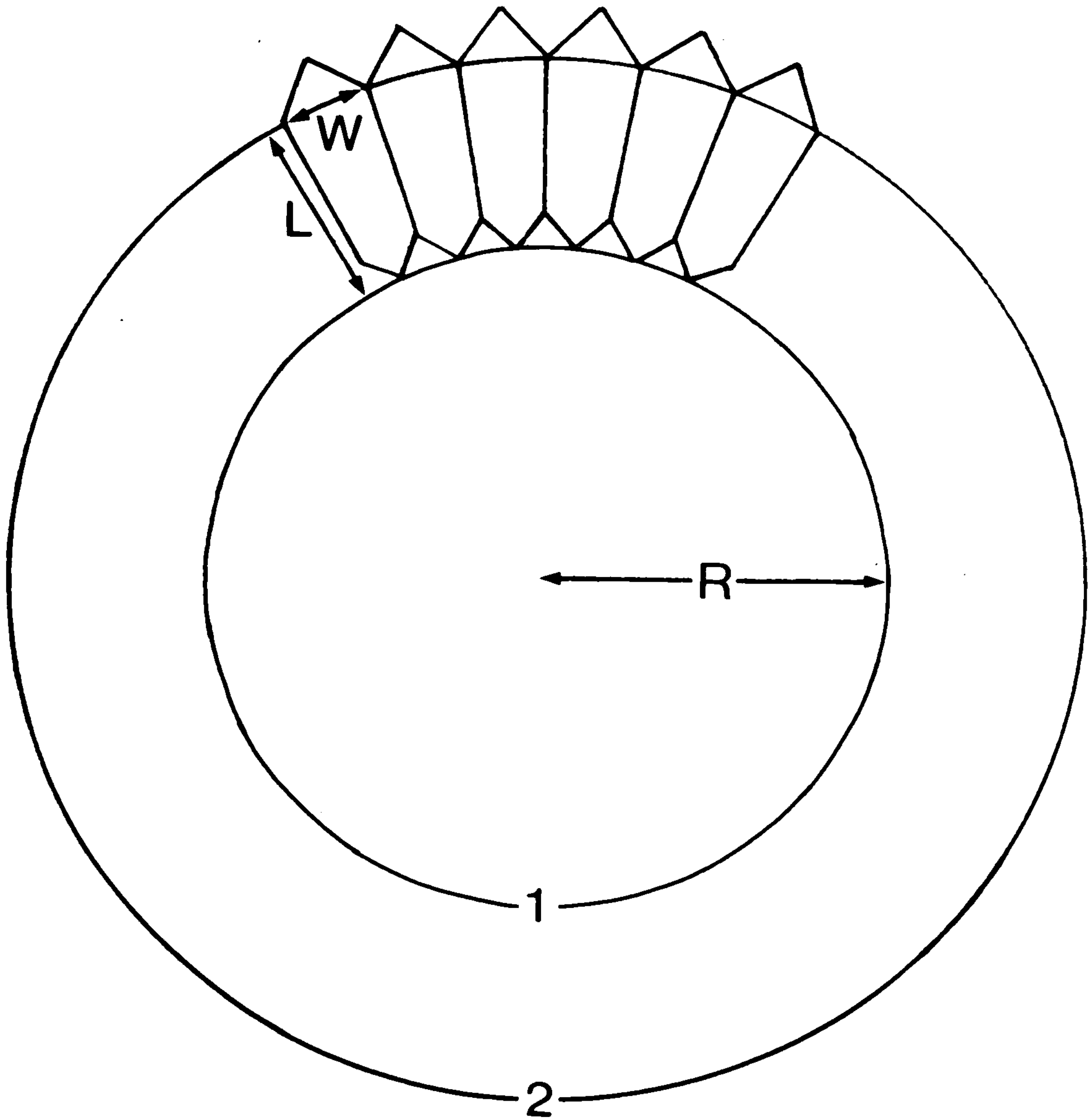

4
4
4
4
3
3
3
2
2
1
P

Figure 43. Model of a discoidal bereniciform colony to show the zooecial budding requirements if a circular colony shape is to be maintained during growth. Full explanation in the text. R, radius of colony at growth stage 1; C_1, circumference of colony at growth stage 1; C_2, circumference of colony at growth stage 2; L, zooecial length (slightly less than measured frontal wall length); W, zooecial width (approximates to frontal wall width if colony radius is large); N_2, number of additional zooecia required per generation of zooecia budded.



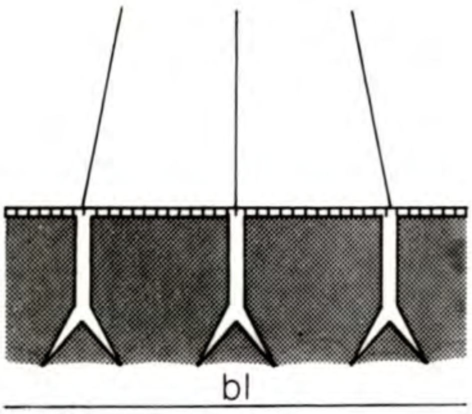
$$C_1 = 2\pi R$$

$$C_2 = 2\pi(R+L)$$

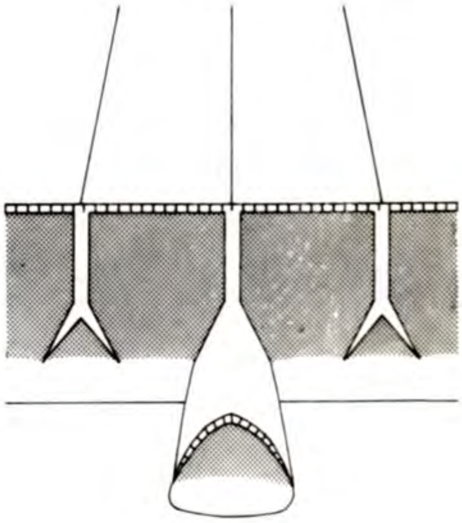
$$C_1 - C_2 = 2\pi L$$

$$Nz = \frac{2\pi L}{W}$$

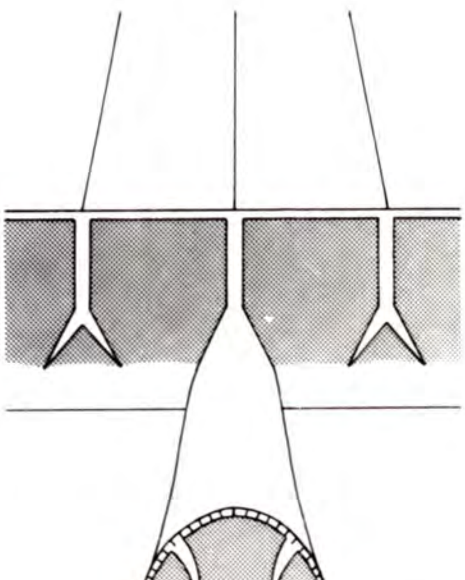
Figure 44. Diagram showing three growth stages (1-3) in the formation of a peripheral subcolony. A portion of colony growth margin is viewed obliquely from above. Zooecial chambers are stippled; the edges of zooecial frontal walls are hatched; bl, distal fringe of the basal lamina.



1



2



3

Figure 45. Idealized septal trace pattern in a bereniciform zoarium with zig-zag zooecia (based on observations of an undescribed species of Serpentipora). Zooecia are partitioned off by the formation of transverse septa (ts) resembling hemiphragms (h). Intercalation of new longitudinal zooecial rows is achieved by the division of a septum (ds). A single zooecium is stippled. Colony growth direction is indicated by the arrow.

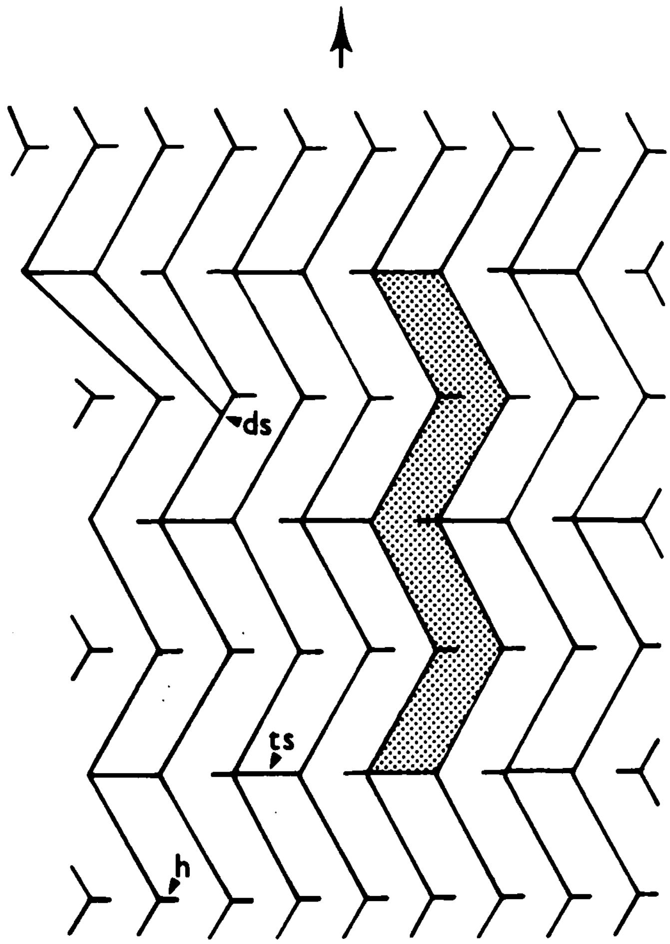
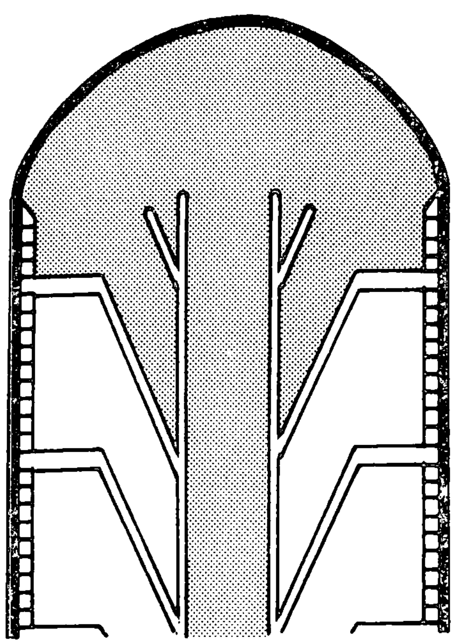
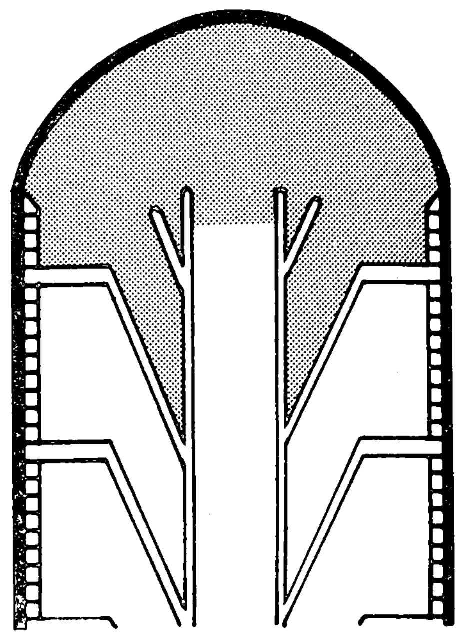

ds
ts
h

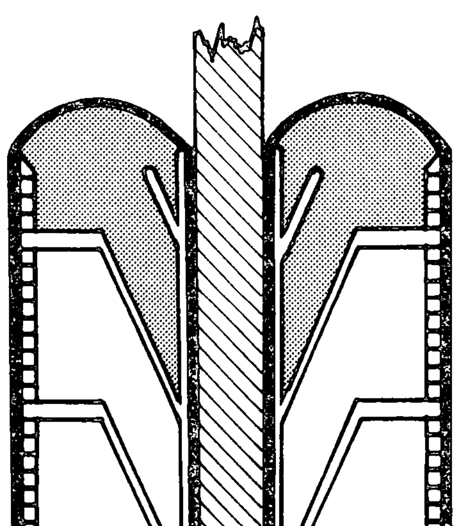
Figure 46. Diagrammatic longitudinal sections of the distal growth tip in <u>Entalophora annulosa</u> to show four possible interpretations of soft tissue disposition during life. Cuticle is shown as a thick black line and zooecial frontal walls are indicated by horizontal hatching. Hypostegal coelom of the common bud is stippled. An axial lumen (labelled 'al' in branch D) is present in all branches but is occupied by a substrate (cross-hatched) in branch C.



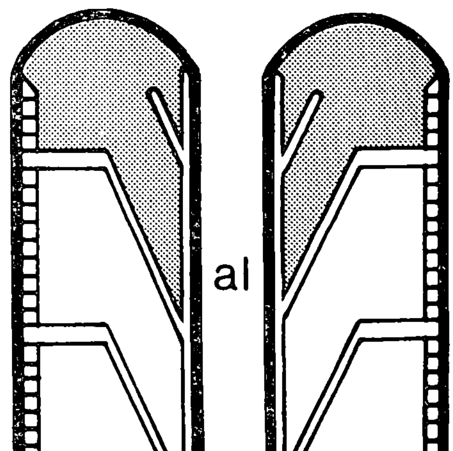
A



B



C



D

Figure 47. Diagram illustrating two modes of frond division occurring in diastoporidiform zoaria. Transverse zoarial sections show three growth stages (1 to 3) in each mode of division. In mode A, the medial budding lamina divides completely and the division is accomplished within the plane of the lamina. In mode B, the budding lamina divides partially to form a Y-shaped fork.

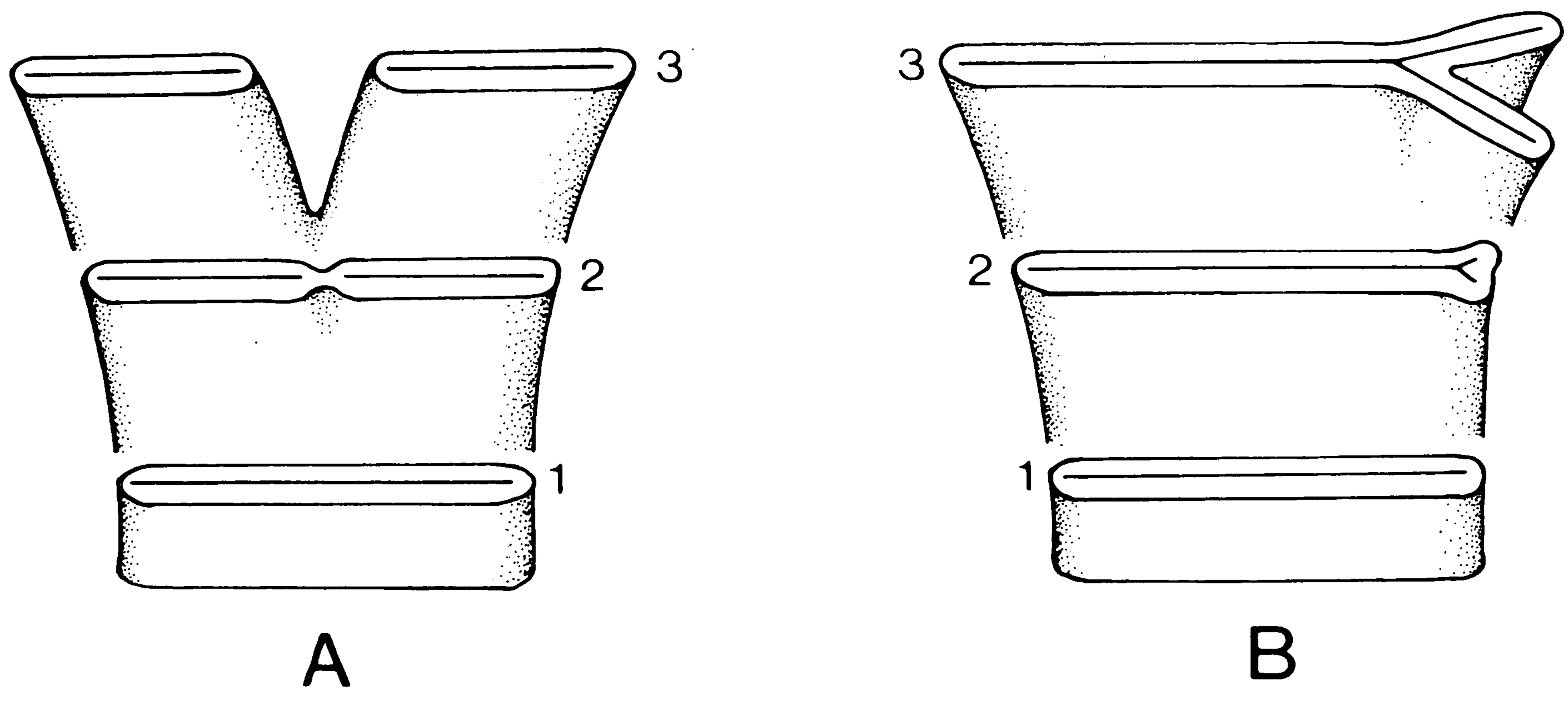

3
2
1
A
3
2
1
B

Figure 48. Reticuliporiform frond. Arrows indicate growth direction and an earlier growth stage is arrowed and labelled '1'. The growth margin (gm) is evenly stippled and reveals a division (d) of the median budding lamina. The basal surface of the zoarium is labelled 'bs'.

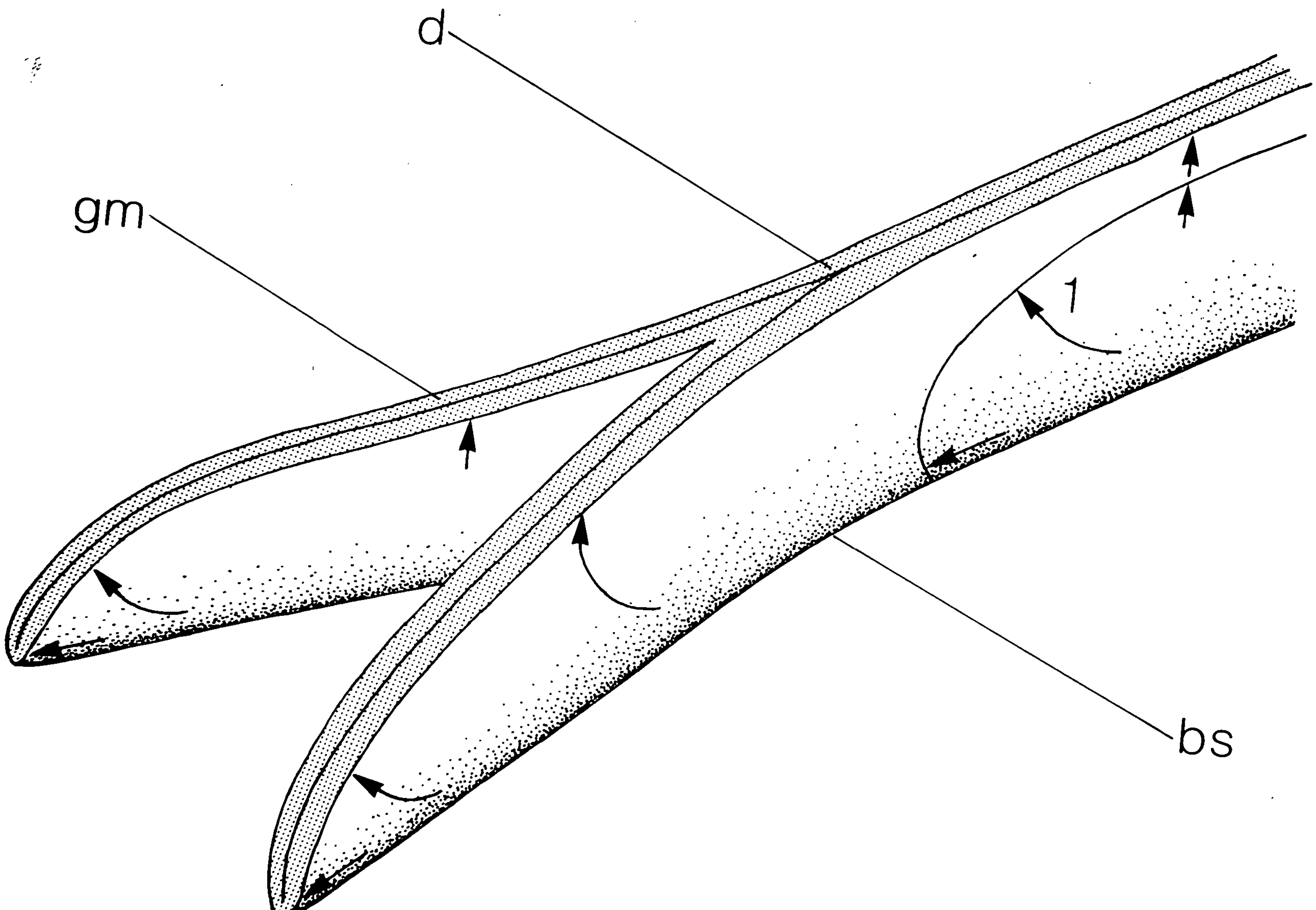

d
gm
1
bs

Figure 49. Diagram showing the symmetrical dichotomy of a reticuliporiform zoarial frond. Two growth stages (1 and 2) are labelled on the middle diagram which is an external lateral view of a frond. The series of transverse sections (A to E) and the longitudinal section were cut from the positions indicated on the external view. Both the longitudinal and the transverse sections reveal the medial budding lamina. The growth margin at the two stages of growth is indicated by a dotted line.

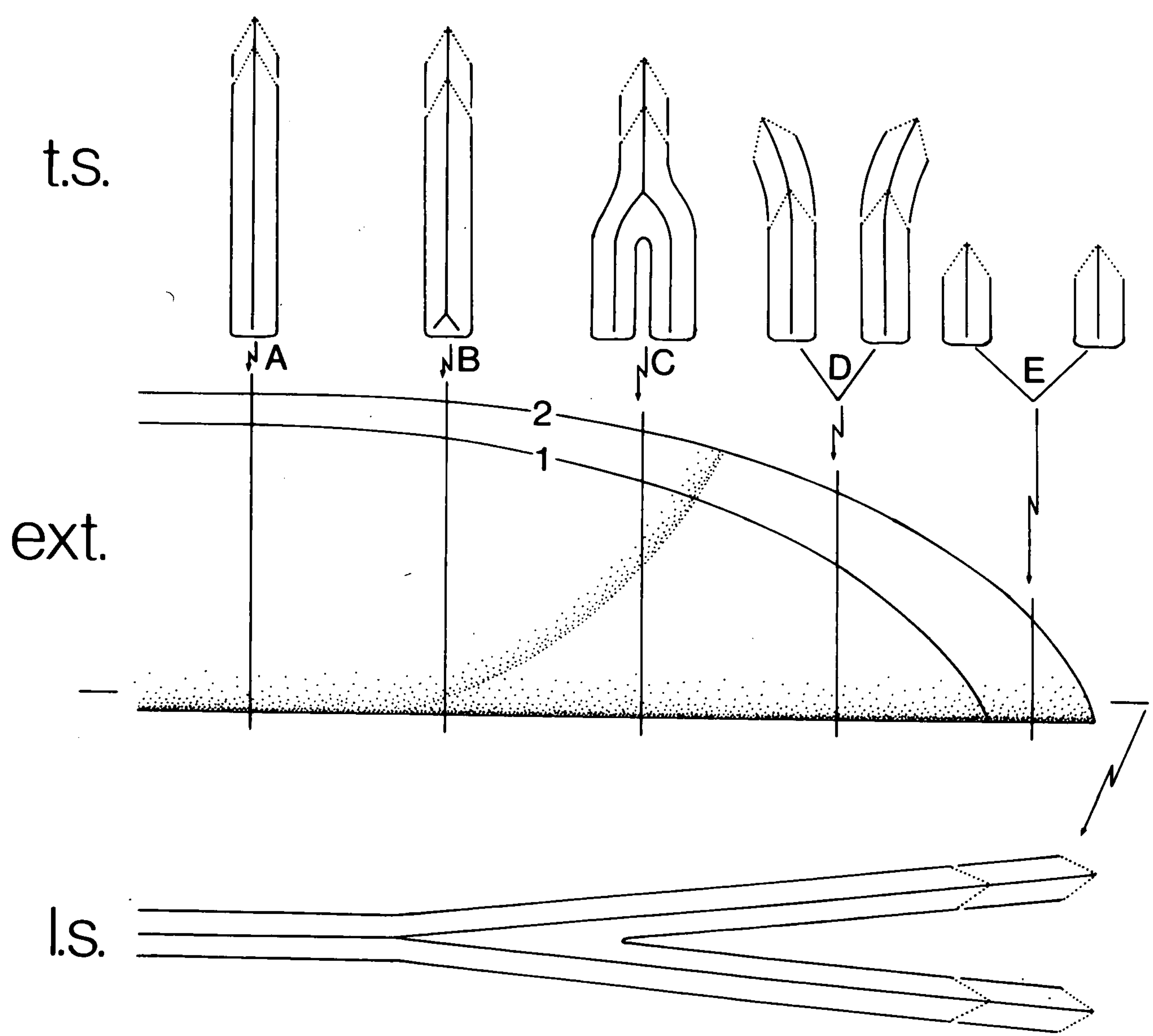

t.s.
A
B
C
D
E
2
1
ext.
l.s.

Figure 50. Diagram showing the asymmetrical division of a reticuliporiform zoarial frond. Transverse sections (A to D) are taken at the positions indicated on the external view.

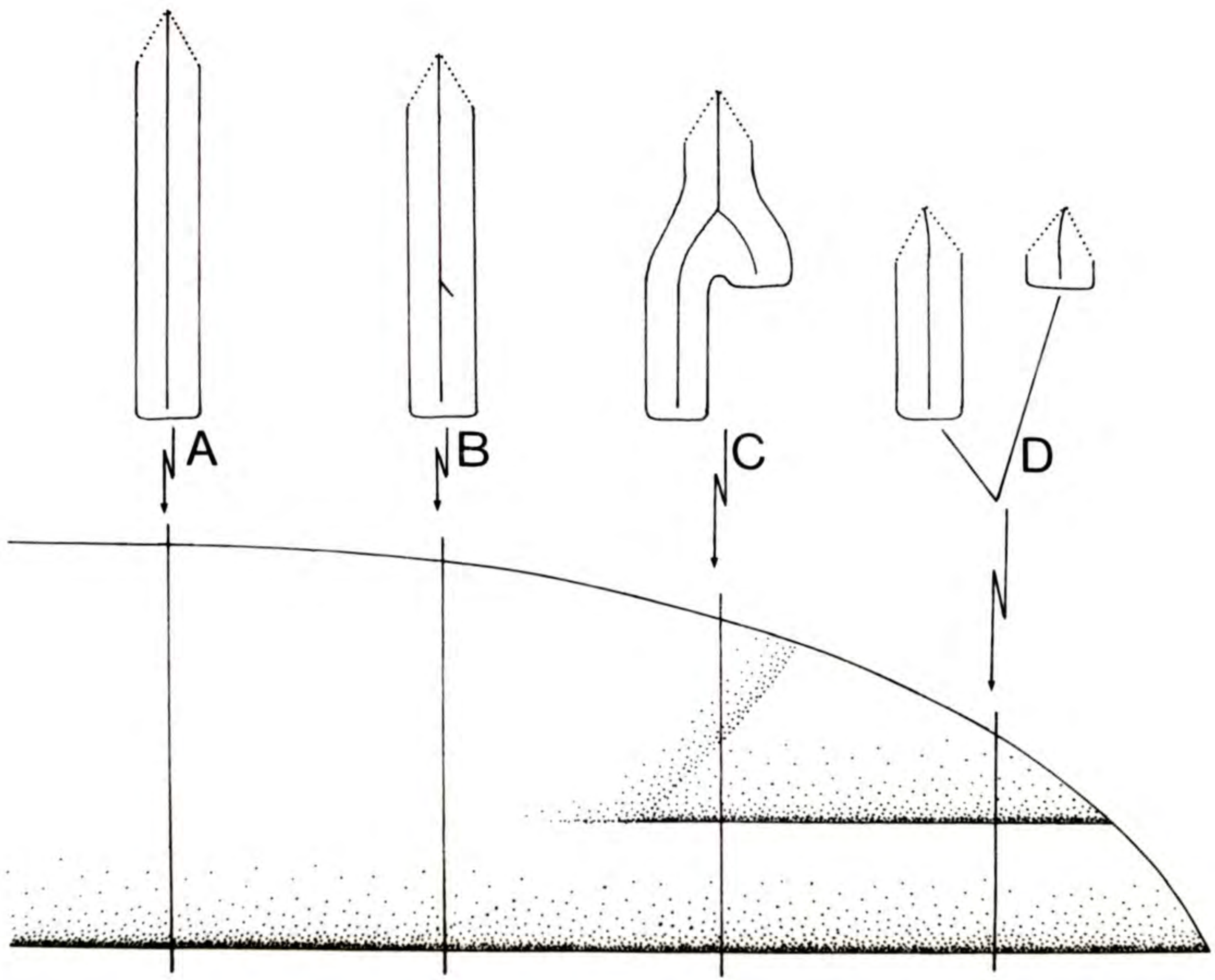
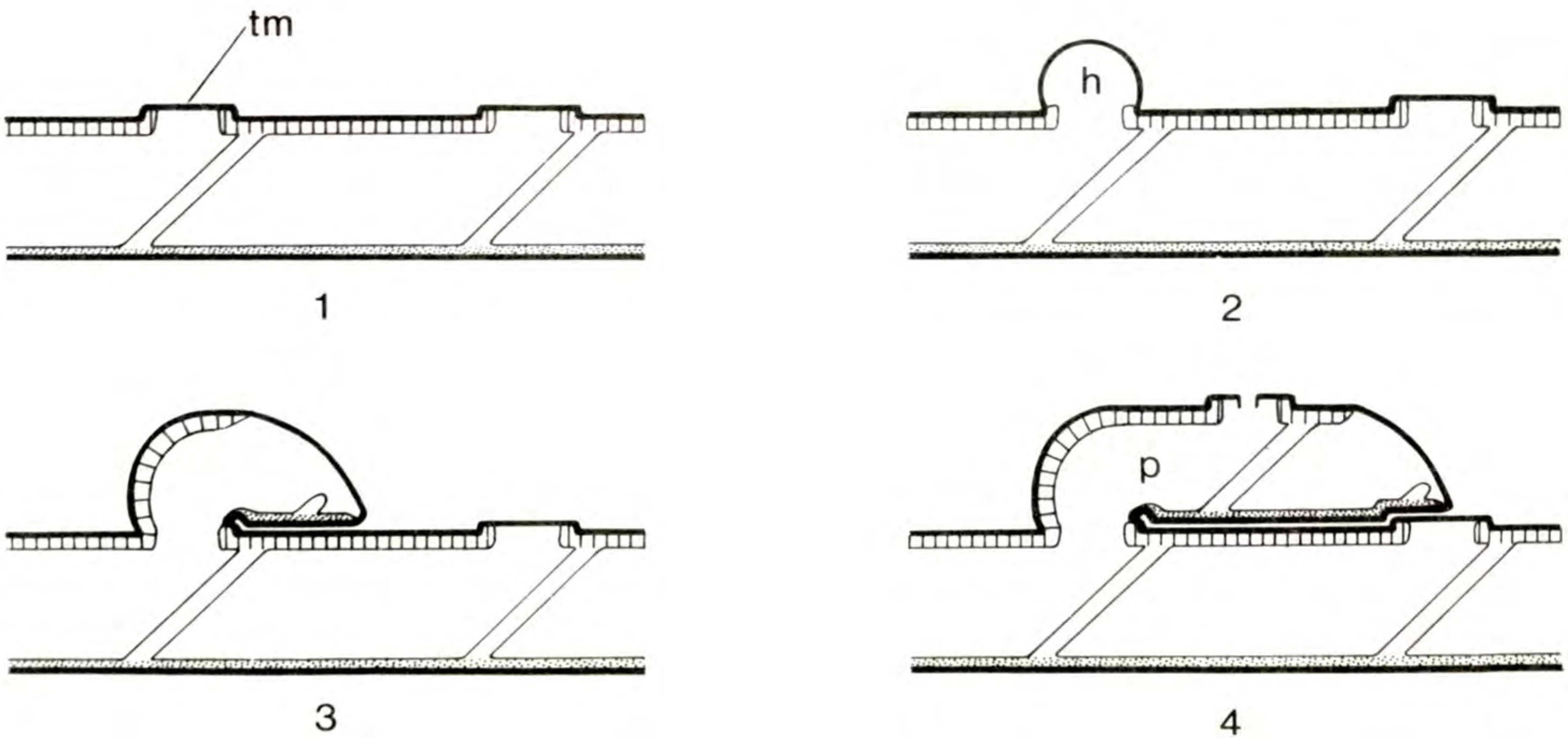

A
B
C
D

Figure 51. Longitudinal sections showing inferred growth stages in the formation of a fan-shaped frontally-budded subcolony. Basal lamina is stippled, zooecial frontal walls are indicated by vertical hatching, inter-zooecial walls are unshaded, and cuticle is shown in black. The terminal membrane (tm) covering the skeletal aperture of a zooid inflates to form a balloon-like expansion (growth stage 2) enclosing a rudimentary hypostegal coelom (h). The expansion increases in size and begins to secrete calcareous skeleton and overgrow established zooids (growth stage 3). The first complete zooid (growth stage 4) within the frontally-budded subcolony is known as the pseudoancestrula (p).



1 2 3 4

Figure 52. Growth pattern of a portion of an idealized Alveolaria colony depicted in longitudinal zoarial section. The six growth stages (A to F) correspond to those shown in figure 53 . Apparent exterior body walls bounding subcolonies are indicated with solid lines; zoarial frontal surfaces covered by hypostegal coelom during life are dotted. Gaps between exterior walls separating adjacent subcolonies are greatly exaggeraged. Growth stage F shows a complete cycle of growth comprising a tabular stage (ts) and an erect stage (es).

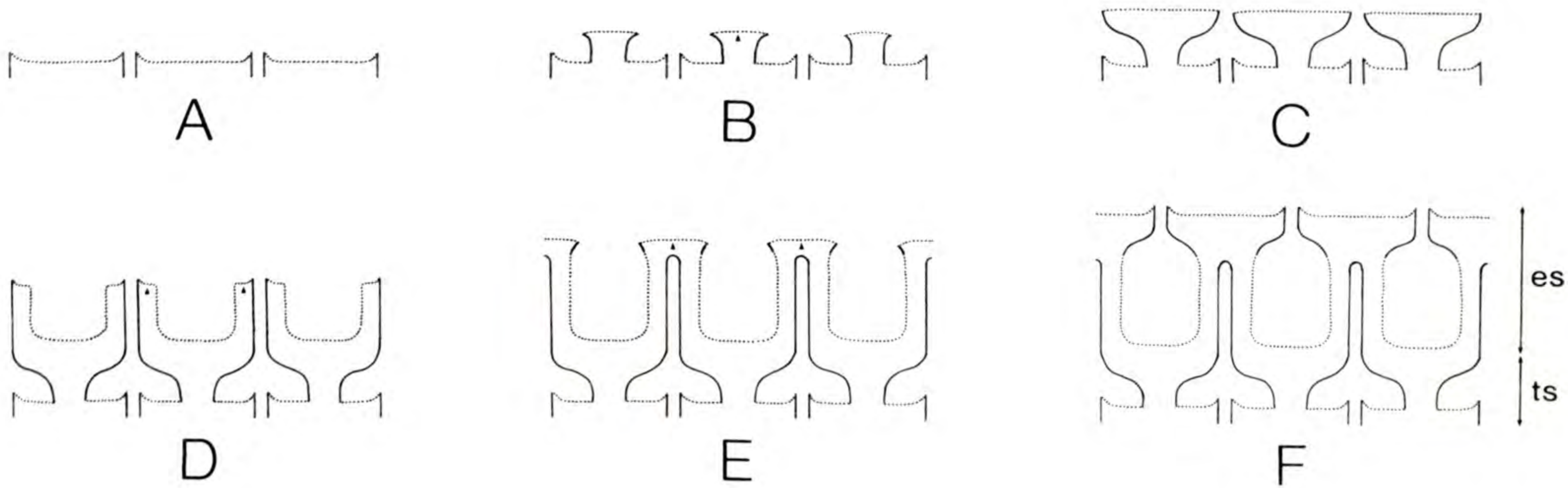
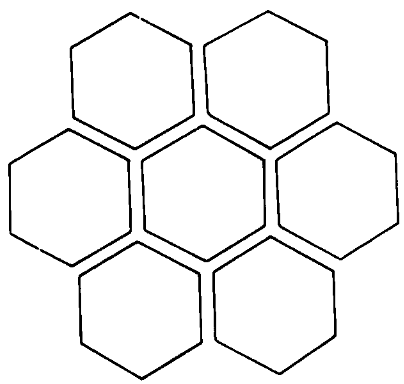
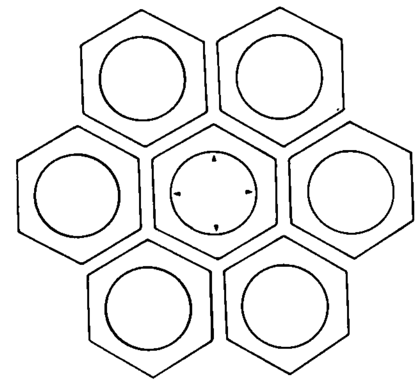
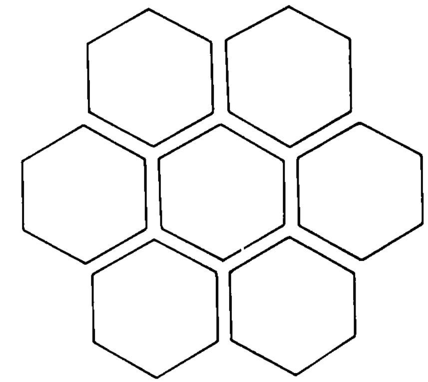
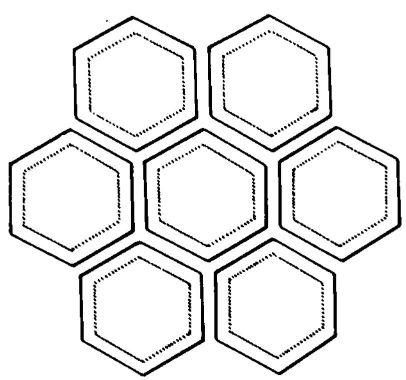

A
B
C
D
E
F
es
ts

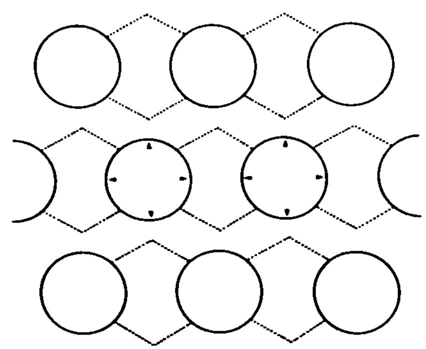
Figure 53. Growth pattern of a portion of an idealized <u>Alveolaria</u> colony. Views of the colony surface are depicted in 6 growth stages (A to F). Apparent exterior body walls bounding subcolonies are indicated with solid lines; zoarial frontal surfaces covered by hypostegal coelom during life are dotted. Outlines of growing subcolonies are either circular (stages B and E) or, when adjacent subcolonies are juxtaposed, hexagonal (stages A, C, D and F). The very slight gap which is between the apparent exterior walls of juxtaposed subcolonies is greatly exaggerated in this figure.


A


B


C


D


E

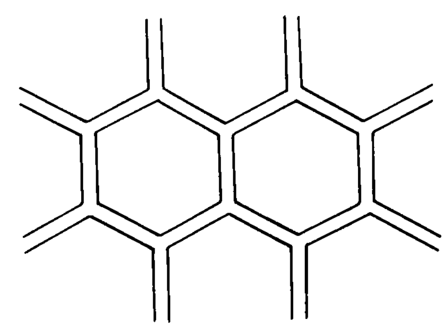
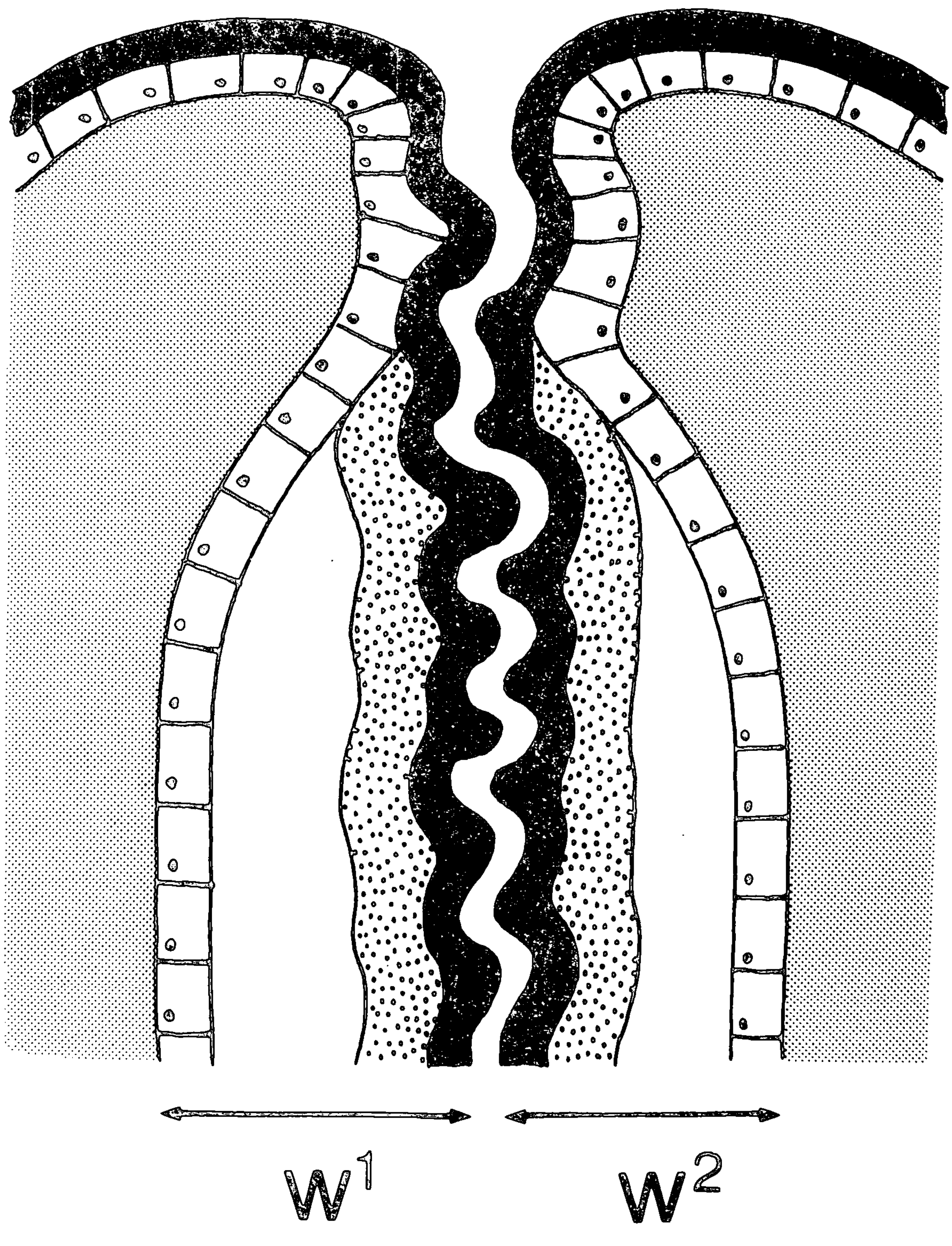
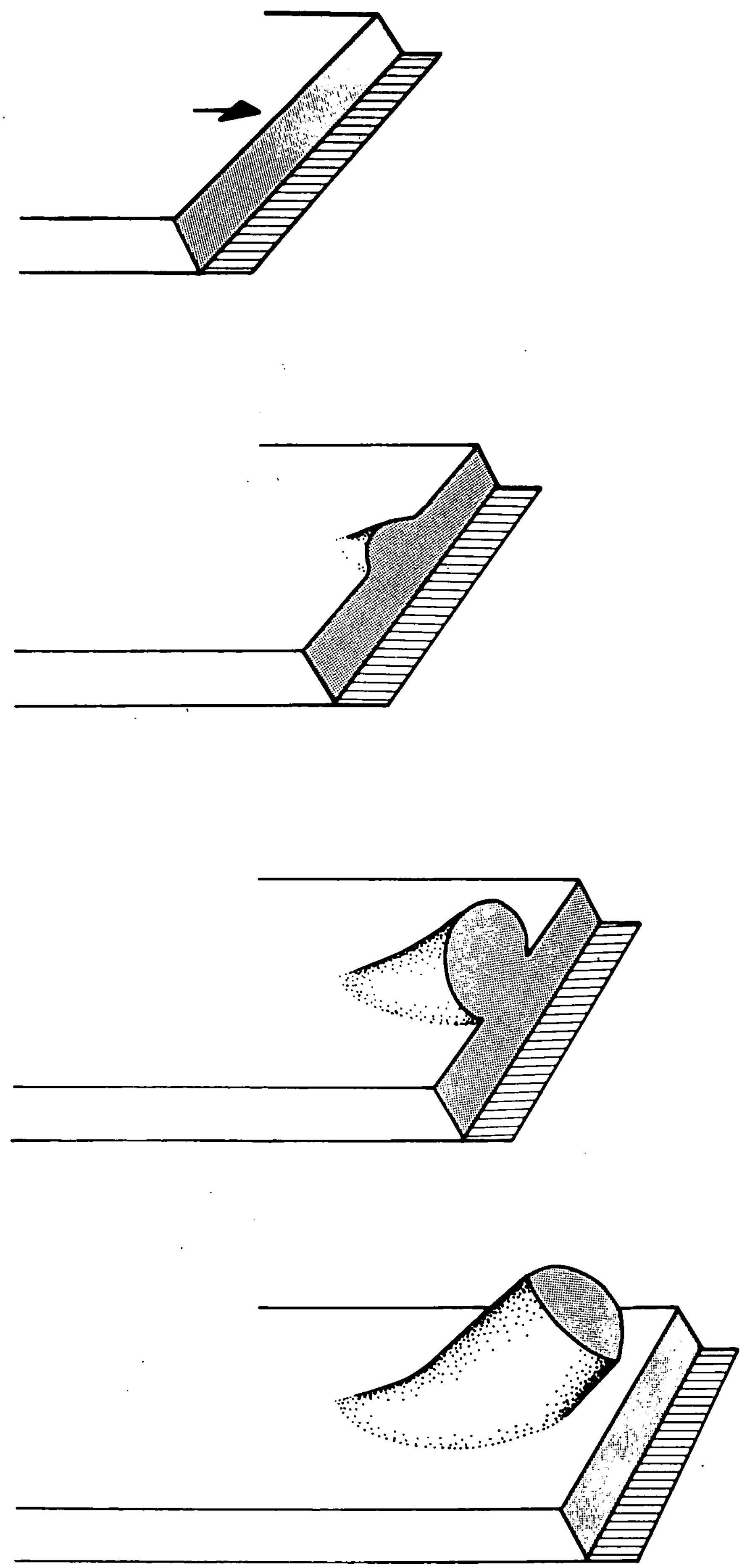

F

Figure 54. Reconstruction of inferred cuticle and secretory epithelium disposition at the growing edges of juxtaposed bounding walls of adjacent subcolonies in Alveolaria. The inferred exterior body walls (W^1 and W^2) bounding each subcolony consist of a cuticle (black), a primary skeletal layer (coarse stipple), a secondary skeletal layer (unshaded), and an epithelial layer (shown as rectangular cells with nuclei). Cuticles of juxtaposed walls interdigitate. Hypostegal coelom is shown by fine stippling. Compare with the growing edge of the unilamellar adnate colony depicted in figure 2 .



W^1
W^2

Figure 55. Diagram depicting 4 growth stages (A-D) in the formation of an erect vinculariiform branch at the growth margin of the adnate unilamellar base of a *Collapora microstoma* colony. Fine stippling indicates common bud (growth margin and growth tip); the distal fringe of the basal lamina is shown by horizontal hatching.



A

B

C

D

Figure 56. Diagrammatic transverse section through a vinculariiform branch of '_Mecynoecia_' _bajocina_. Zooecia are arranged in 10 radial rows, one of which is indicated by stippling. Zooecial budding occurs around a central zoarial axis and zooecia begin as triangular buds (1), acquire a pentagonal shape (2), and finally a hexagonal form (3) before opening at the zoarial surface (4 and 5).

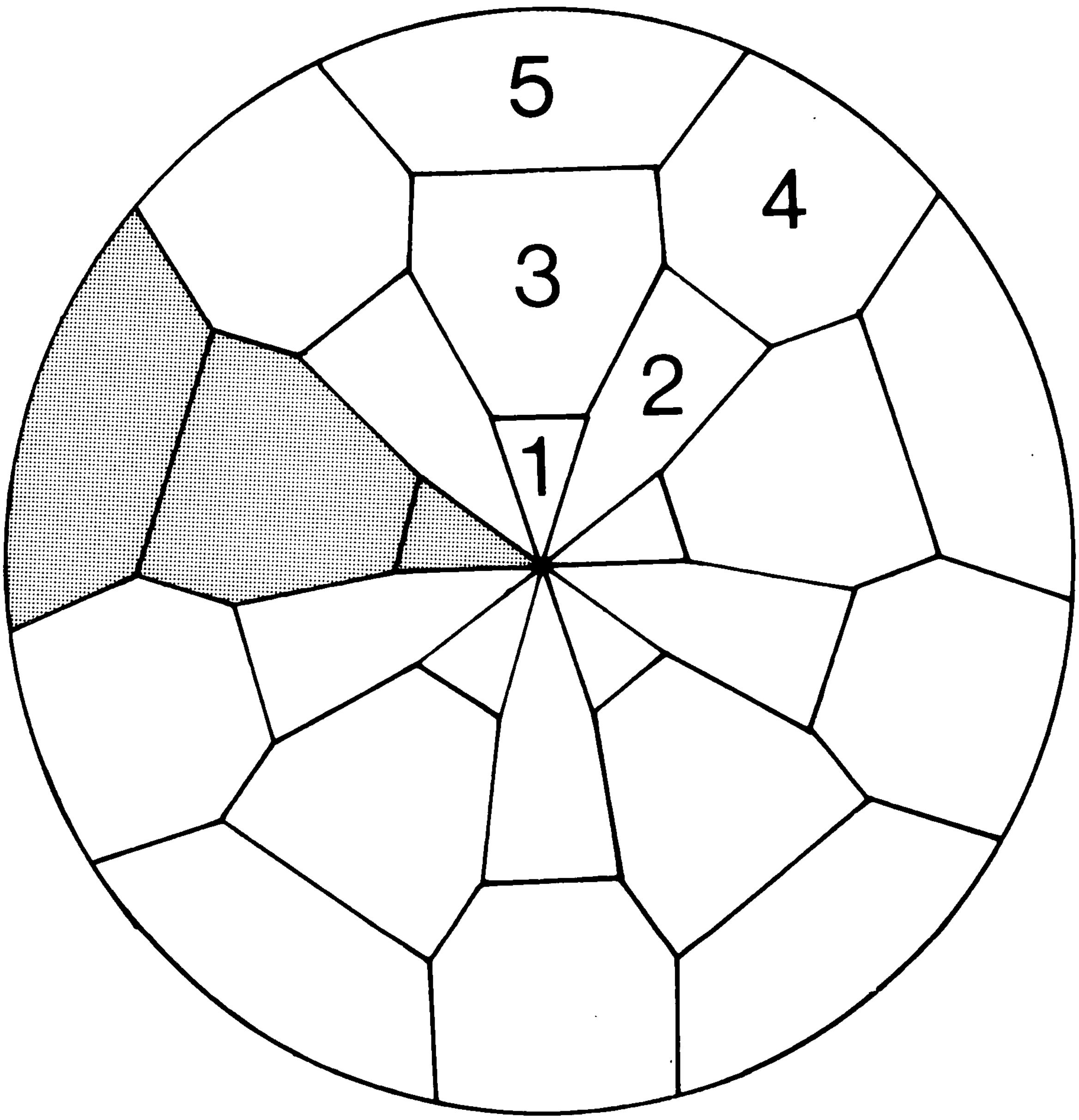

5
4
3
2
1

Figure 57. Simplified external aspects of a helico-spiral branch of _Terebellaria_ from which the basal parts have been omitted. A, lateral aspect; B, branch viewed from above looking down upon the growth tip with proximal whorls of the growth margin obscured by projecting ledges of zooecia. Stipple indicates the common bud (growth margin and growth tip). Arrows indicate directions of colony growth inferred from zooecial orientation.

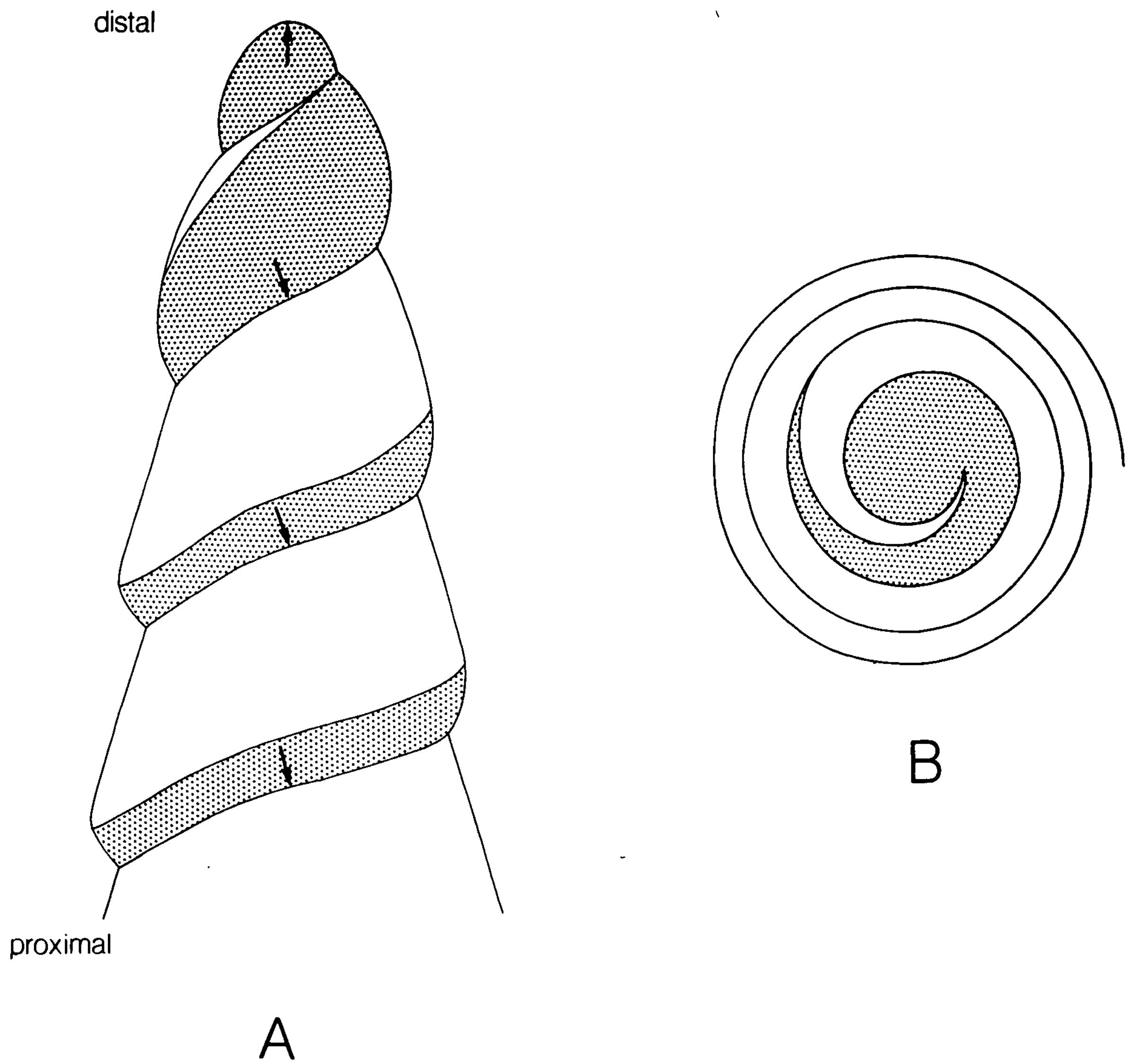
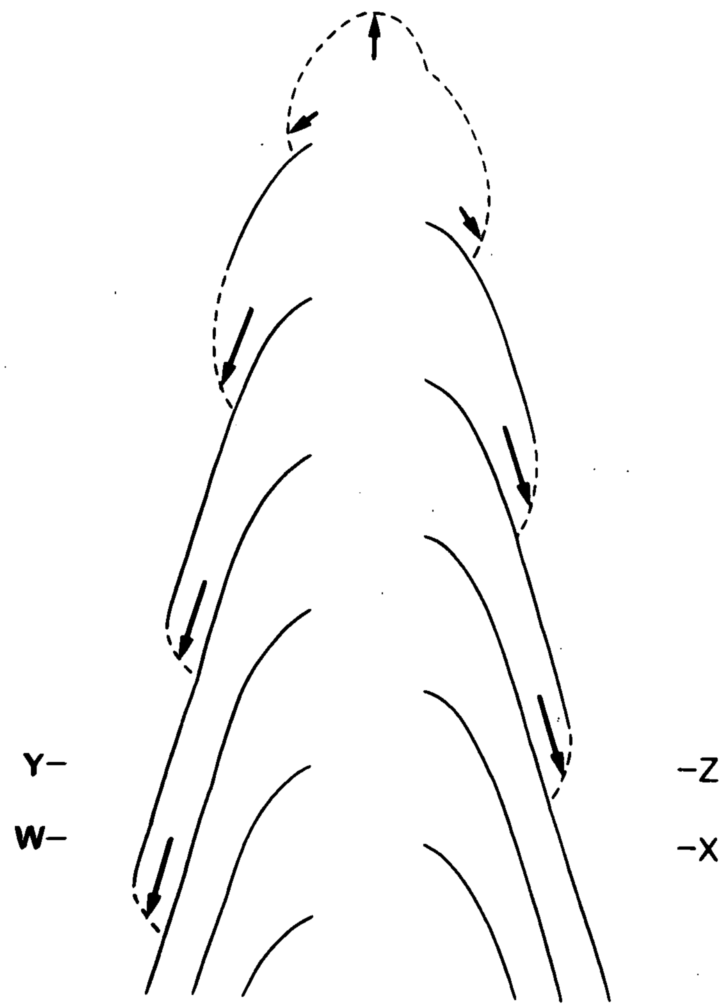
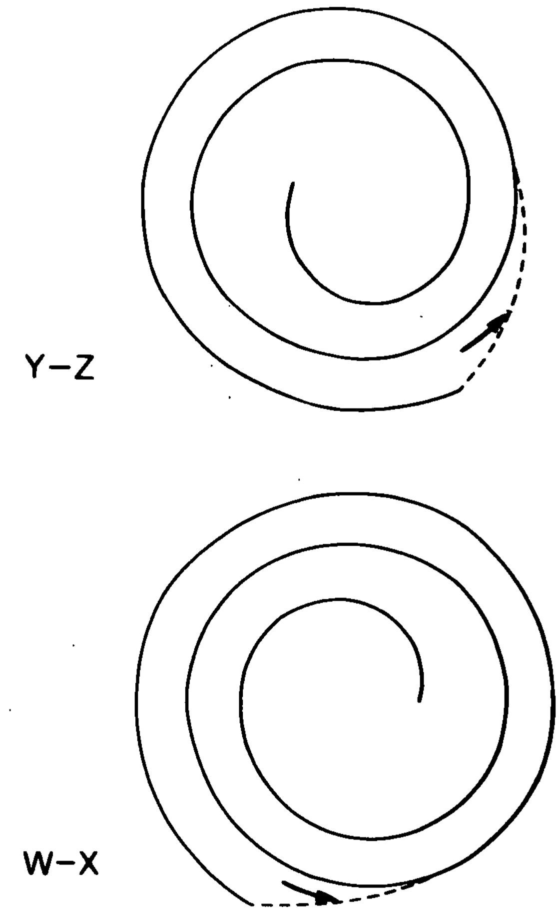

distal
proximal
A
B

Figure 58. Zoarial sections taken from the helico-spiral *Terebellaria* branch shown in figure 57 . A, longitudinal zoarial section; B, transverse zoarial sections cut at the two levels indicated on the longitudinal section. Common bud is represented by broken lines. Solid lines represent zooecial frontal walls. The axial region in the longitudinal section devoid of zooecial frontal walls is the endozone. The origin of the spiral formed by zooecial frontal walls in the transverse sections occurs on the periphery of the axial endozone.

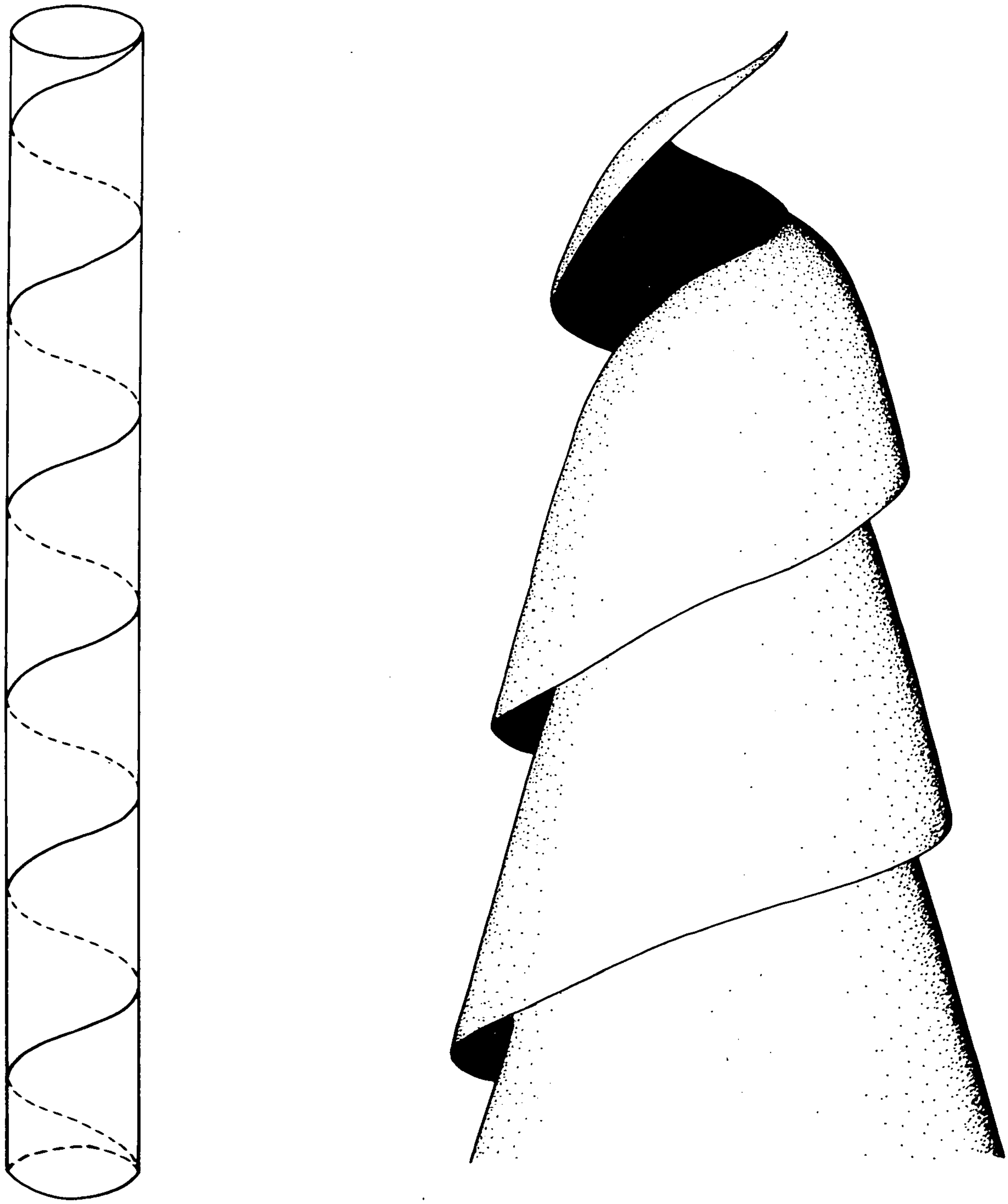


A



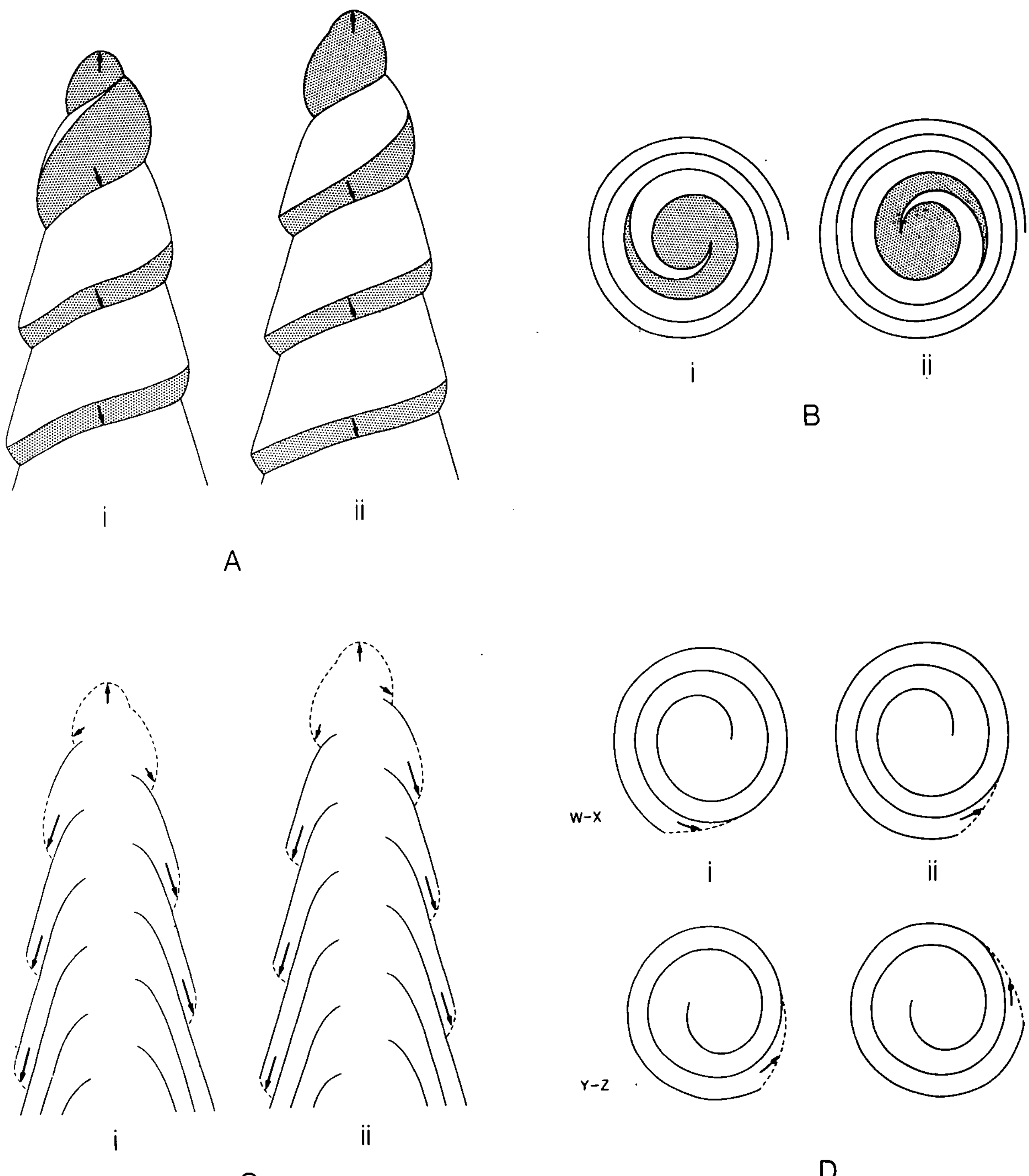
B

Figure 59. Three-dimensional aspects of the helico-spiral Terebellaria branch shown in figures 57 and 58 . A, the helical exozonal trace (indicated by a solid line when on the near side and dashed when on the reverse side of the cylindrical endozone) which represents the line along which axial walls of omega endozonal zooecia met the periphery of the endozone and gave rise to the exozonal budding lamina. B, surface formed of zooecial frontal walls over which the exozonal budding lamina subsequently extends; its inner edge is the helical exozonal trace, its outer edge occurs at the growth margin and extends towards the colony base during growth.



A B

Figure 60. Addition of an arbitrary increment of growth to the _Terebellaria_ branch illustrated in figures 57-59 . In all cases diagrams labelled 'i' are before growth, 'ii' after growth. A, external lateral aspects. B, external aspects viewed from above the growth tip. C, longitudinal zoarial sections. D, transverse zoarial sections.



i
ii
A
i
ii
B
i
ii
C
W-X
i
ii
Y-Z
D

Figure 61. Interpretation of growth at the transition between endozone and exozone in *Terebellaria*. Longitudinal half sections of three growth stages, 'i' - 'iii'. A detailed explanation of the sequence of events is given on p.230. Interzooecial walls and budding lamina, black; zooecial frontal walls, hatched; inner epithelium lining interzooecial walls, dashed line; outer epithelium, dotted line. The hypostegal coelom of the common bud (growth tip and growth margin) is enclosed between the inner and outer epithelia. Zooecial apertures have been omitted for simplicity.

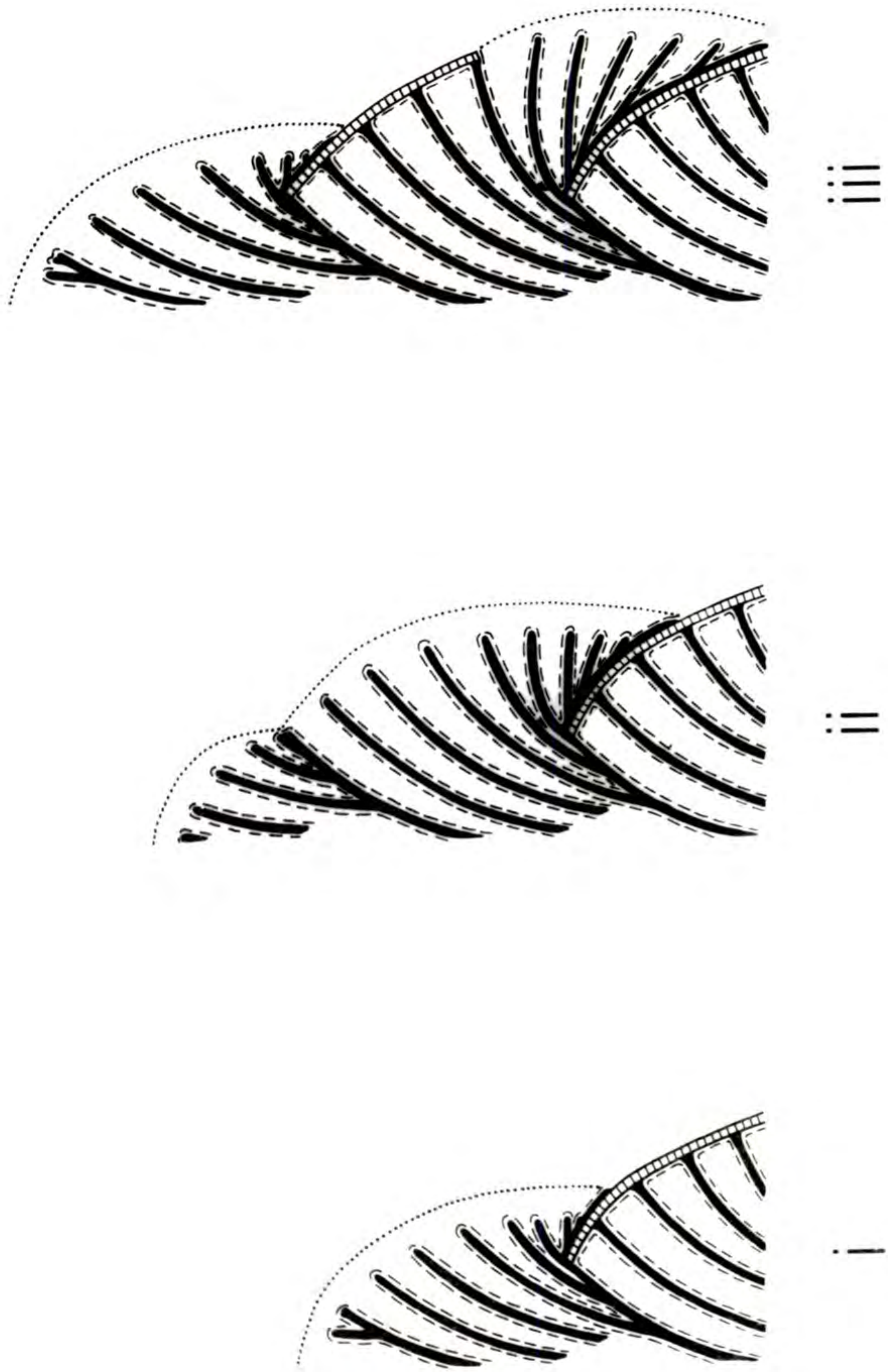
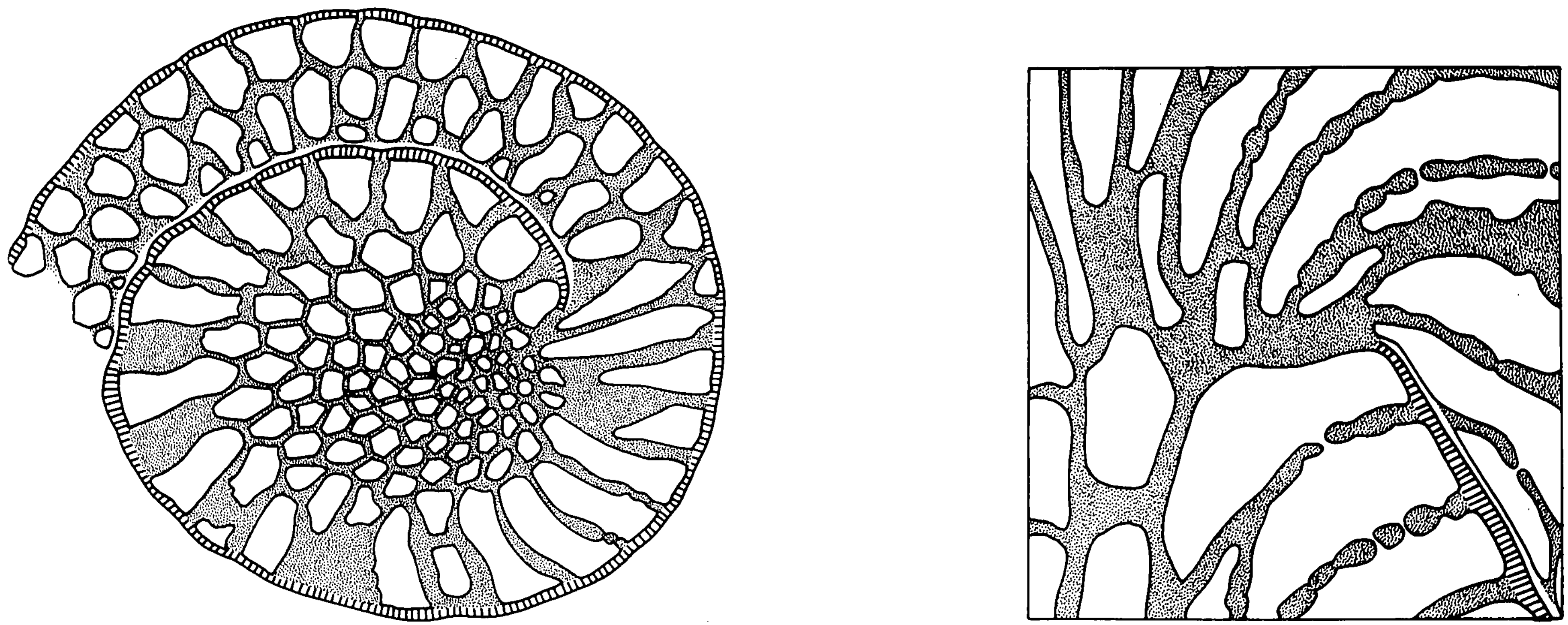


Figure 62. Camera lucida drawings to illustrate zooecial configuration in sections of helico-spiral branches of Terebellaria. Stipple, interzooecial walls; white, basal budding lamina; hatched, zooecial frontal walls.

A, part of a transverse zoarial section showing an axial endozone, lacking zooecial frontal walls, in which zooecia are sectioned approximately transversely. The endozonal budding locus is the region occupied by the smallest zooecia. Strongly reflexed zooecia near to the boundary between endozone and exozone are almost longitudinally sectioned. BMNH D2111g, 'Bathonian,Ranville'. X40

B, part of a longitudinal section at the transition between endozone and exozone. The axial interzooecial wall of an omega endozonal zooecium, slightly obliquely sectioned, gives rise to its own frontal wall (stippled) and the exozonal budding lamina which covers it. Endozonal budding has a locus above the axial wall of the omega zooecium. Interzooecial walls have pores and constrictions. BMNH D2111j, 'Bathonian, Ranville'. X80.



A

B

Figure 63. Camera lucida drawing showing part of the exterior of a Terebellaria zoarium in which horizontal division of the growth margin was occurring. A split in the growth margin was apparently extending from left to right. BMNH 11150d, 'Great Oolite ?locality'. X50.

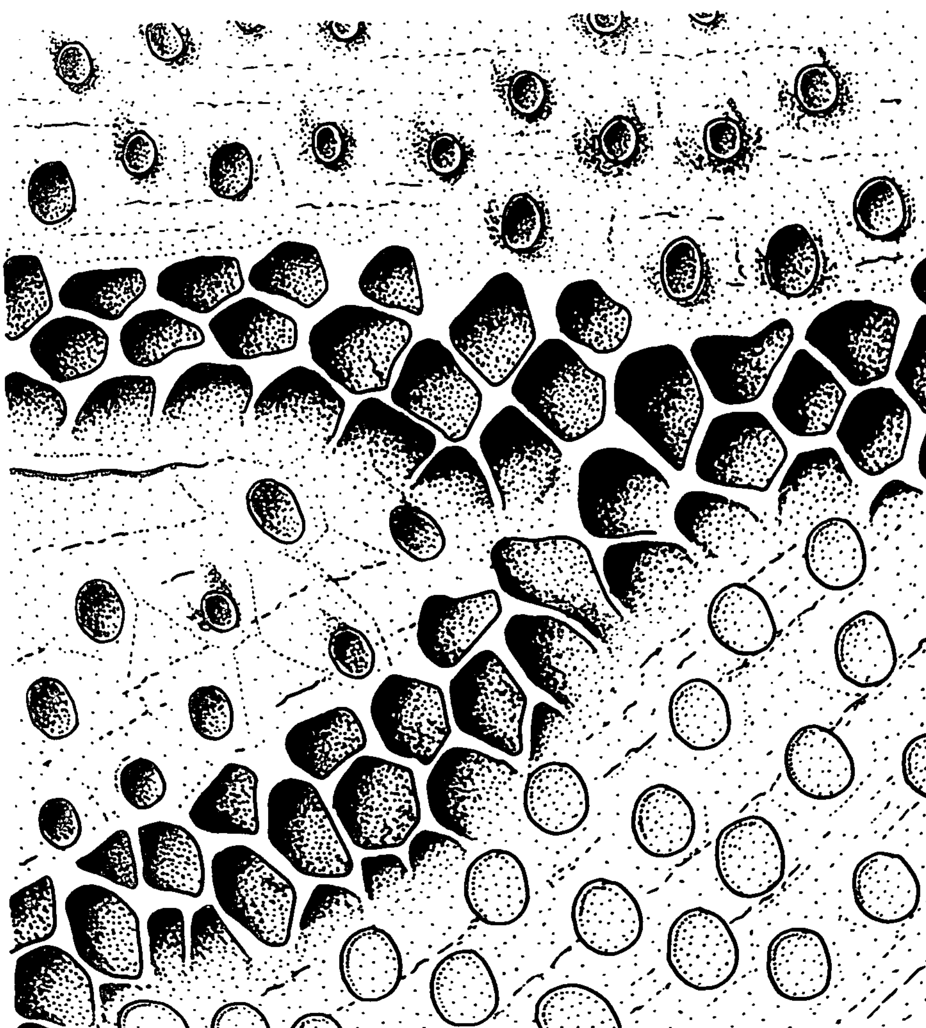


Figure 64. *Terebellaria* branch with an annular exozone. Legend as in figures 57-59.

A, external lateral aspect. Compare with figure 57A.

B, external aspect looking down upon the distal growth tip. Compare with figure 57B.

C, inclined annular exozonal traces occurring on the periphery of the cylindrical endozone. Compare with figure 59A.

D, longitudinal zoarial section. Compare with figure 58A.

E, transverse zoarial sections taken at the levels marked on the longitudinal section. Compare with figure 58B.

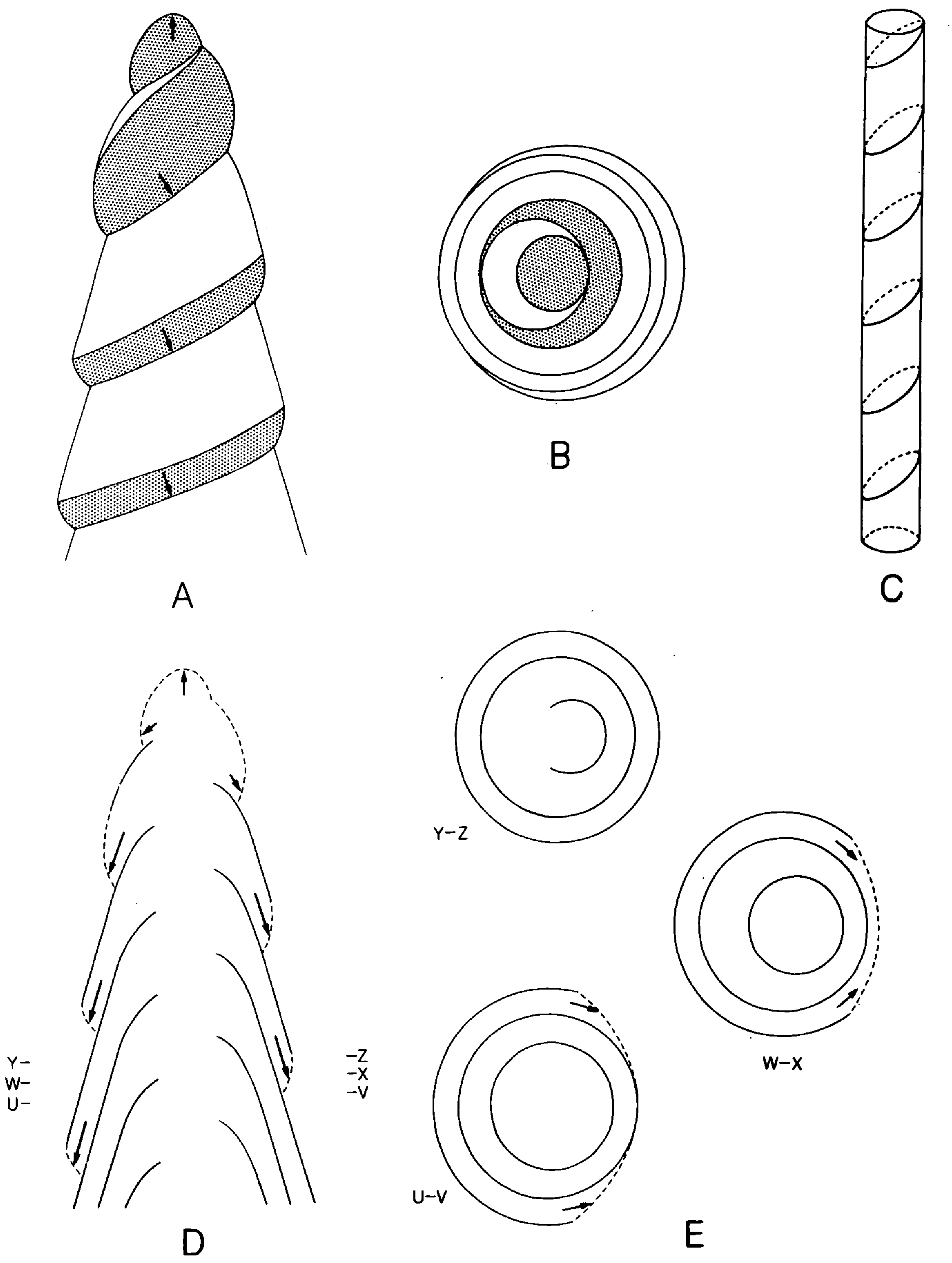

A
B
C
Y-
W-
U-
-Z
-X
-V
D
Y-Z
W-X
U-V
E

Figure 65. Diagrammatic transverse zoarial sections showing rotation of the budding locus (stippled) within the circular endozone during distal branch extension in _Terebellaria_. 5 growth stages, 'i' - 'v'.

A, clockwise rotation giving rise to a branch which is a dextral helicospiral externally.

B, division of the locus and rotation of the two consequent loci in opposite directions prior to their coalescence at the opposite side of the endozone. A new locus forms after an interval of time in which there is no endozonal budding locus. A branch with inclined annular growth margins is produced by this sequence of events.

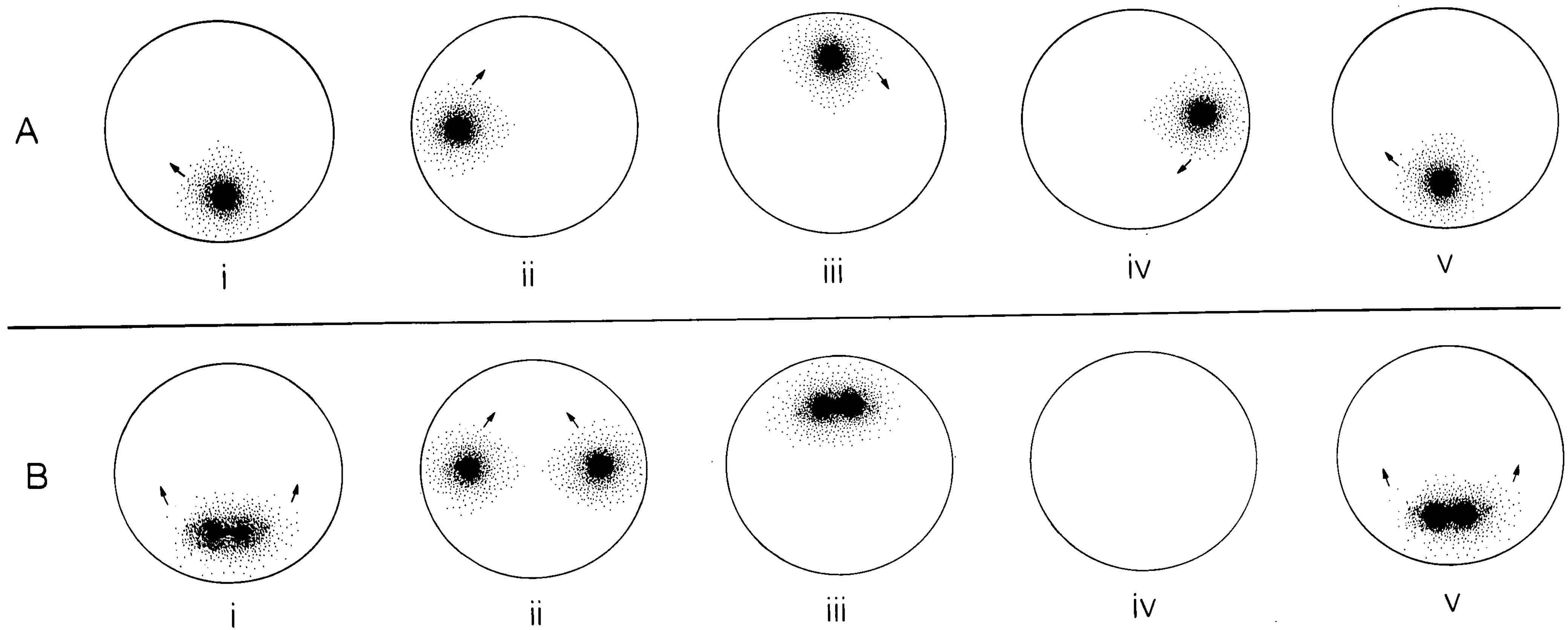

A
i
ii
iii
iv
v
B
i
ii
iii
iv
v

Figure 66. The 6 possible modifications of the exozonal trace consequent upon primary branching of <u>Terebellaria</u> zoaria. A, B and E have been positively identified in fossil zoaria. A, parent branch and both daughter branches have helical traces. B, parent branch and one daughter branch have helical traces, the second daughter branch has annular exozonal traces. C, parent branch has a helical trace, both daughter branches have inclined annular traces. D, parent branch and both daughter branches have annular traces. E, parent branch and one daughter branch have annular traces, the second daughter branch has a helical trace. F, parent branch has an annular trace, both daughter branches have helical traces.

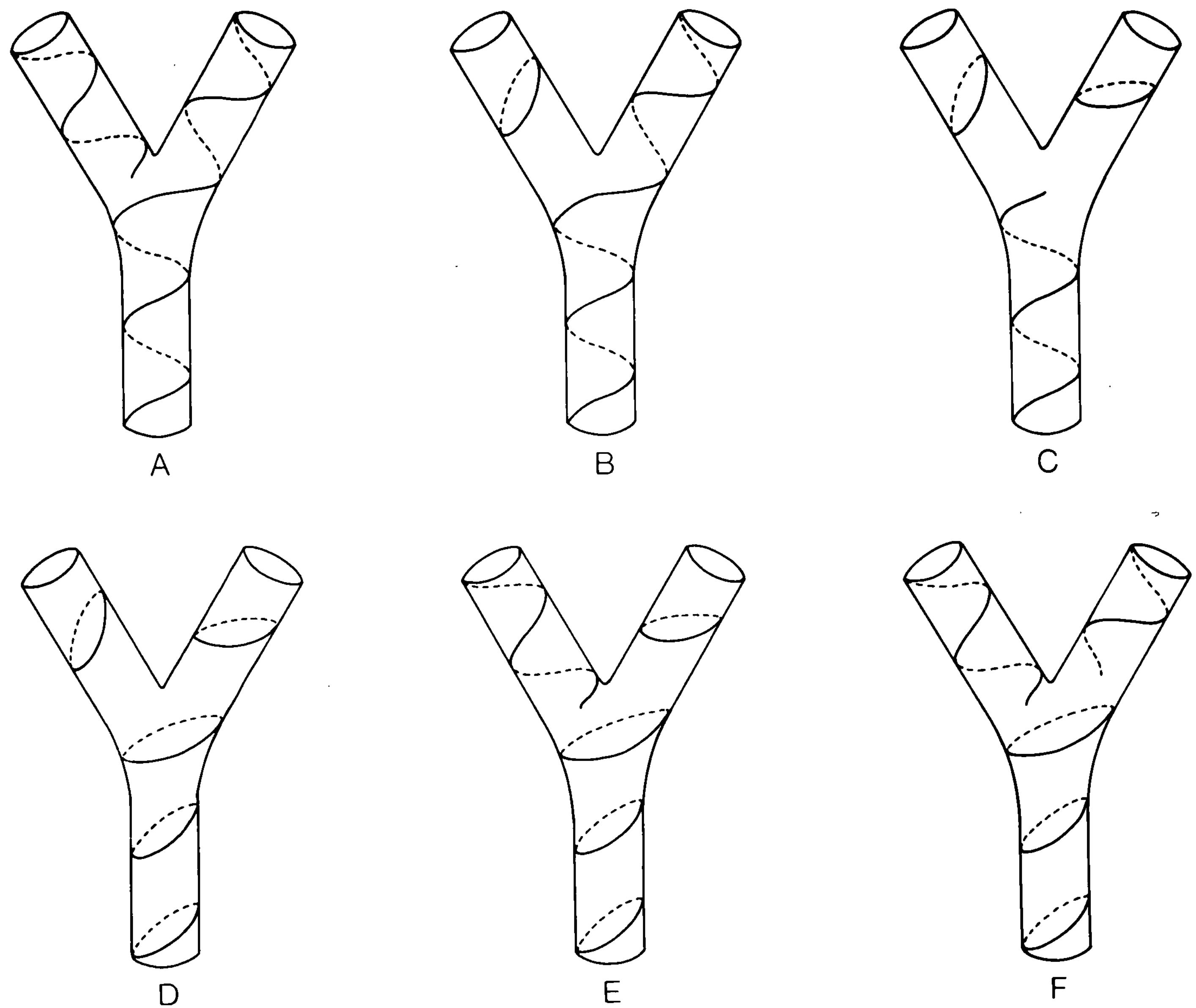
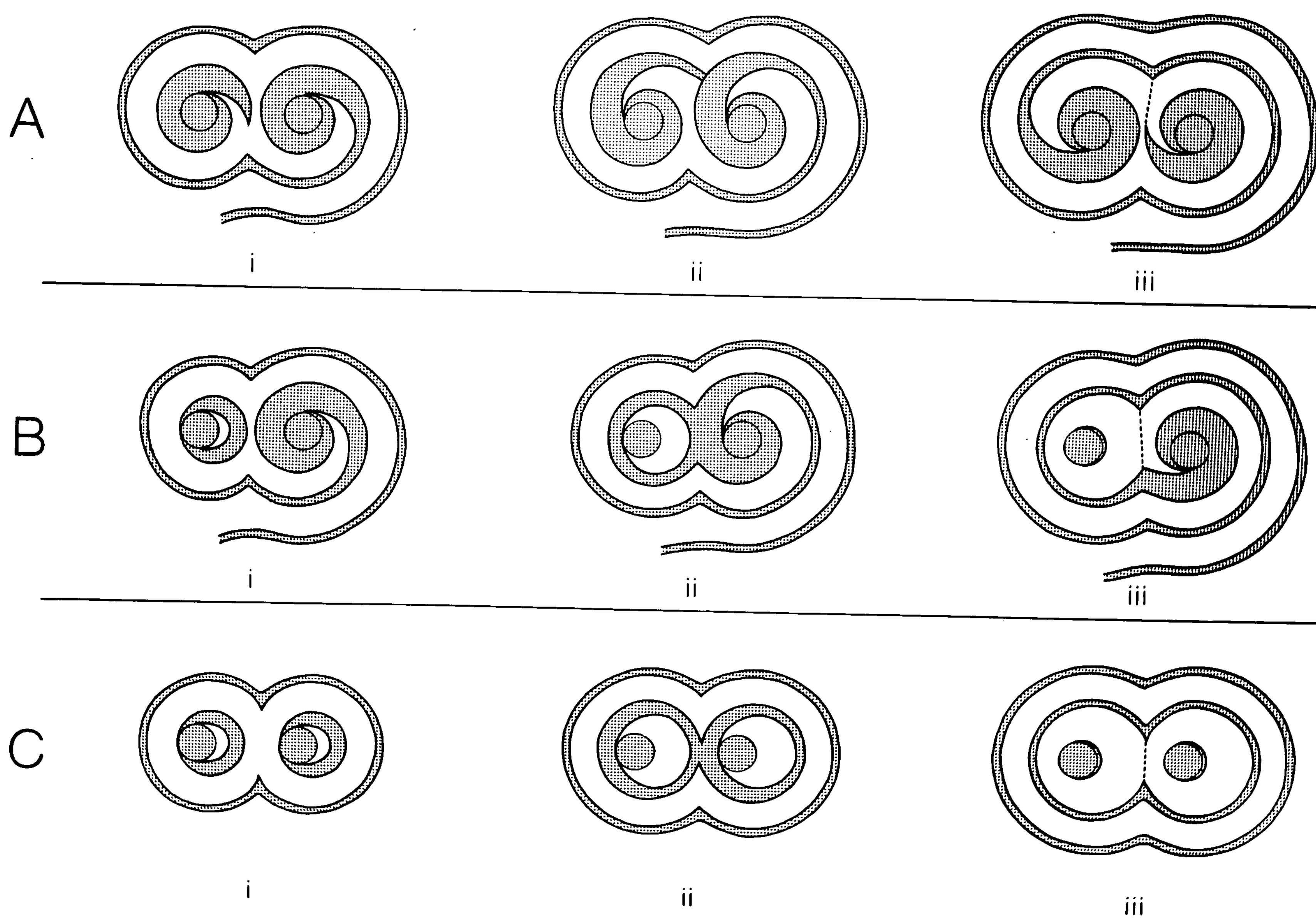

A
B
C
D
E
F

Figure 67. The effect of convergence between basally extending exozonal growth margins of daughter branches at their junction with the parent branch in <u>Terebellaria</u> zoaria. Diagrammatic external aspects looking down upon the distal growth tips. For simplicity and clarity, the effects of angular divergence of daughter branches, and of overlap of more proximal parts of growth margin by autozooecial ledges (as in text-fig. 1B) have been ignored. 3 growth stages ('i'-'iii') are illustrated for each of 3 examples (A-C). Growth margins and growth tips, stippled; lines of anastomosis, dashed. Circular axial parts of the growth tips are endozones.

A, convergence of helico-spiral exozonal growth margins. At growth stage 'i', the helico-spiral margin of the right-hand daughter branch is continuous with that of the parent branch, but that of the left-hand daughter branch terminates at its confluence with an autozooecial ledge on the right-hand daughter branch. Further growth ('ii') results in the meeting of helico-spiral growth margins belonging to each daughter branch. Anastomosis between them occurs and causes the development of a discontinuity in the left-hand helico-spiral growth margin. The helico-spiral growth margin of the parent branch now ('iii') appears to be continuous with that of the left-hand daughter branch, whilst that of the right-hand daughter branch abuts against a ledge of autozooecia on the left-hand branch.

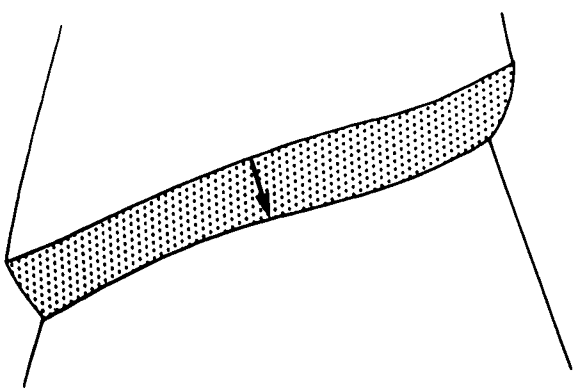
B, convergence of a helico-spiral growth margin with an annular growth margin. Anastomosis of growth margins occurs when they meet at (ii) (compare with Taylor 1976, text-fig.5A in Appendix 2). Successive annular growth margins are incorporated into the helico-spiral growth margin extending down the parent branch.

C, convergence of annular growth margins from daughter branches. Their inclined nature causes anastomosis to be eccentric.

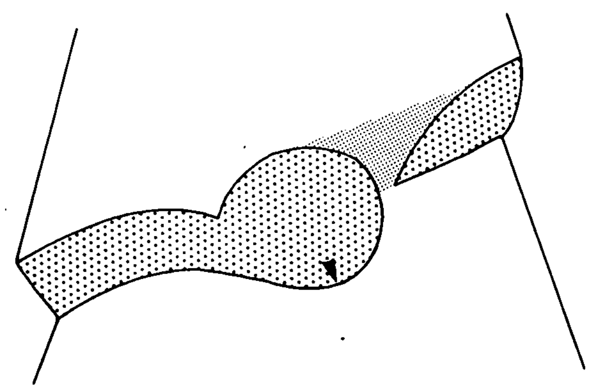


A
B
C
i
ii
iii
i
ii
iii
i
ii
iii

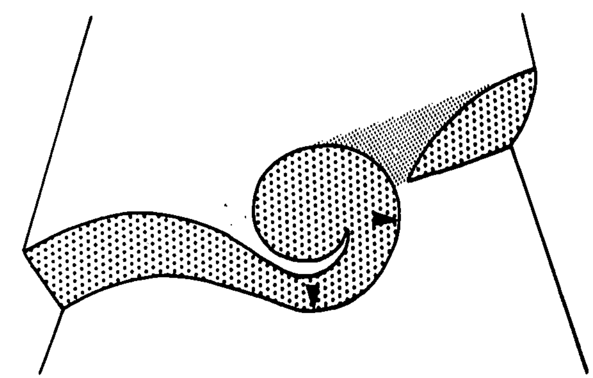
Figure 68. Inferred formation of an adventitious or secondary branch on the exterior of a *Terebellaria* branch in three growth stages ('i'-'iii'). Full explanation on p.238 . Coarse stipple, non-occluded exozonal growth margin; fine stipple, occluded exozonal growth margin; arrows, inferred growth direction.



i



ii



iii

Figure 69. Bivariate paradigm showing the functional efficiency of differing morphological states of a hypothetical structure which performs two equally important functions. Vertical and horizontal axes represent the % efficiency with which the two functions (A and B) are performed. Morphology 1 performs function A with an efficiency of 100% and function B with a negligable efficiency. Morphology 2 performs function B with an efficiency of 100% and function A with a negligable efficiency. A compromise morphology, allotted an arbitrary efficiency of 75% when performing a combination of function A and function B, would have selective advantage over morphologies 1 and 2.

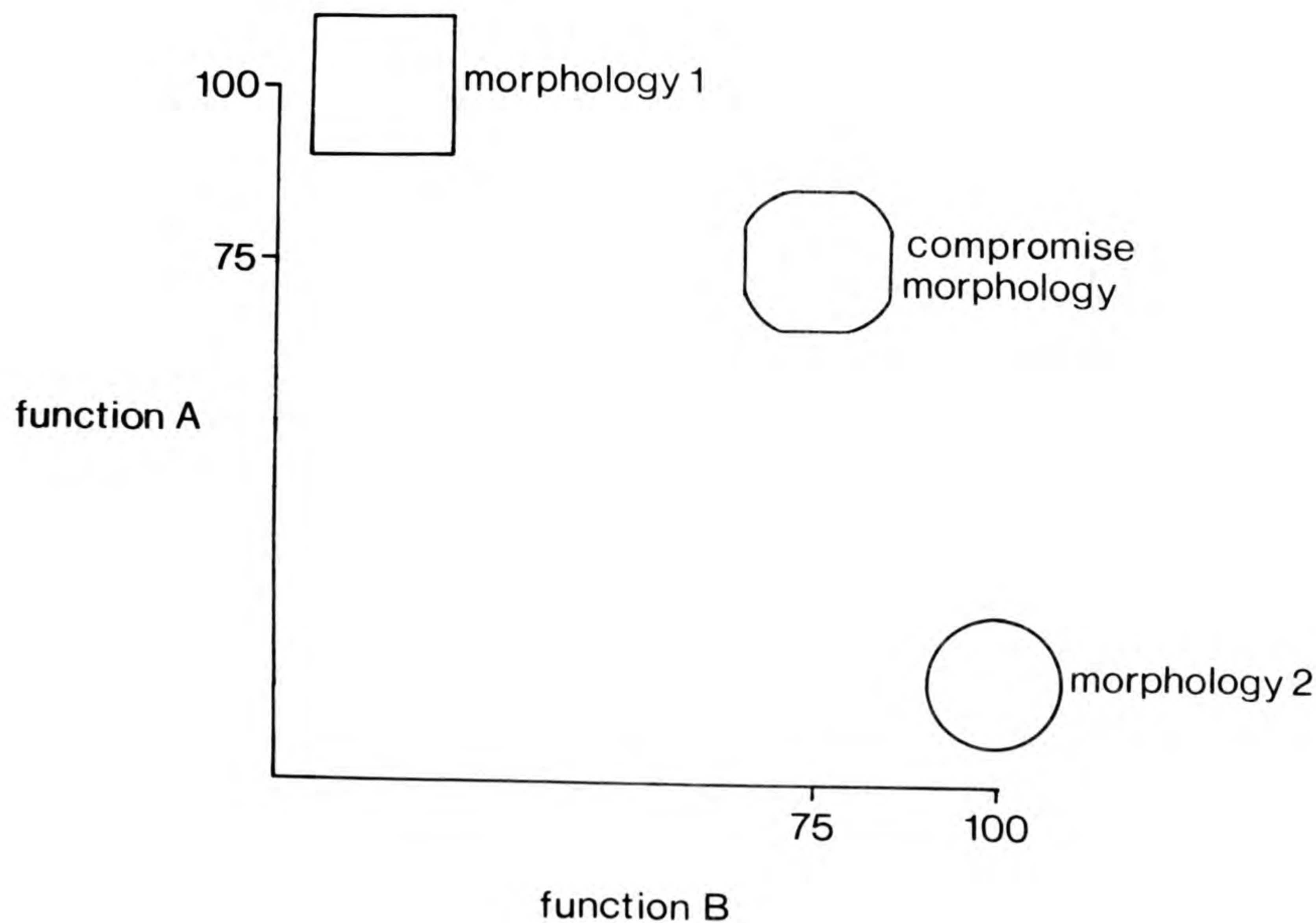

morphology 1
compromise morphology
morphology 2
100
75
function A
75
100
function B

Figure 70. Camera lucida drawing to show the helical zoarial form of the extant cheilostome <u>Spiralaria</u> <u>florea</u> (Busk). BMNH (Zoology Department) 1936. 12.30.261, Melbourne. See p.253 . X25.

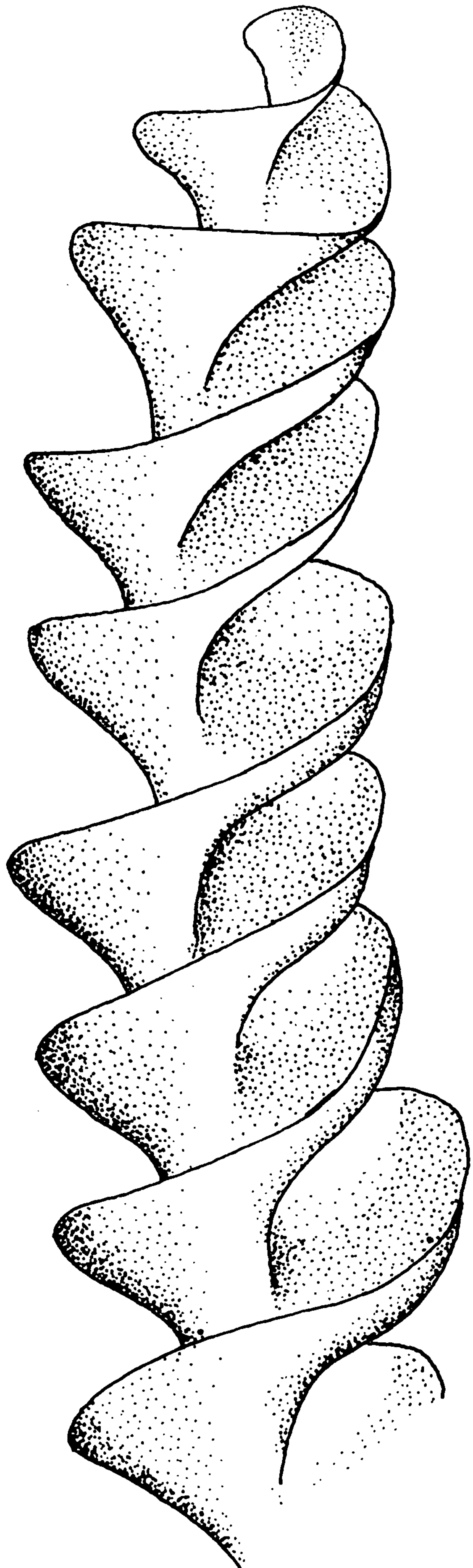


Figure 71. Transverse section through an autozooidal tentacle crown just above the level of the mouth (m). Movements of the lateral cilia on the tentacles evacuate water from within the ring of tentacles. After Ryland (1970).

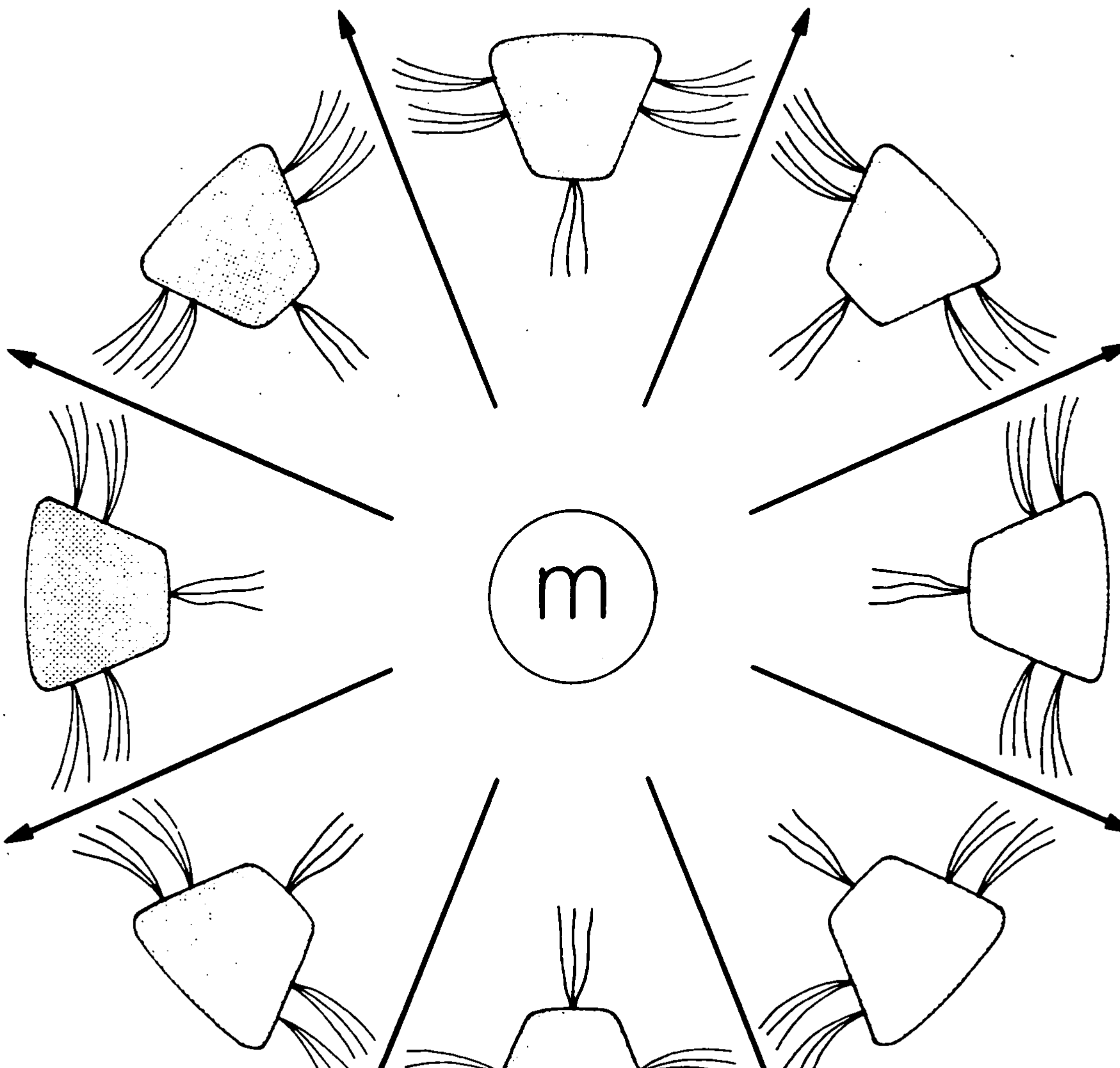

m

Figure 72. Longitudinal section of the tentacles, mouth and pharynx of an autozooid. Arrows indicate the water currents created by the zooid. After Borg (1926).

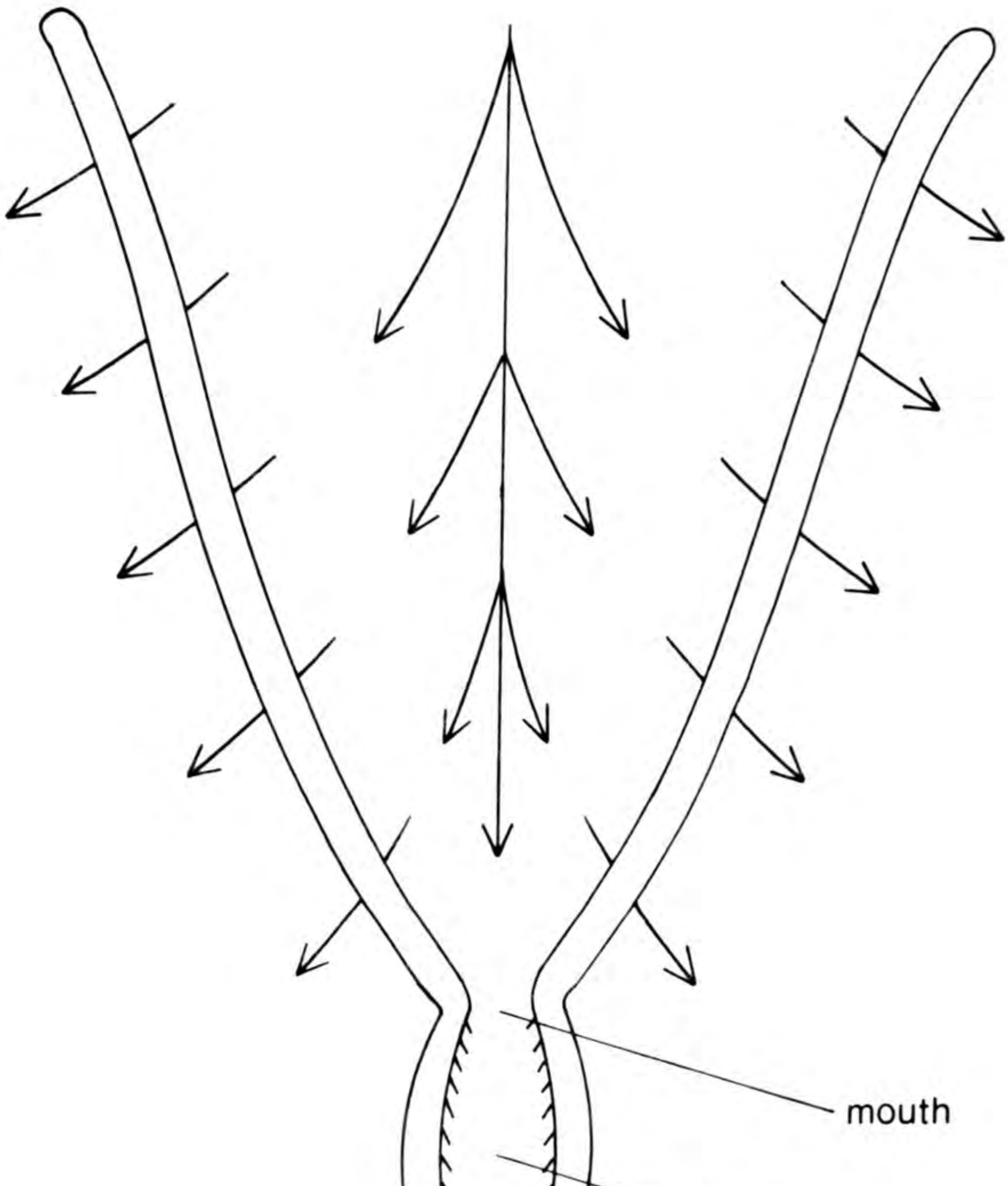

mouth
pharynx

Figure 73. Diagram showing inferred loci of inhalent (indicated by a positive sign) and exhalent (indicated by a negative sign) water current flow at the colony surface of a bryozoan in which autozooecial apertures (indicated by circles) are hexagonally close-packed.

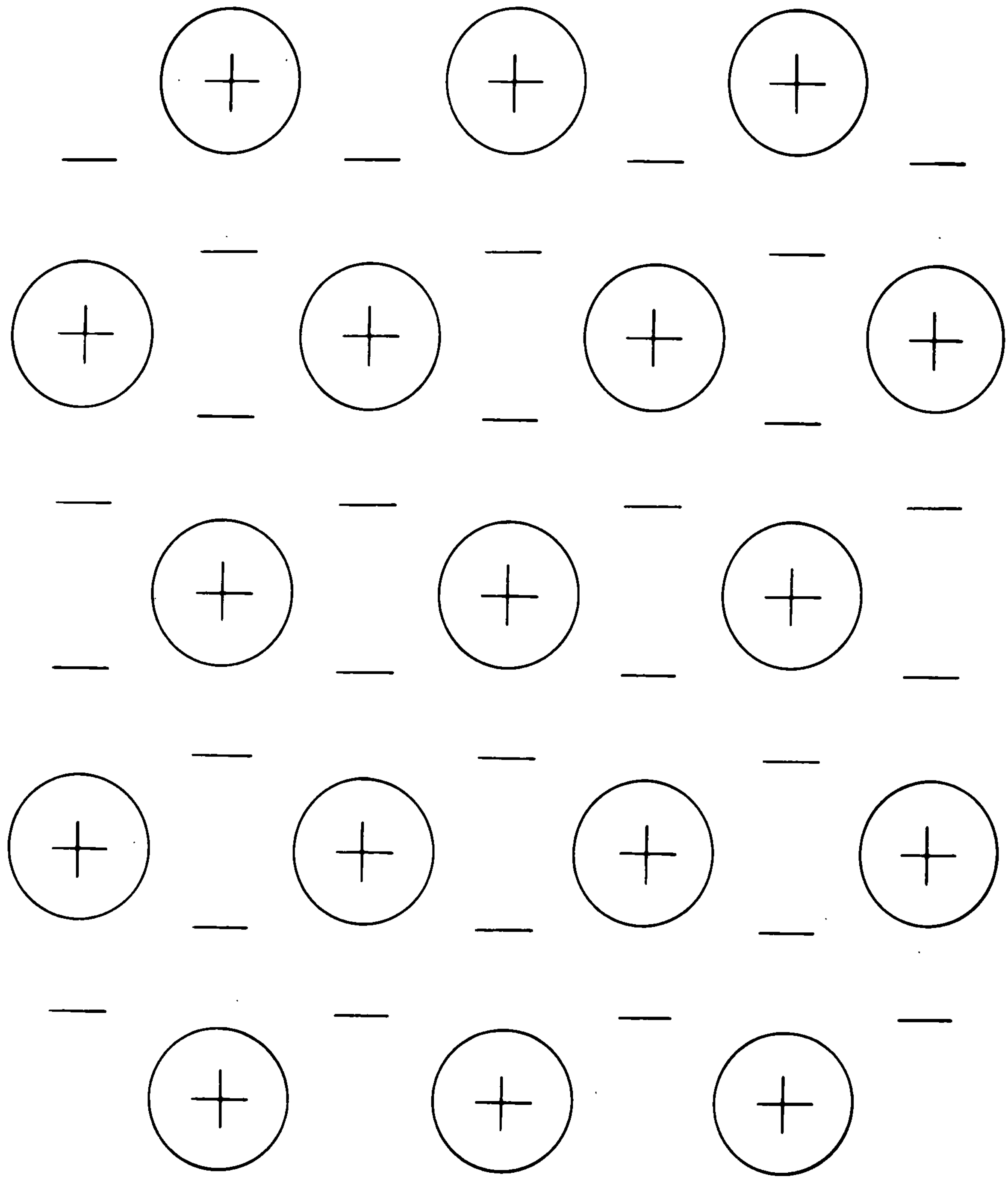


Figure 74. Diagram showing inferred loci of inhalent (indicated by a positive sign) and exhalent (indicated by a negative sign) water current flow at the colony surface of a bryozoan in which autozooecial apertures (indicated by circles) are arranged in rows. Inhalent flow loci are concentrated above the rows, exhalent flow loci between the rows.

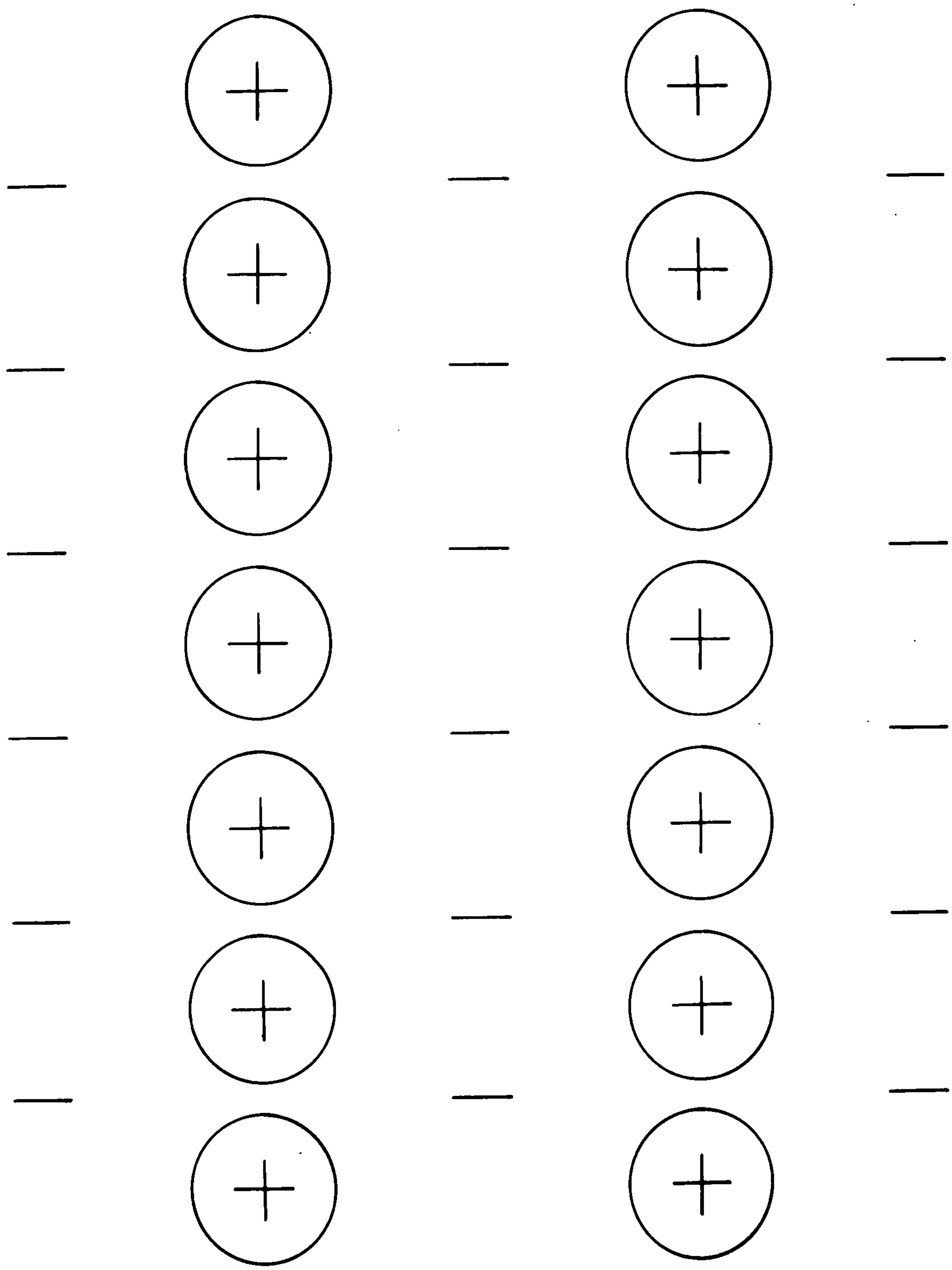


Figure 75. Diagram of a portion of a vinculariiform <u>Spiropora elegans</u> branch showing nodes of apertures and internodes formed of zooecial frontal walls. Loci of inhalent flow are situated above the nodes, loci of exhalent flow above the internodes.

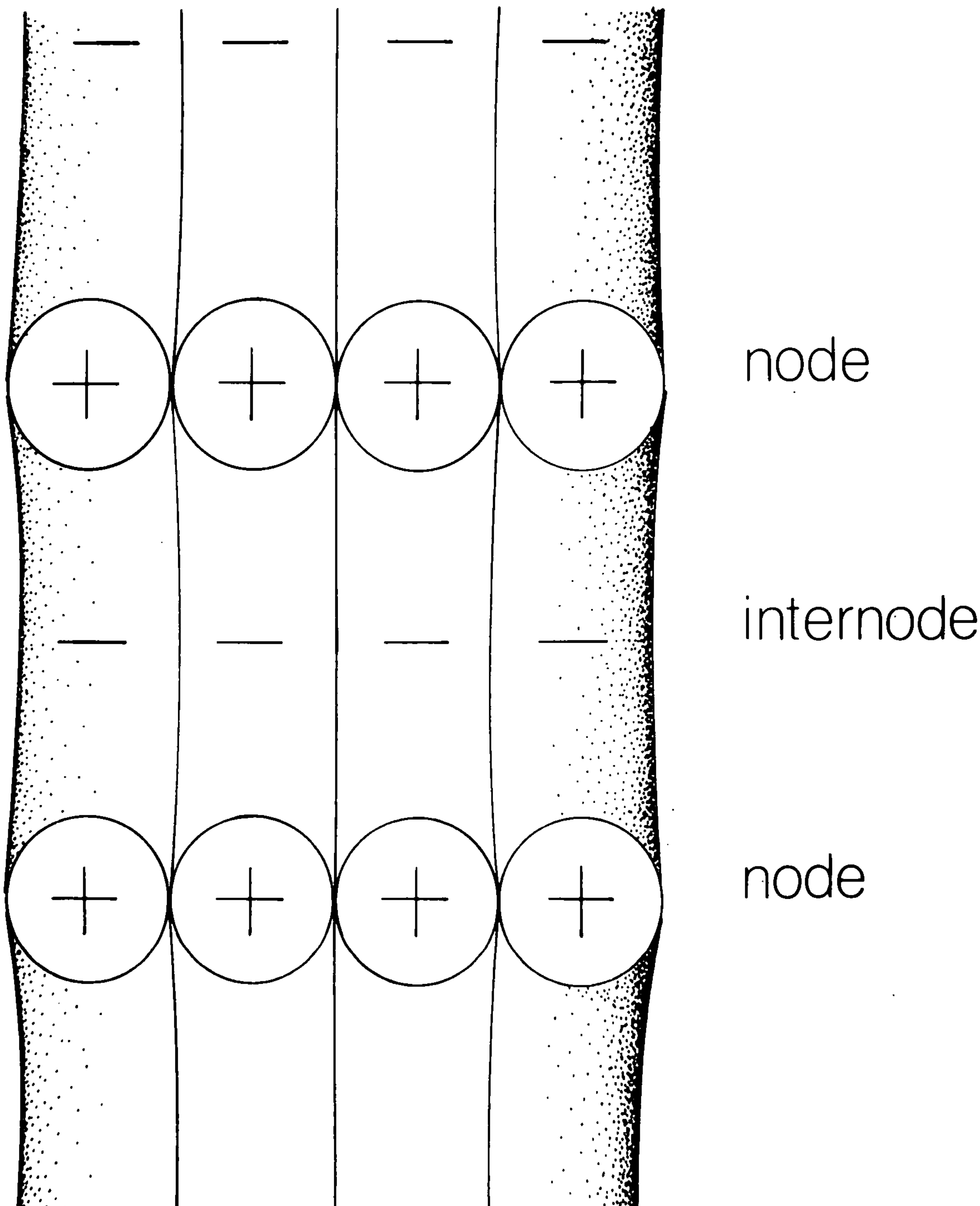
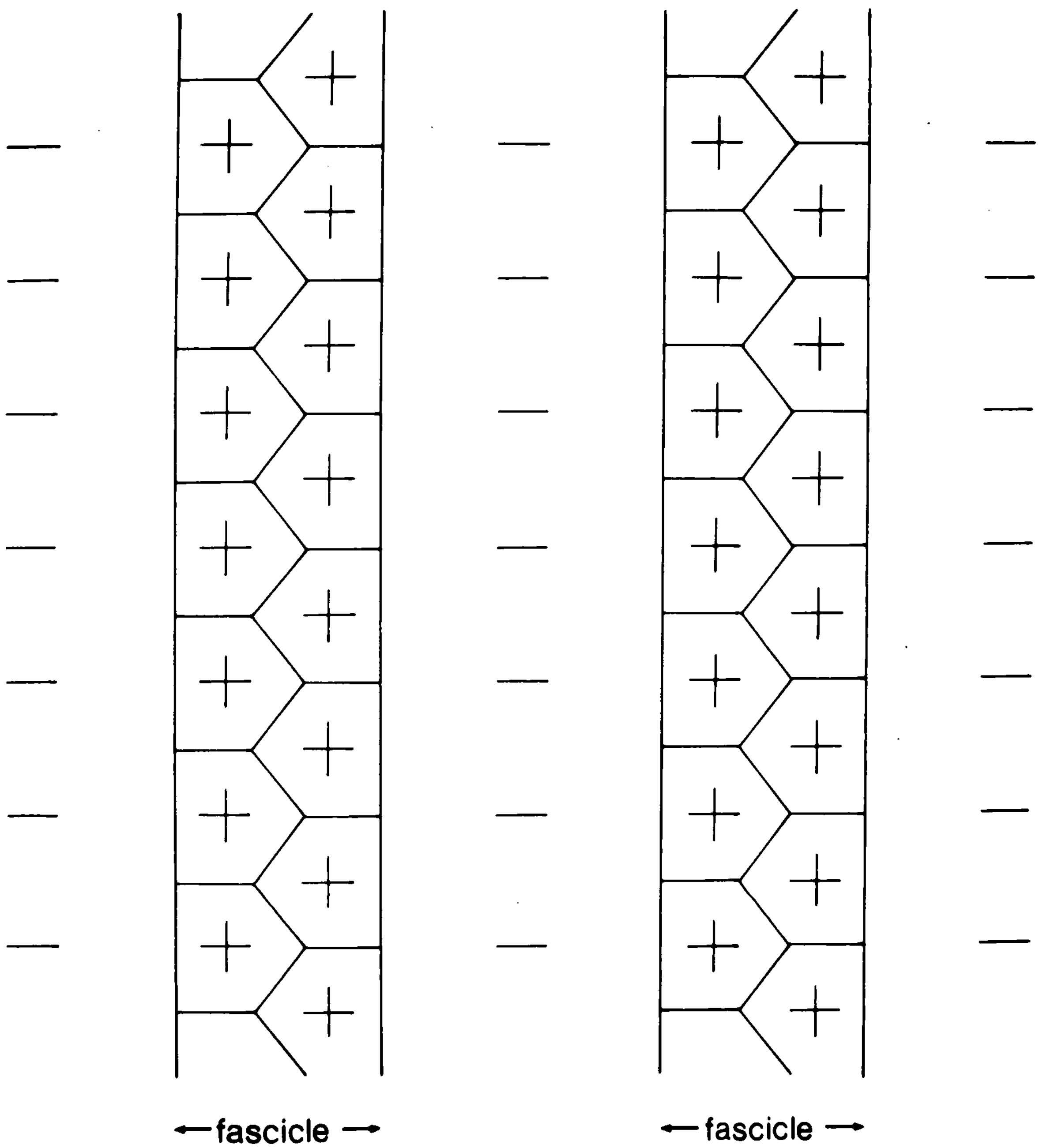

node
internode
node

Figure 76. Diagram showing inferred loci of inhalent and exhalent water current flow at the colony surface of a bryozoan in which autozooecial apertures (pentagonal in shape) are arranged in biserial linear fascicles. Loci of inhalent flow are situated above the fascicles, exhalent flow departs above interfascicular regions.



fascicle
fascicle

Figure 77. Diagram showing inferred loci of inhalent (indicated by a positive sign in the central fascicle) and exhalent water current flow at the colony surface of a bryozoan (e.g. *Meandropora*) in which polygonal autozooecial apertures are arranged in circular fascicles. Loci of exhalent flow between the hexagonally close-packed fascicles are indicated by a negative sign.

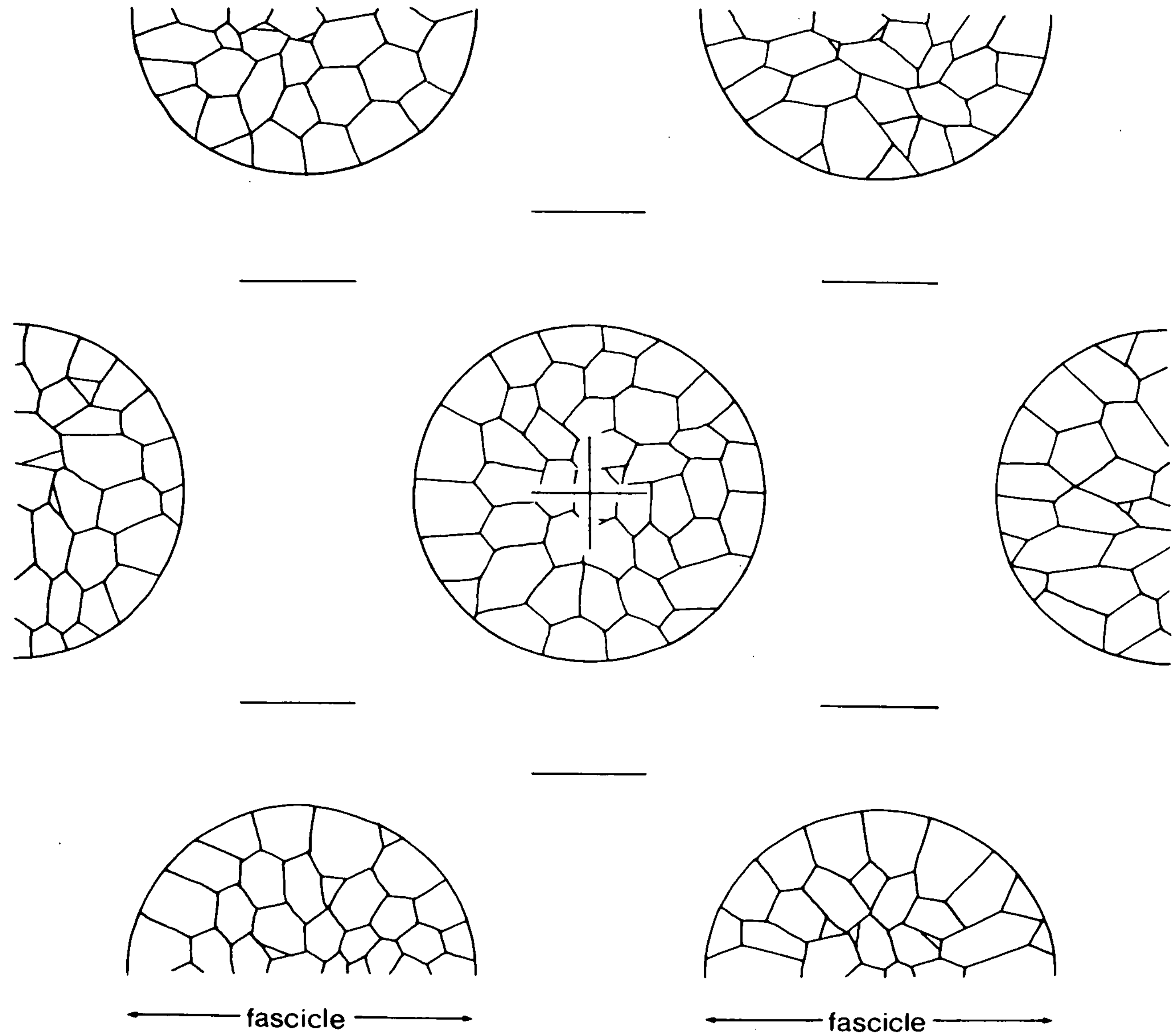
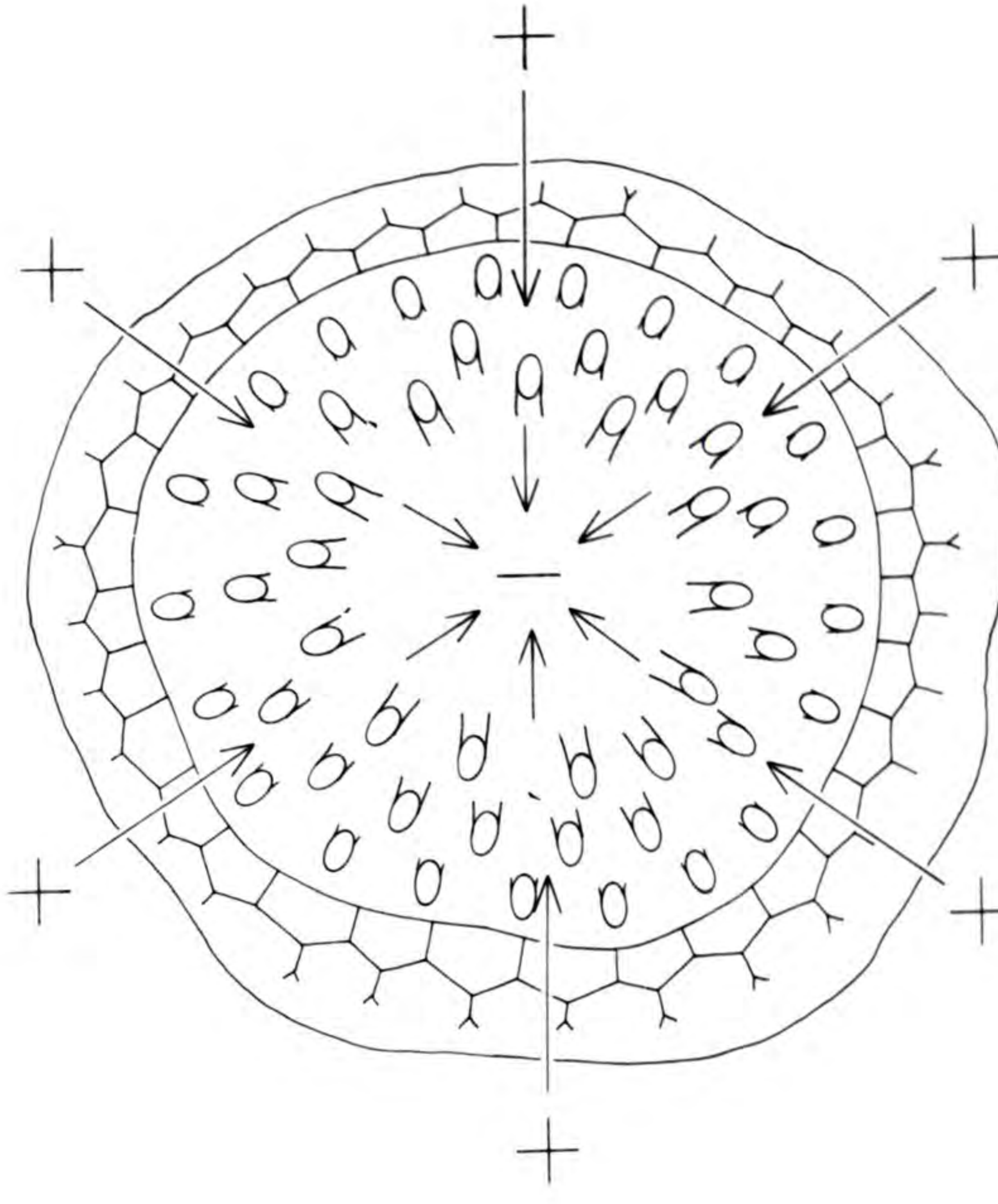

fascicle
fascicle

Figure 78. Inferred extrazooidal current system created by a discoidal bereniciform colony with ontogenetically zoned autozooids. The upper diagram is a view of the colony surface showing the radial flow of inhalent currents (arrowed and indicated by positive signs) and the upward flow of exhalent water leaving the colony above its central region devoid of feeding autozooids. The lower diagram is a profile which shows lengthening of peristomes proximally through the zone of feeding zooids and the extrazooidal water current system deduced.



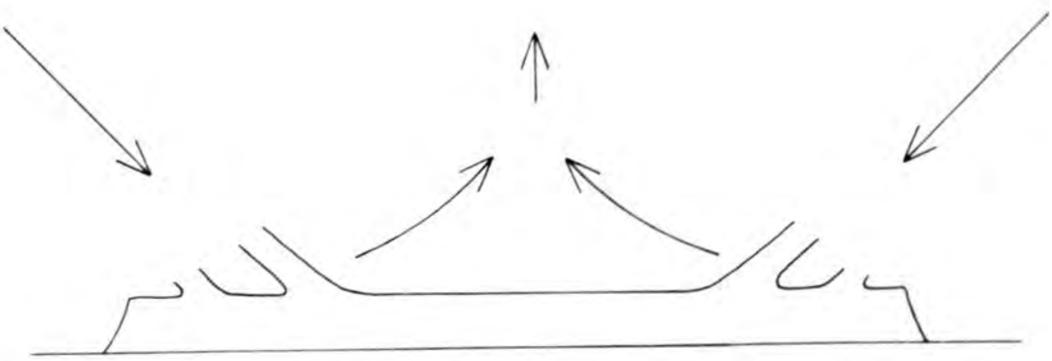


Figure 79. Colonial water current system inferred to have developed along _Terebellaria_ branches during life. Small arrows indicate the overall direction of water flow created by the cooperative action of feeding zooids within zone 2 (indicated by crosses). A distal flow of water exchanged between consecutive bands of feeding zooids may have resulted in a net exhalent flow above the branch apex (large arrow).

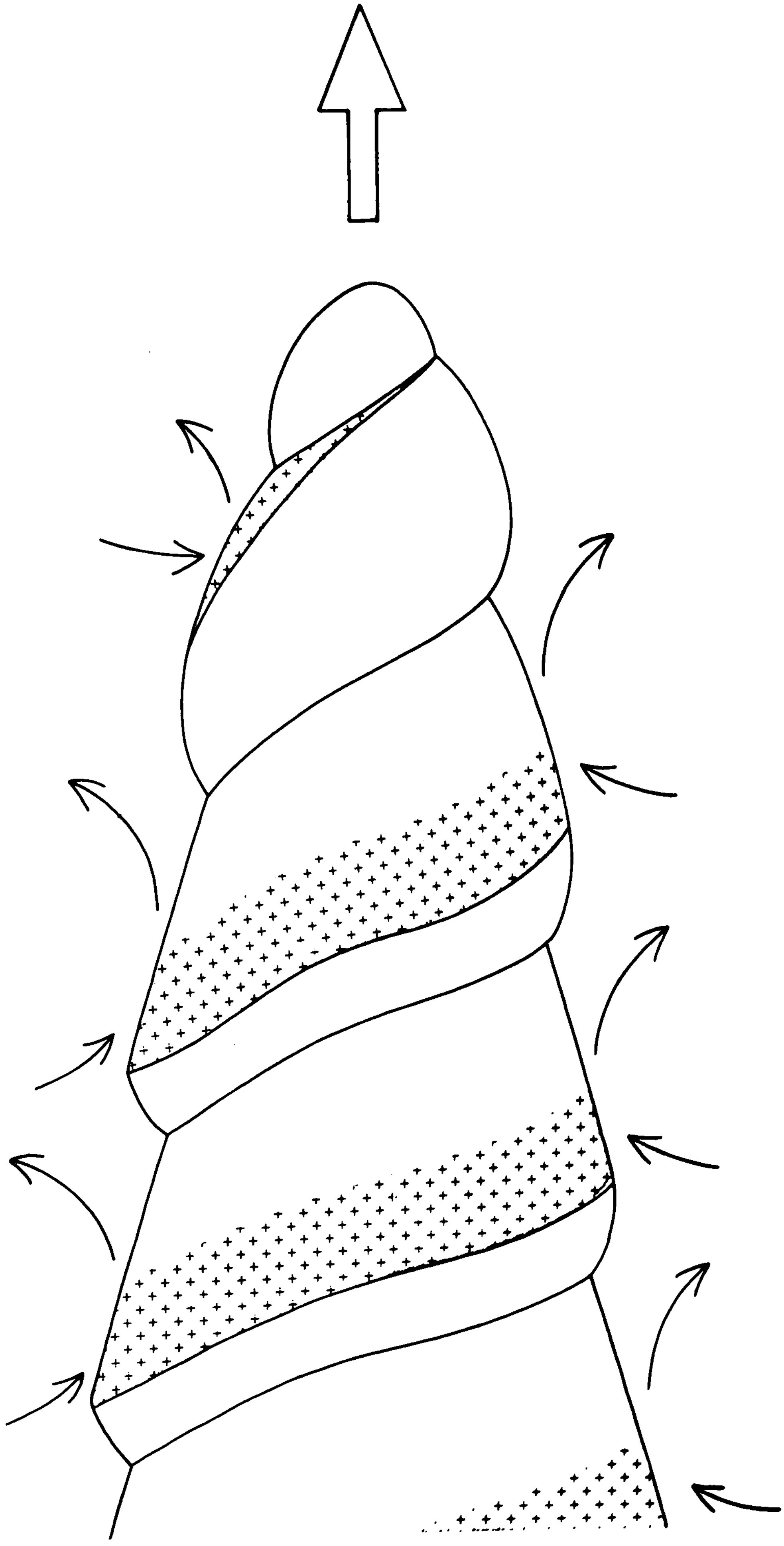


Figure 80. Diagrammatic section through a colony with monticules. Small arrows show the feeding currents created by individual autozooids (indicated by a 'V' sign) and large open arrows show the extrazooidal currents established. Autozooidal inhalent currents focus on intermonticular regions because autozooid tentacle crowns are held at right angles to the colony surface. Monticule summits possess a lower concentration of feeding autozooids and function as chimneys of exhalent flow.

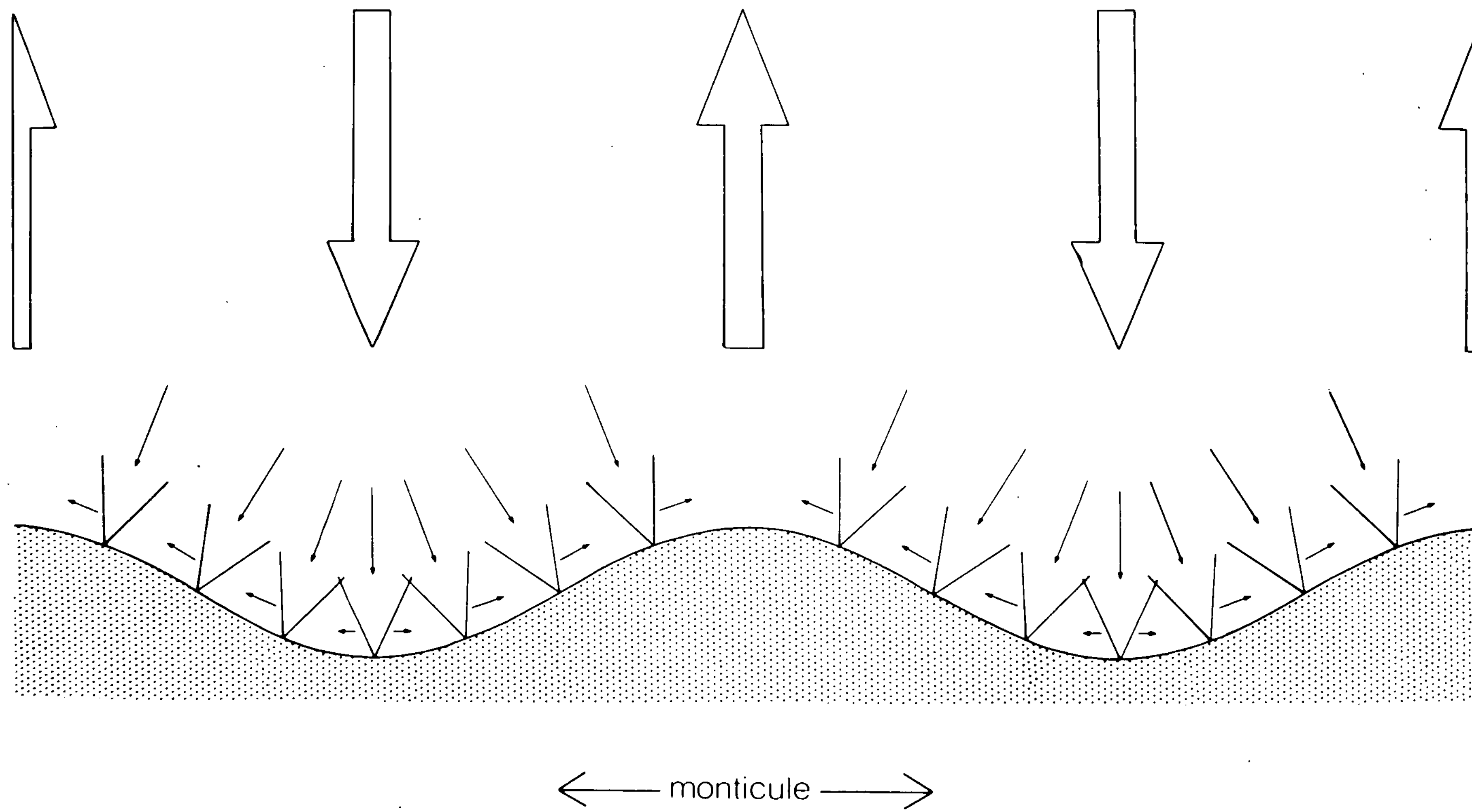

monticule

Figure 81. Diagrammatic transverse section through an adnate subtriangular branch of Idmonea triquetra. Inferred autozooidal water current are indicated by small arrows. Because autozooid tentacle crowns (shown by a V-sign) are directed away from the apex of the subtriangular branch, the branch apex functions as a chimney of exhalent flow (shown by a large open arrow).

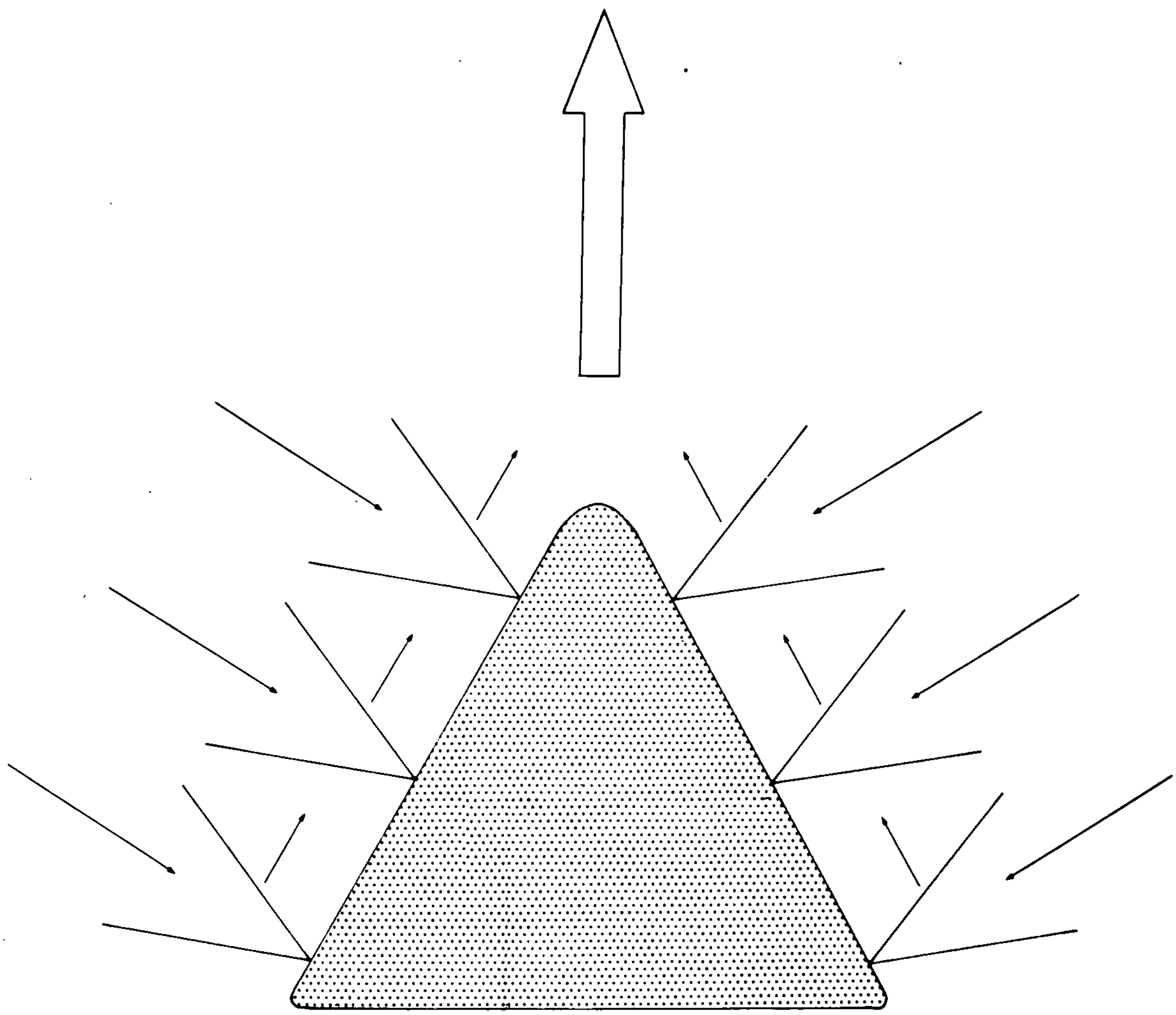


Figure 82. Diagrammatic view of the reticulate upper surface of a <u>Reticulipora</u> colony. Crosses indicate the zone of inferred feeding zooids which create an extra-zooidal flow (arrowed) of water through the zoarium from its upper to its basal surface.

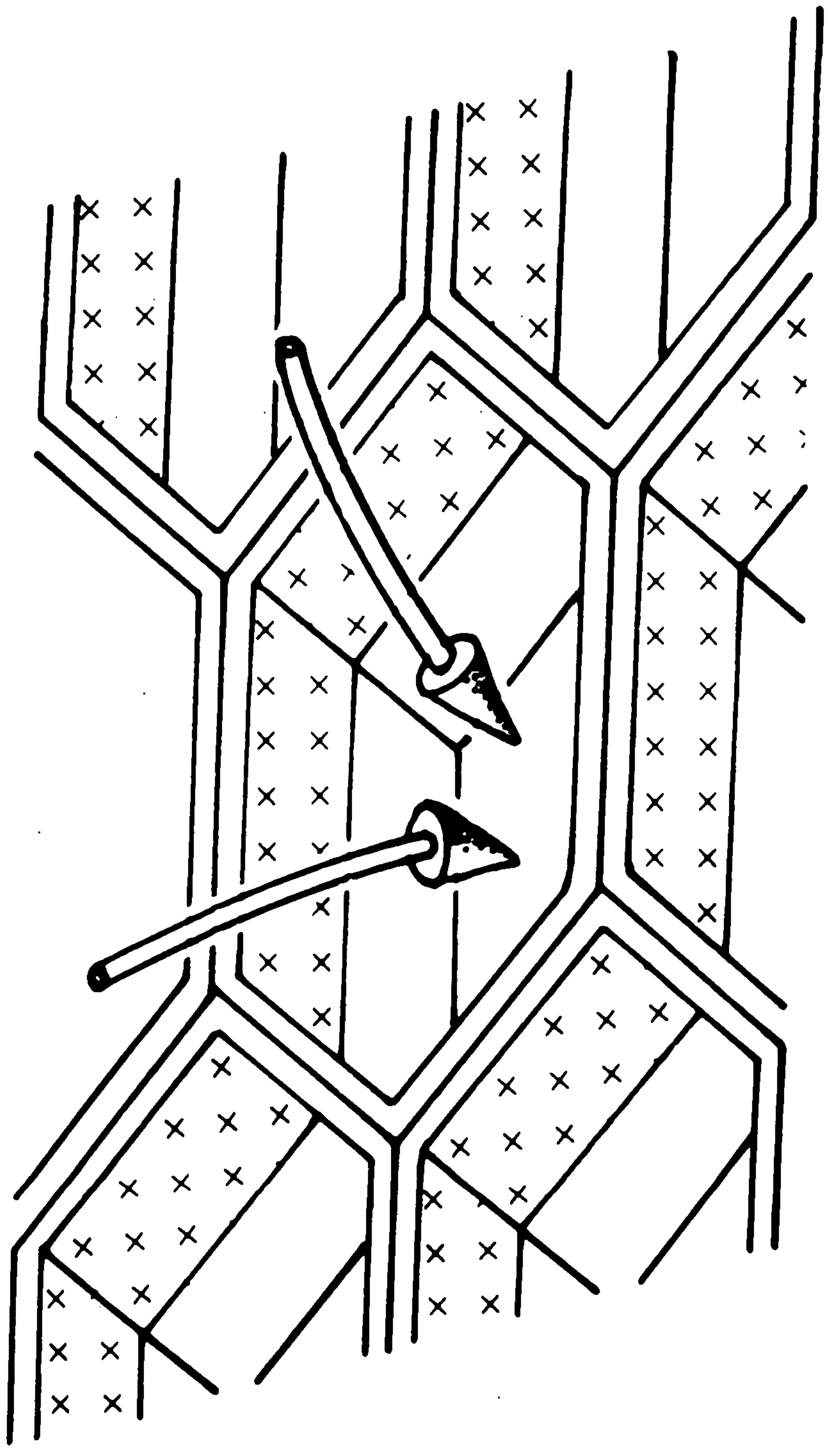


Figure 83. The spatial competitive abilities of stomatoporiform (i) and discoidal bereniciform (ii) adnate tubuloporinid colonies. The finely stippled area represents a hypothetical spatial competitor with an encompassing growing zone. In both possible outcomes (1 and 2) the stomatoporiform branch is ultimately overgrown by the hypothetical competitor, directly in outcome 1 and indirectly in outcome 2 where lobes of the competitor converge proximal to the growth tip by overgrowing the zoarial lateral walls of the stomatoporiform branch. There exist 3 possible outcomes to the meeting of the bereniciform colony and the hypothetical spatial competitor; in outcome 1 the bereniciform colony overgrows the spatial competitor, in outcome 2 neither organism is able to overgrow the other, in outcome 3 the bereniciform colony is overgrown by the spatial competitor.

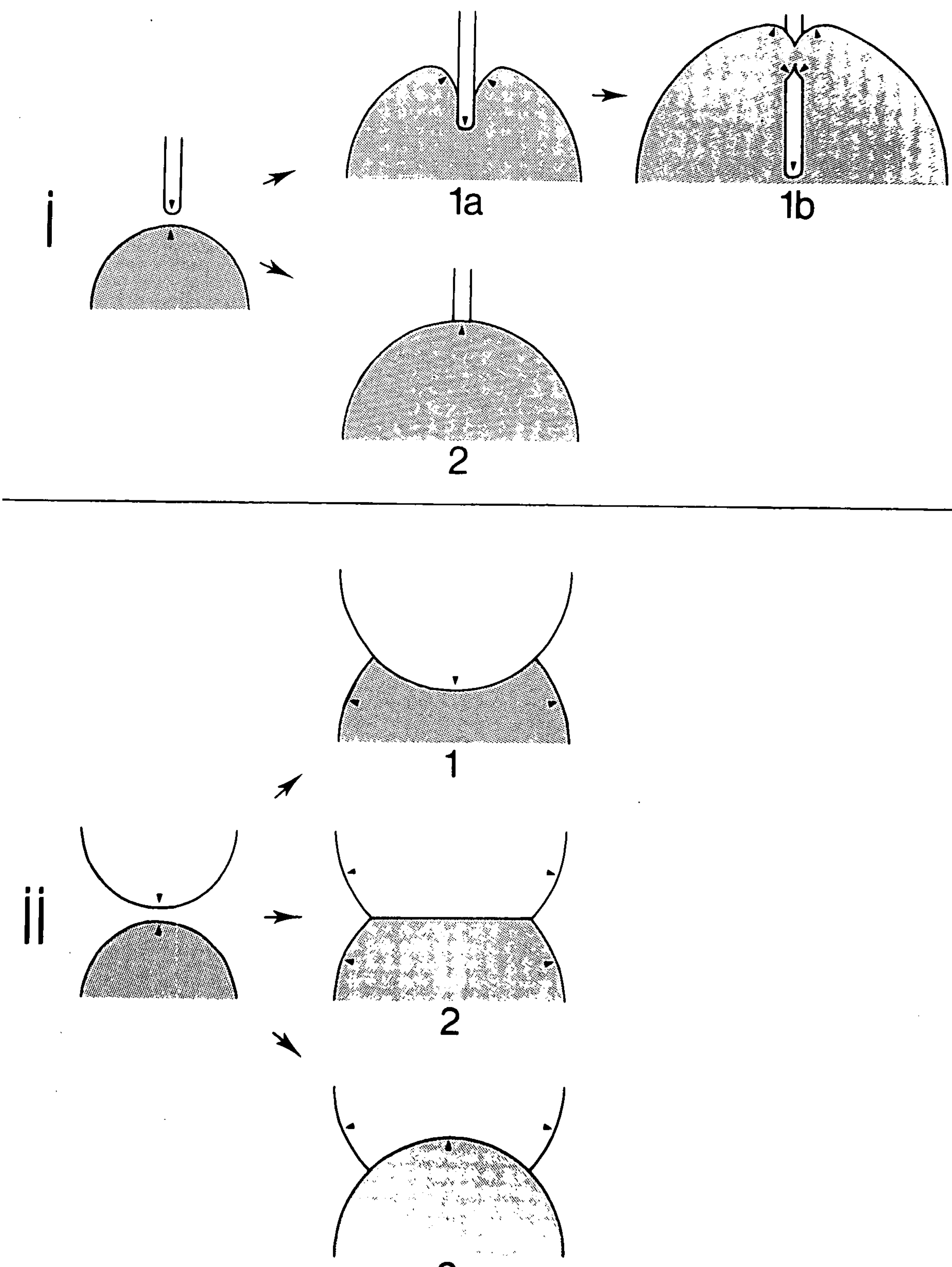

i
1a
1b
2
ii
1
2
3

Figure 84. Possible phylogenetic relationships between the suborders Tubuloporina and Cerioporina. Boxes to the right contain features correlated with retention or loss of hypostegal coelom during zooidal ontogeny. The polyphyletic origin of one or both of the suborders seems probable.

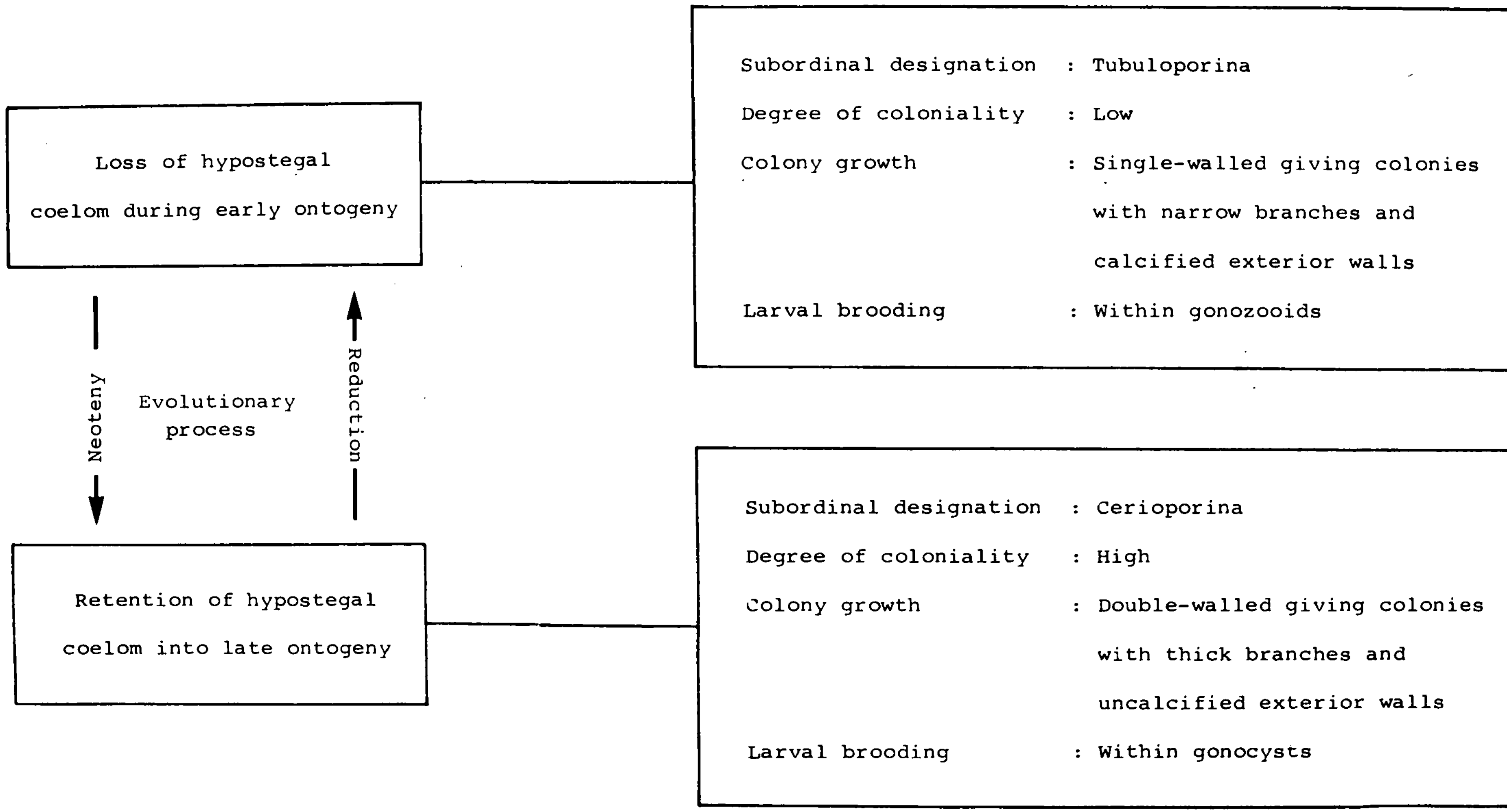

Loss of hypostegal
coelom during early ontogeny
Neoteny
Evolutionary
process
Reduction
Retention of hypostegal
coelom into late ontogeny
Subordinal designation : Tubuloporina
Degree of coloniality : Low
Colony growth : Single-walled giving colonies
with narrow branches and
calcified exterior walls
Larval brooding : Within gonozooids
Subordinal designation : Cerioporina
Degree of coloniality : High
Colony growth : Double-walled giving colonies
with thick branches and
uncalcified exterior walls
Larval brooding : Within gonocysts

Figure 85. Known stratigraphical ranges of the
15 tubuloporinid species studied.

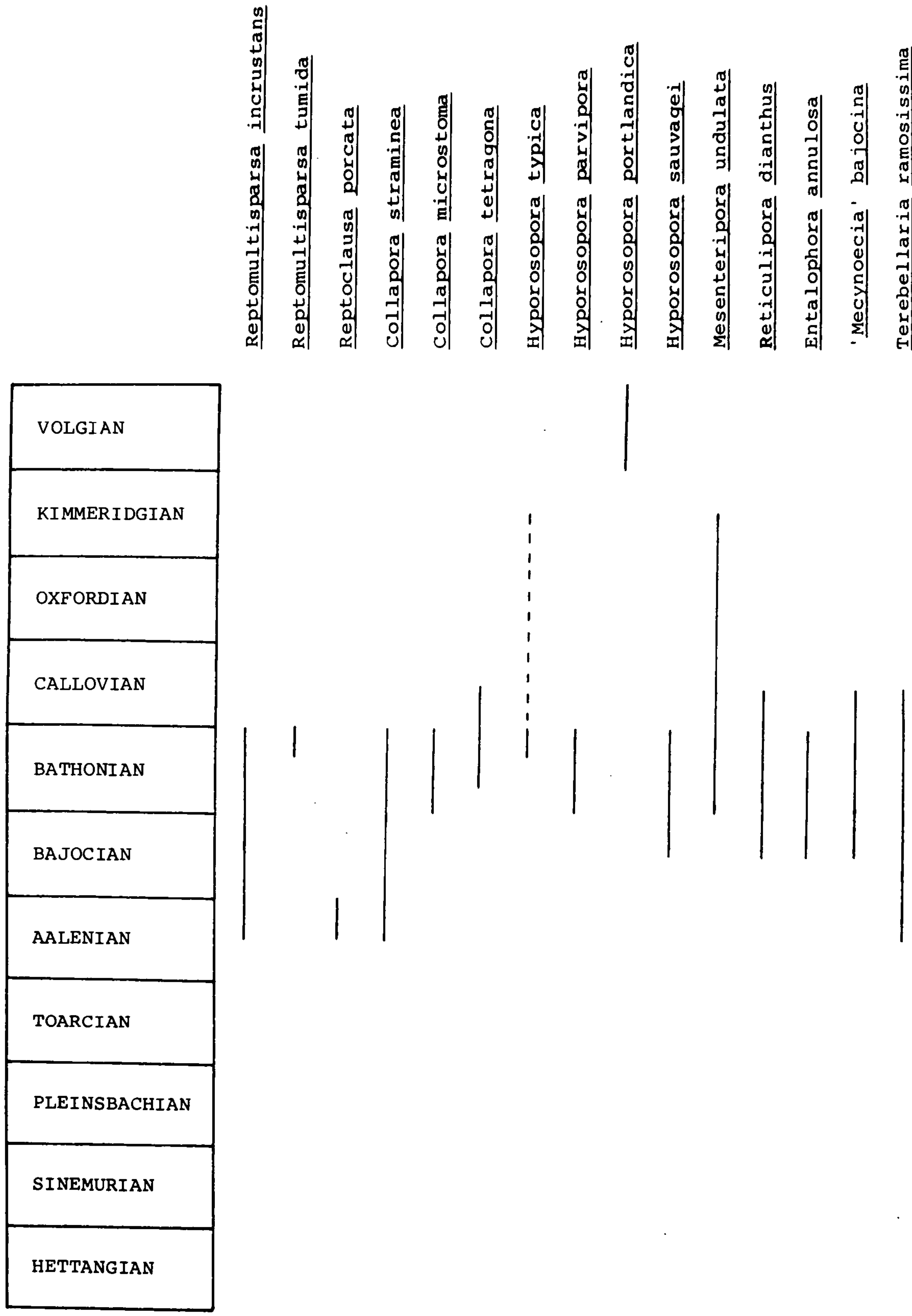

VOLGIAN
KIMMERIDGIAN
OXFORDIAN
CALLOVIAN
BATHONIAN
BAJOCIAN
AALENIAN
TOARCIAN
PLEINSBACHIAN
SINEMURIAN
HETTANGIAN
Reptomultisparsa incrustans
Reptomultisparsa tumida
Reptoclausa porcata
Collapora straminea
Collapora microstoma
Collapora tetragona
Hyporosopora typica
Hyporosopora parvipora
Hyporosopora portlandica
Hyporosopora sauvagei
Mesenteripora undulata
Reticulipora dianthus
Entalophora annulosa
'Mecynoecia' bajocina
Terebellaria ramosissima

Figure 86. Clade diagram of tubuloporinid generic diversity in the Jurassic (J), Cretaceous (C), Tertiary/Pleistocene (T+P) and Holocene (H). Constructed using data in the Treatise (Bassler 1953). Figures indicate the number of genera per 10 m.y. in each period of time. Horizontally lined area = total genera given in the Treatise. Vertically lined area = number of genera recalculated using studies on Jurassic tubuloporinids which suggest that only 16 out of Bassler's 27 listed genera should be accepted.

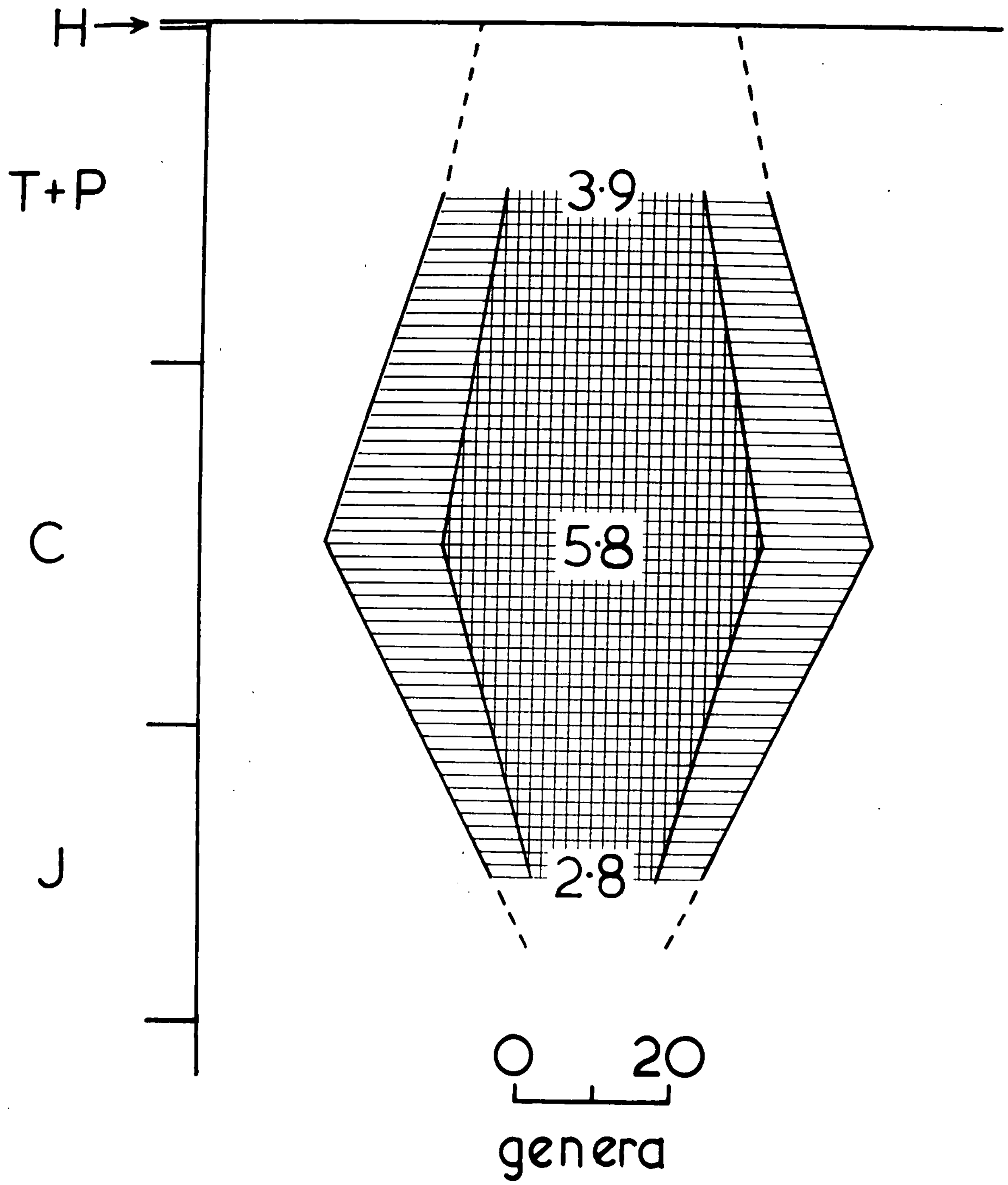

H
T+P
C
J
3·9
5·8
2·8
0
20
genera

Fig. 87. Reptomultisparsa incrustans (d'Orbigny) PT 541-7. Upper Bathonian, St. Aubin Member, Carriere des Campagnettes, Ranville, Normandy. Showing autozooecia and a growth margin terminating at apivot point. Bar represents 1 mm.

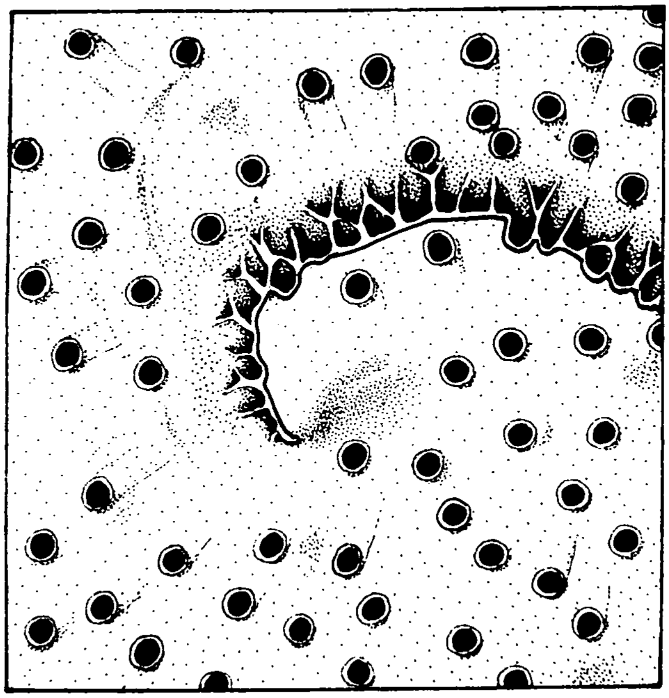


Figure 88. _Reptomultisparsa_ _incrustans_ BMNH 60221
'Bathonian, Ranville' Camera lucida
drawing of zooecial layers in transverse
section. Stipple, zooecial frontal
walls; black, zooecial chambers.
Bar represents 1 mm.

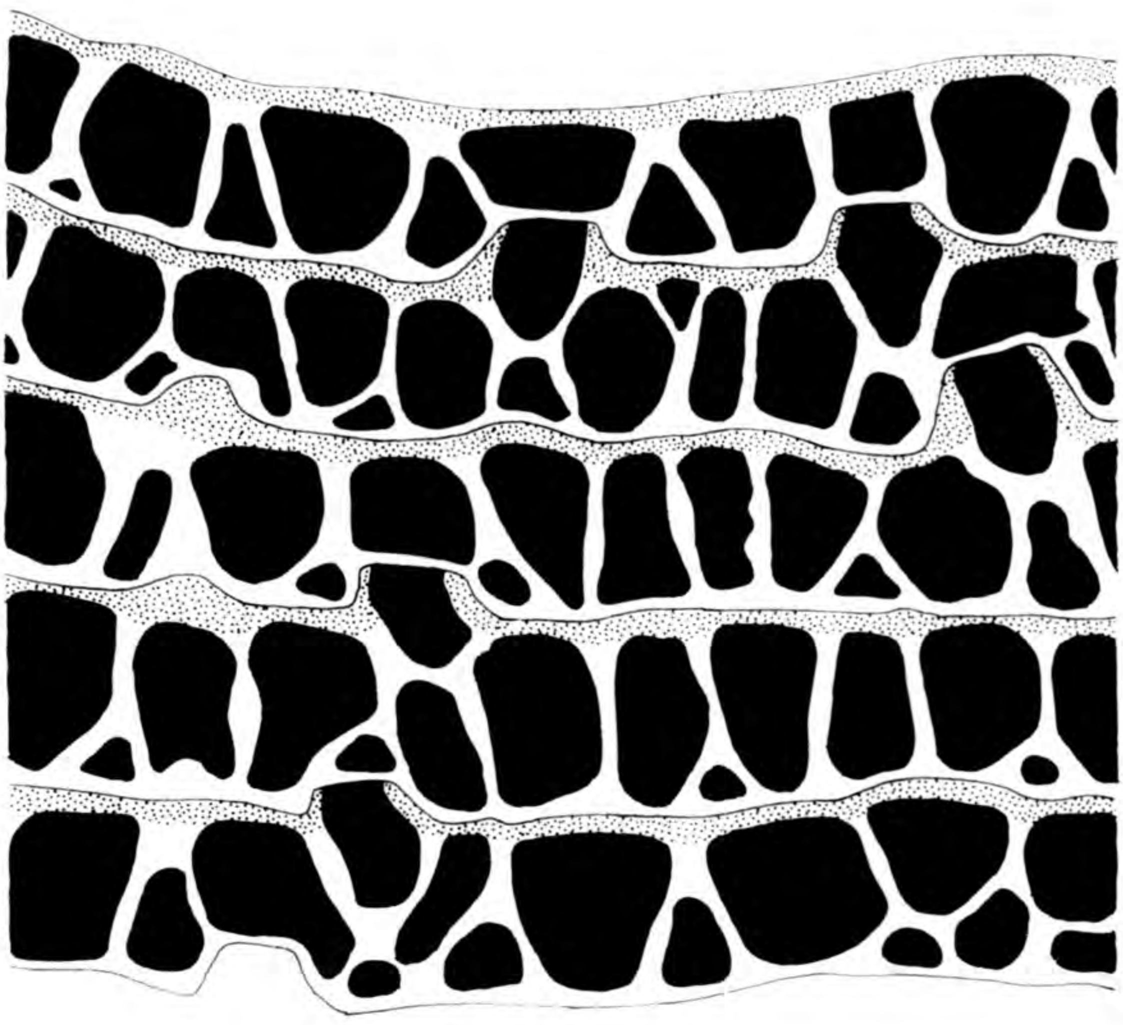


Fig. 89. Reptomultisparsa tumida sp. nov. BMNH D13346 (holotype). Upper Bathonian, Bradford Clay, Bradford-on-Avon, Wiltshire. A group of autozooecia and an inflated gonozooecium. Bar represents 1 mm.

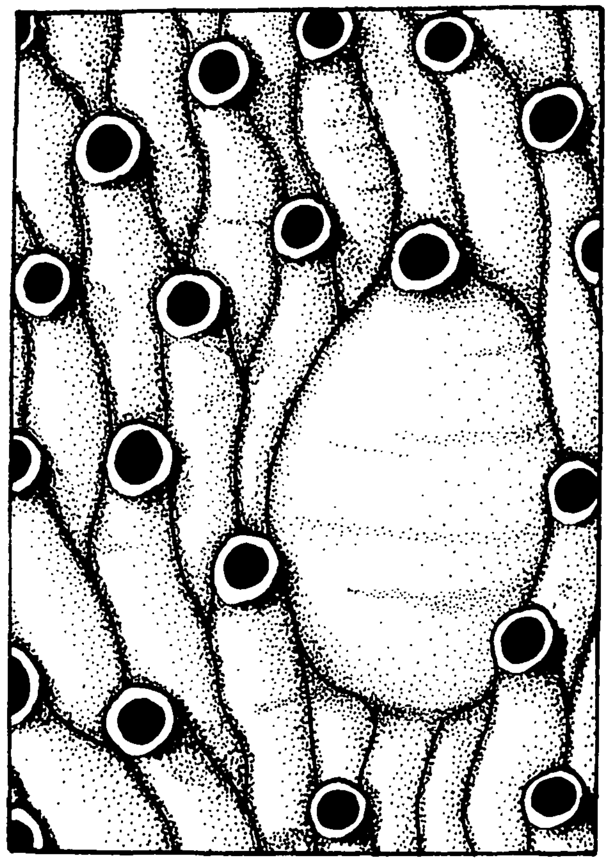


Fig. 90. <u>Collapora</u> <u>straminea</u> (Phillips)
PT A3-93. Bajocian, Millepore Bed, Yons Nab, Yorkshire. Broken vinculariiform branch with a gonozooecium and a group of autozooecia. Bar represents 1 mm.

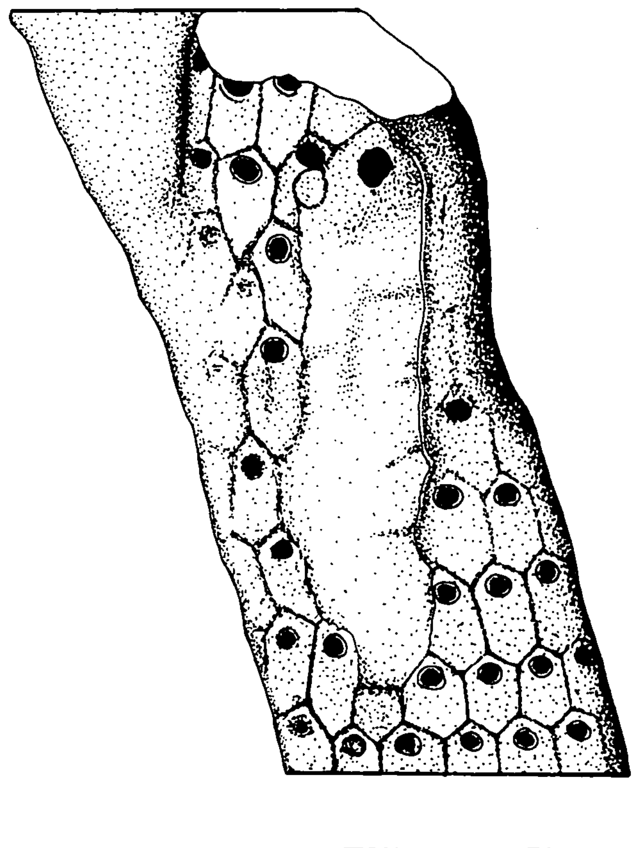


Fig. 91. <u>Collapora</u> <u>straminea</u> (Phillips)
BMNH B4566. 'Bathonian, Ranville'. More probably from the Ragstones of the Cotswolds. Autozooecia on a vinculariiform branch partly obscured by matrix. Bar represents 1 mm.

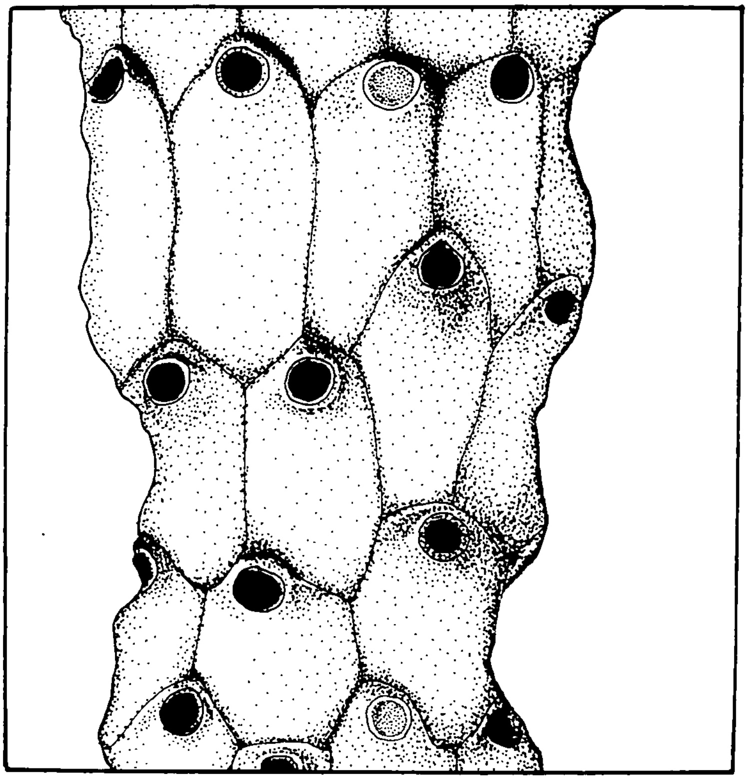


Fig. 92. _Collapora_ _straminea_ (Phillips) PT A3-70. Bajocian, Millepore Bed, Yons Nab, Yorkshire. Kenozooecia and some autozooecia where one branch has grown up against another. Bar represents 1 mm.

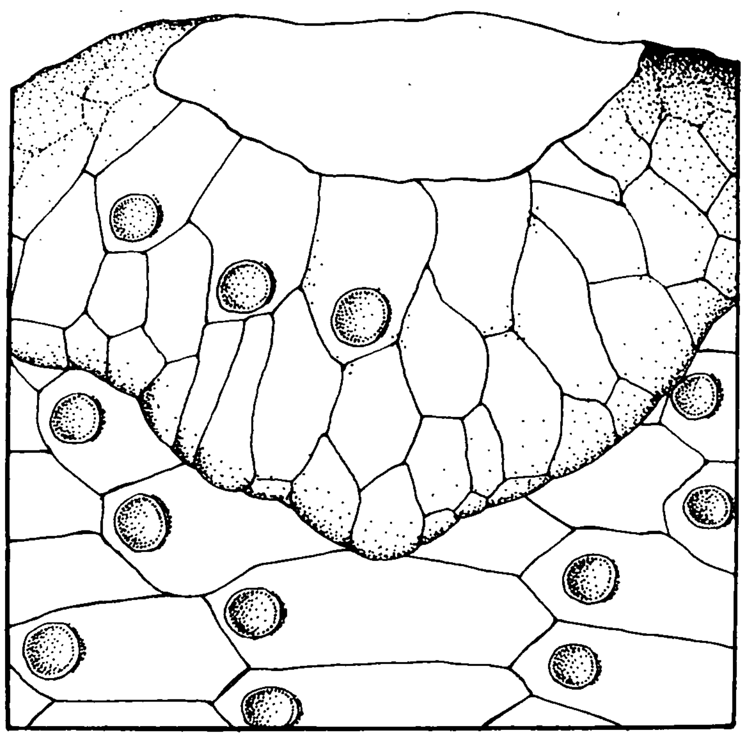


Figure 93. _Collapora_ _straminea_ PT A3-44 Bajocian, Millepore Bed, Yons Nab, North Yorkshire. Camera lucida drawing of a transverse section through a vinculariiform branch. Stipple, zooecial frontal walls; black, zooecial chambers. Bar represents 1 mm.

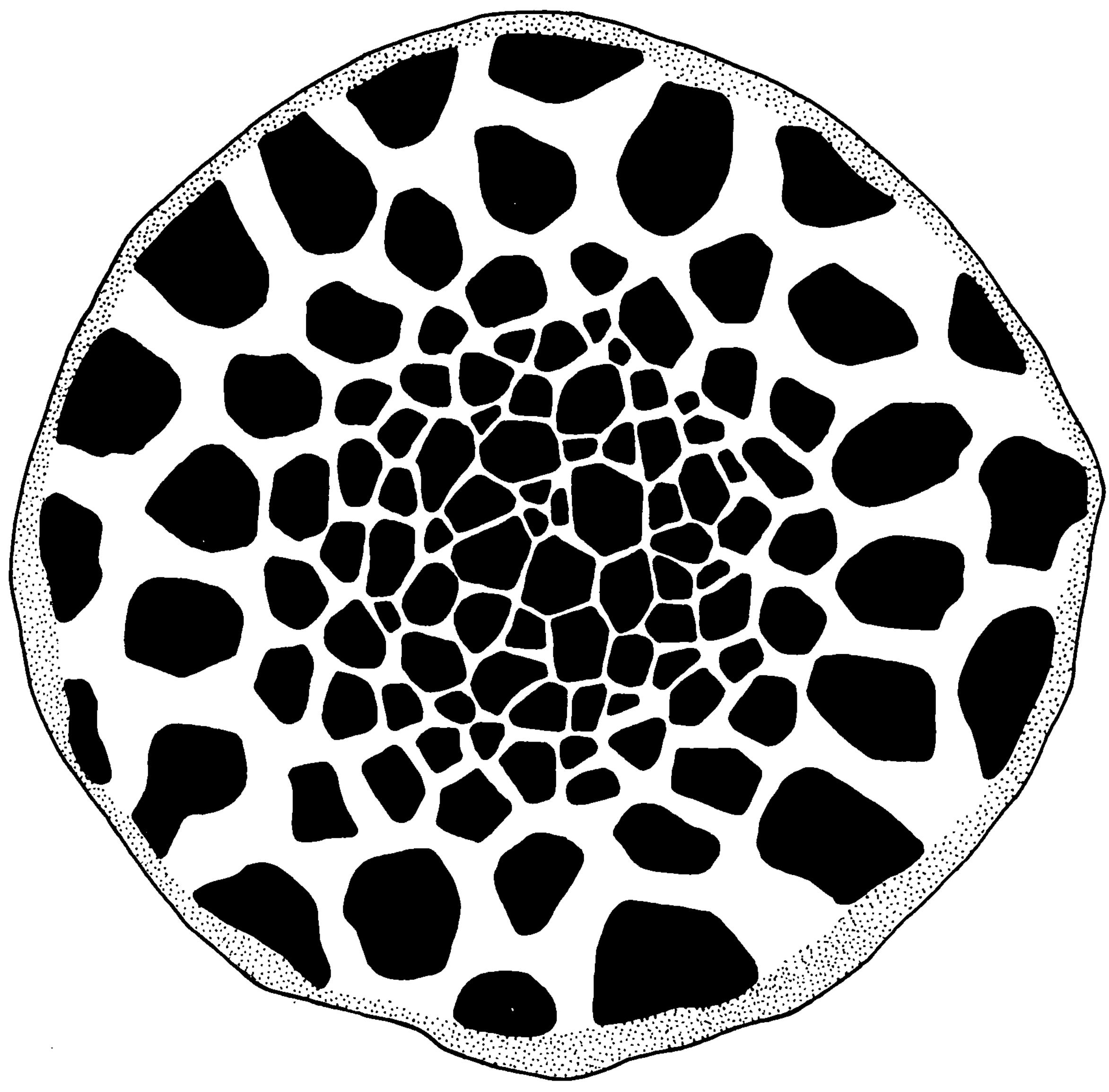


Fig. 94. <u>Collapora</u> <u>microstoma</u> (Michelin)
BMNH D21498. Bathonian, Great
Oolite, Thrapston, Northamptonshire.
A gonozooecium and a group of auto-
zooecia, some occluded by terminal
diaphragms, in a bereniciform
zoarium. Bar represents 1 mm.

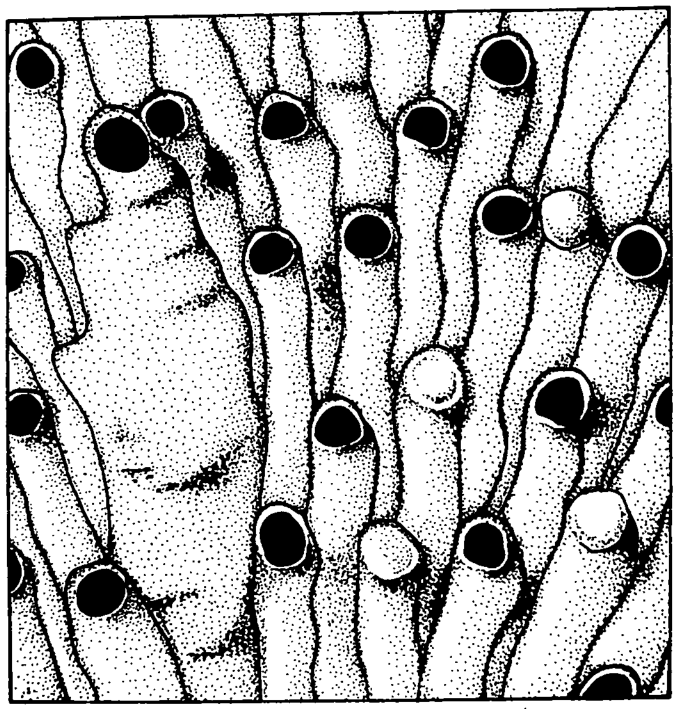


Fig. 95. Collapora microstoma (Michelin) BMNH D52645e. Upper Bathonian, Bradford Fossil Bed, Sunhill, Gloucestershire. Occluded auto-zooecia from a lamellar overgrowth on an erect branch. Bar represents 1 mm.

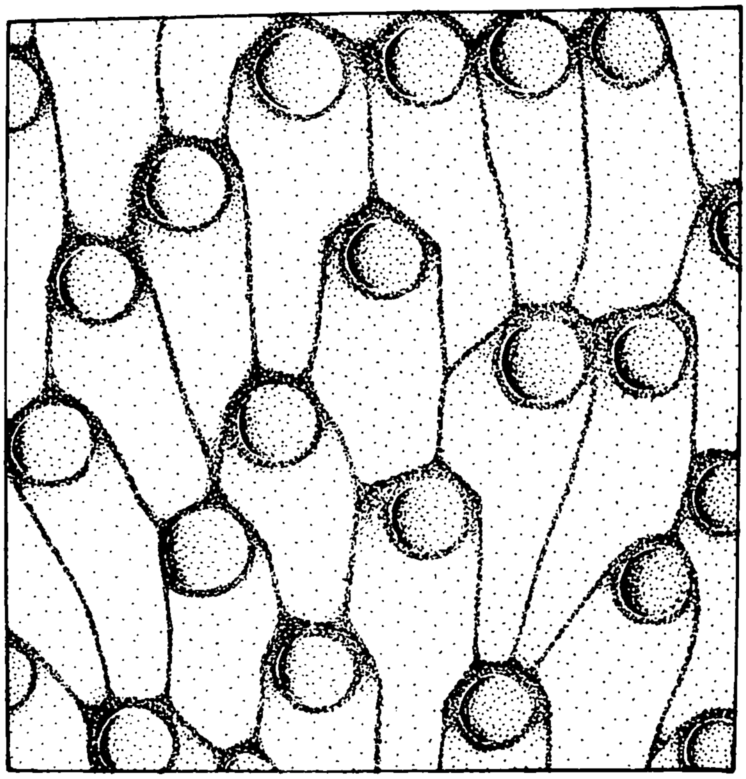


Fig. 96. Collapora microstoma (Michelin) BMNH D52645g. Upper Bathonian, Bradford Fossil Bed, Sunhill, Gloucestershire. Zooecia in an abraded frontally-budded intra-zoarial overgrowth on an erect branch. Bar represents 1 mm.

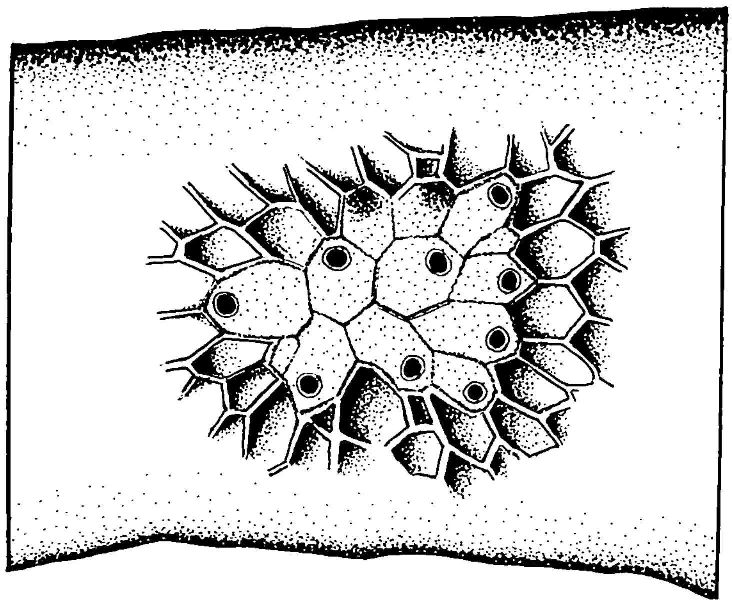


Fig. 97. Collapora tetragona (Lamouroux)
PT 549-5. Upper Bathonian, St. Aubin Member, Carriere des Campagnettes, Ranville, Normandy. A quadrate branch with autozooecia. Bar represents 1 mm.

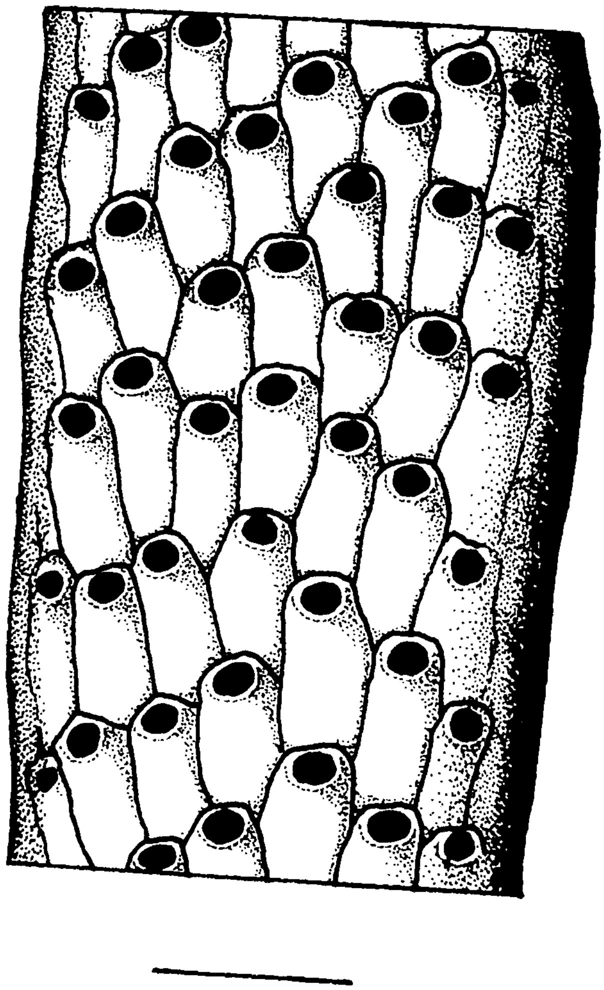


Fig. 98. _Hyporosopora_ _typica_ Canu and Bassler PT A4-lla. Upper Bathonian, Bradford Clay, Bradford-on-Avon, Wiltshire. Autozooecia with 1 complete gonozooecium and a portion of a second. Bar represents 1 mm.

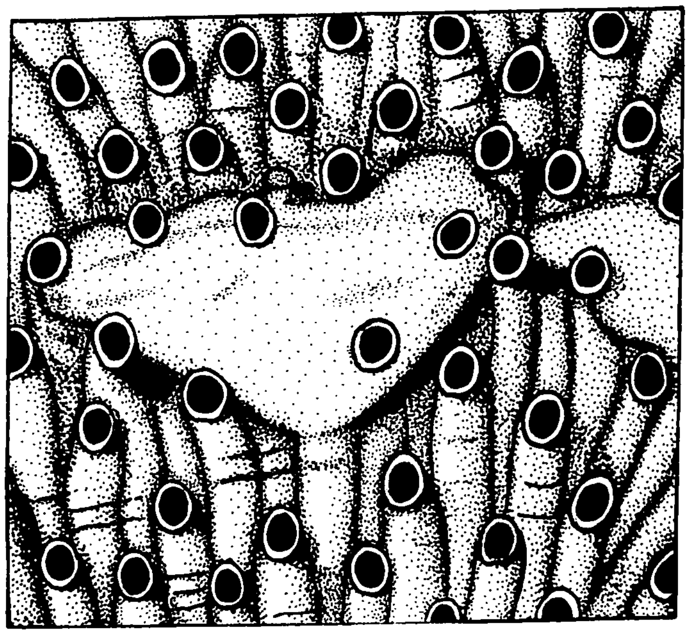


Fig.99. _Hyporosopora_ _parvipora_ (Canu and Bassler) PT 67-15. Bathonian, White Limestone, Woodeaton, Oxfordshire. Gonozooecium, autozooecia, and a growth margin. Bar represents 1 mm.

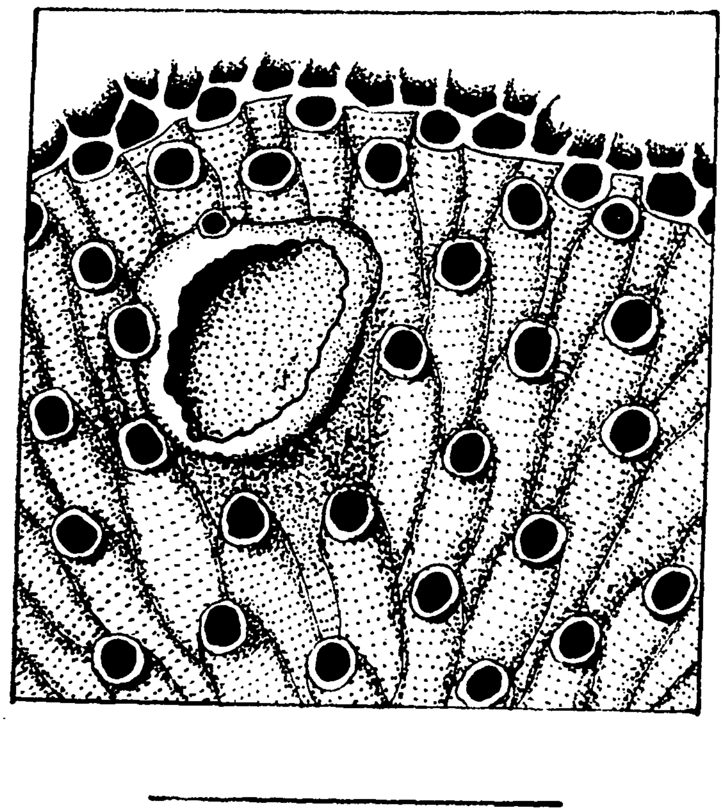


Fig. 100 Hyporosopora portlandica (Gregory) BMNH D47325. Portlandian, Portland Stone, either Tisbury, Wiltshire, or Portland, Dorset. Autozooecia and a gonozooecium. Bar represents 1 mm.

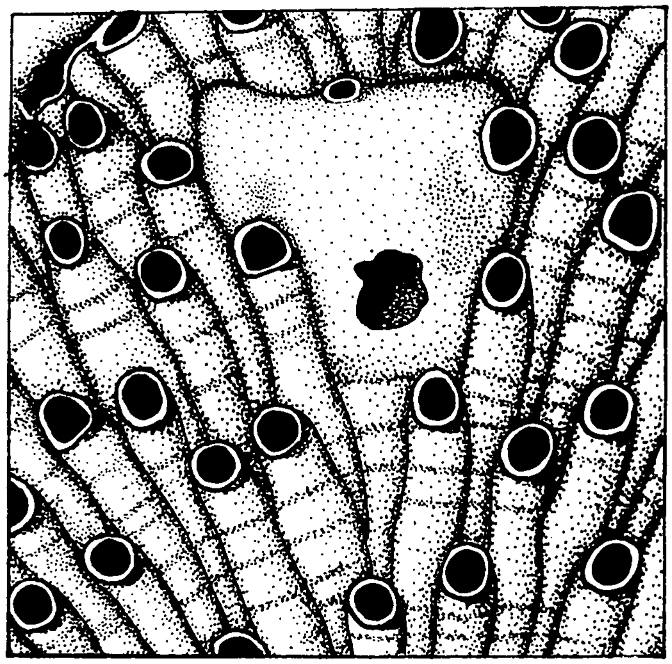


Fig. 101. <u>Hyporosopora</u> <u>sauvagei</u> (Gregory) PT B708. Upper Bathonian, Boueti Bed, Herbury, Dorset. Gonozooecium and a group of autozooecia. Bar represents 1 mm.

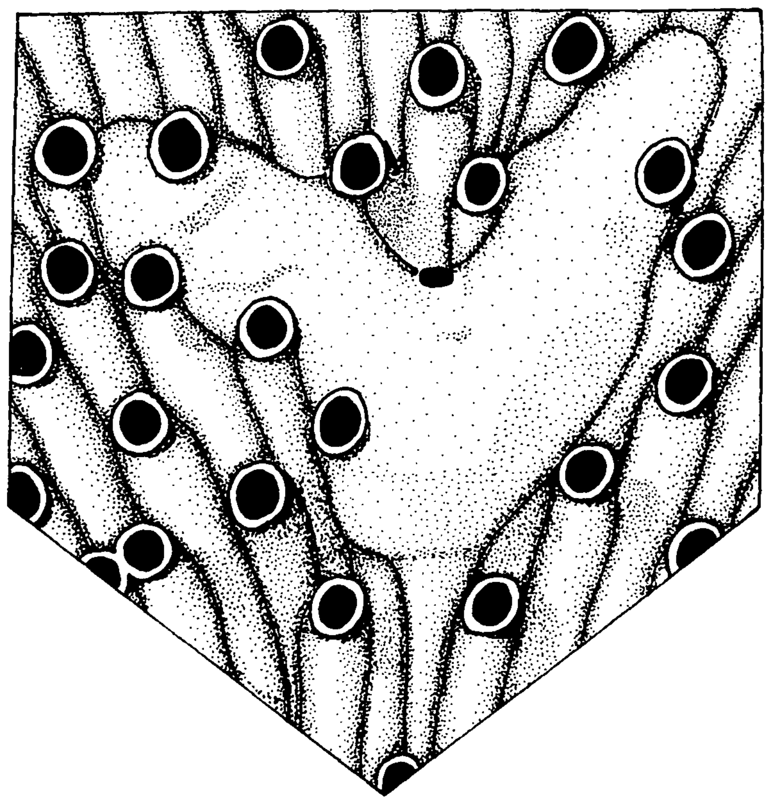


Fig.102. Mesenteripora undulata (Michelin)
PT 641-1. Upper Bathonian, Langrune Member caillasse, Luc-sur-mer, Normandy. Gonozooecium, autozooecia and a growth margin. Bar represents 1 mm.

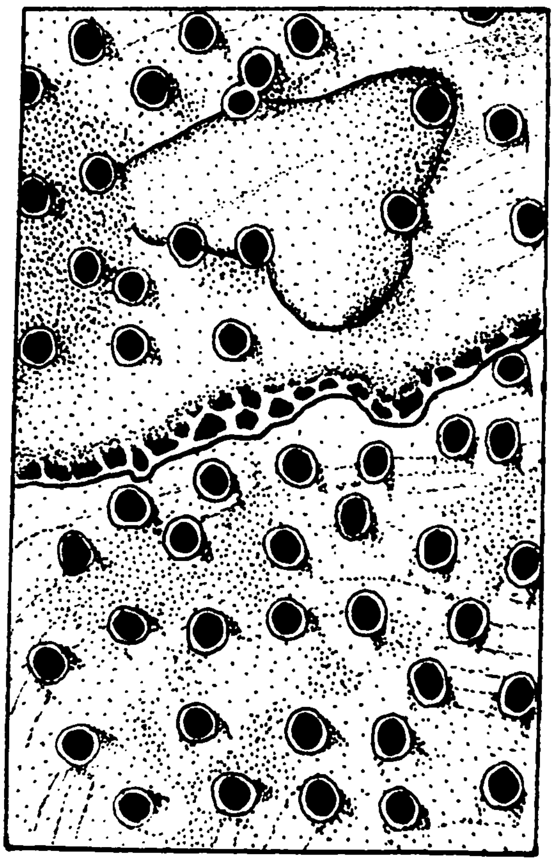


Fig. 103. Mesenteripora undulata (Michelin)
BMNH D13416. Upper Bathonian,
Bradford-on-Avon, Wiltshire.
Autozooecia are crossed by
transverse ridges. Bar represents
1 mm.

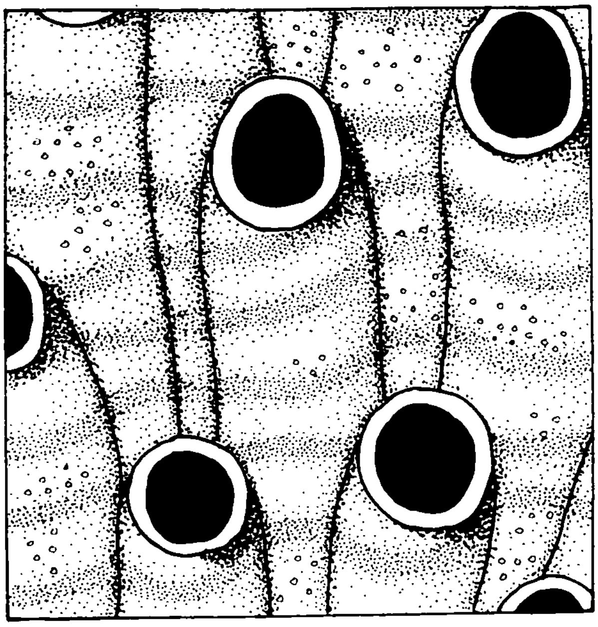


Fig. 104. *Reticulipora dianthus* (de Blainville)
PT 546-1. Upper Bathonian, St. Aubin Member, Carriere des Campagnettes, Ranville, Normandy. Group of occluded autozooecia. Bar represents 1 mm.

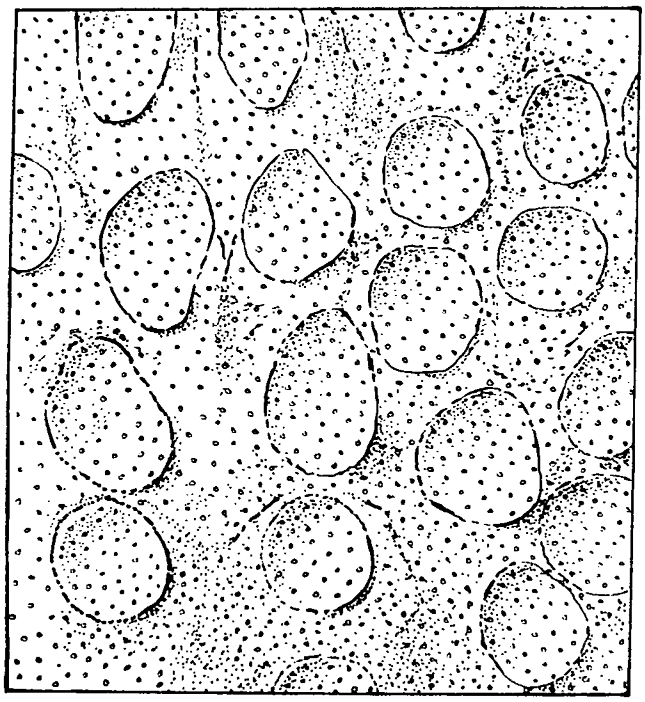


Fig. 105. Entalophora annulosa (Michelin)
PT 608-3. Upper Bathonian, Langrune Member, Luc-sur-mer, Normandy. Vinculariiform branch with autozooecia. Bar represents 1 mm.

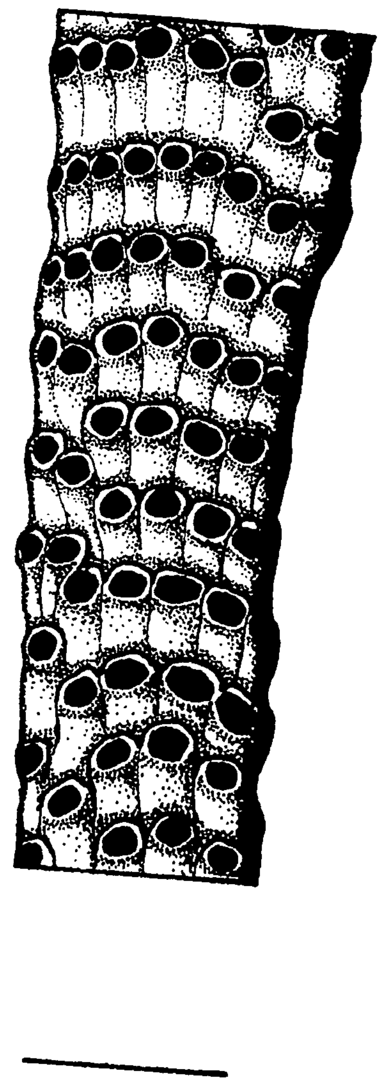


Fig. 106. '*Mecynoecia*' *bajocina* (d'Orbigny) PT 157. Bajocian, Microzoa Bed, Shipton Gorge, Dorset. Autozooecia on a vinculariiform branch with an apical growth tip preserved. Bar represents 1 mm.

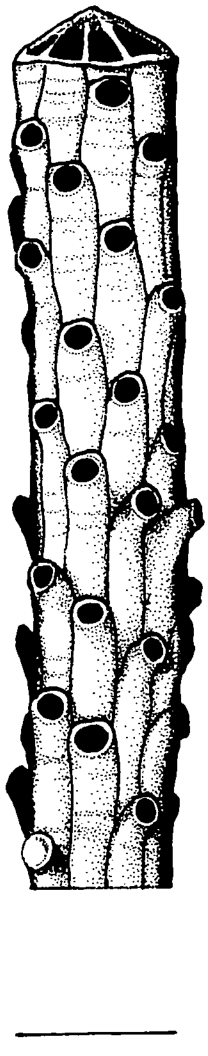


Fig. 107. _Terebellaria_ _ramosissima_ Lamouroux BMNH D2111. Bathonian, Ranville, Normandy. Gonozooecium and occluded exozonal autozooecia. Colony growth direction was from top to bottom. Bar indicates 1 mm.

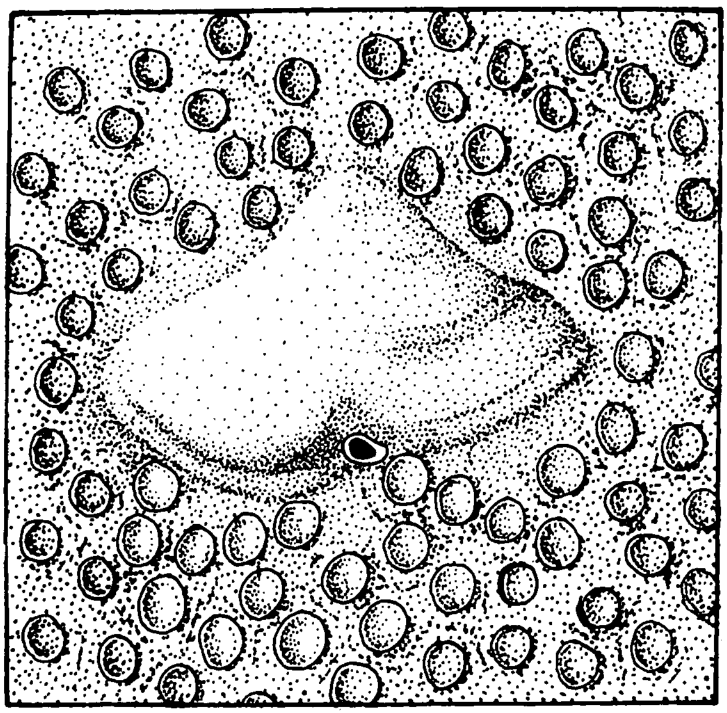


Figure 108. Vertical and horizontal sections through the Upper Bathonian of St. Aubin-sur-mer, Normandy. The horizontal section begins in the east where the concrete casing on the cliff terminates. Reefs are dashed in the horizontal section.

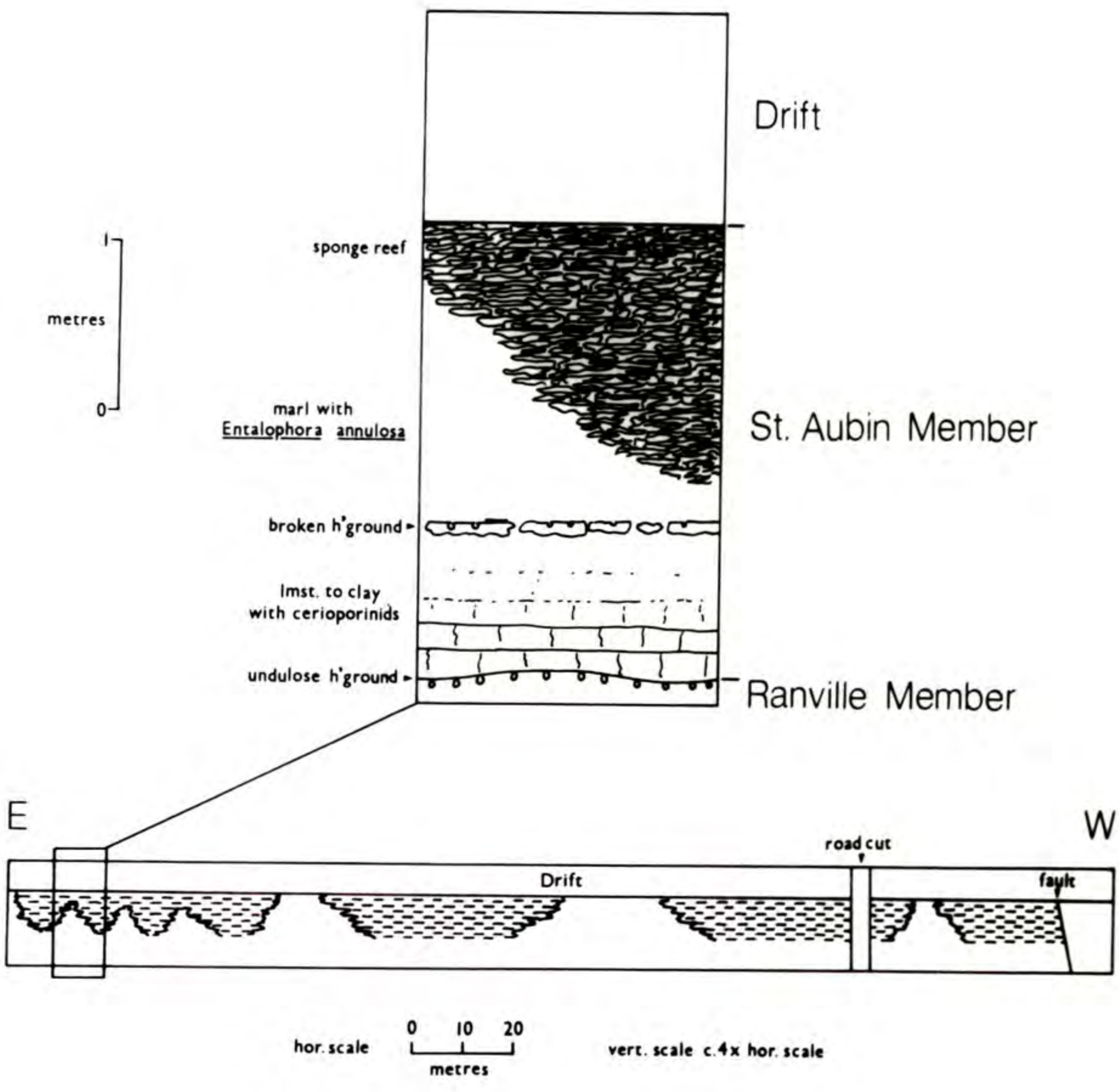

Drift
sponge reef
1
metres
0
marl with
Entalophora annulosa
St. Aubin Member
broken h'ground
lmst. to clay
with cerioporinids
undulose h'ground
Ranville Member
E
W
road cut
Drift
fault
hor. scale
0 10 20
metres
vert. scale c.4x hor. scale

Plate 1. SEM photomicrographs of polished and etched zoarial sections.

Fig.a. Reptomultisparsa incrustans PT 541-1B Upper Bathonian, St. Aubin Member, Carriere des Campagnettes, Ranville, Normandy. Transverse section through two zooecia and part of an overgrowing zoarial layer. Arrowhead indicates the junction between overgrowing (upper right) and overgrown (lower left) zoarial layers. X500.

Fig.b. Collapora straminea PT A3-100 Bajocian, Millepore Bed, Yons Nab, Yorkshire. Transverse zoarial section at the endozone-exozone boundary. Zooecia in the exozone possess an outer laminar layer (arrowed) absent from zooecia in the endozone (right). X500.

a

b

Plate 2. Collapora straminea. SEM photomicrographs of polished and etched zoarial sections.

Fig.a. PT 73 Upper Aalenian, Lower Freestone, Cleeve Hill, Gloucestershire. Transverse zoarial section showing inner and outer laminar layers, and interzooecial pores. X500.

Fig.b. PT A3-100 Bajocian, Millepore Bed, Yons Nab, Yorkshire. Transverse zoarial section showing deflection of wall laminae in the vicinity of an interzooecial pore (arrowed). X500.

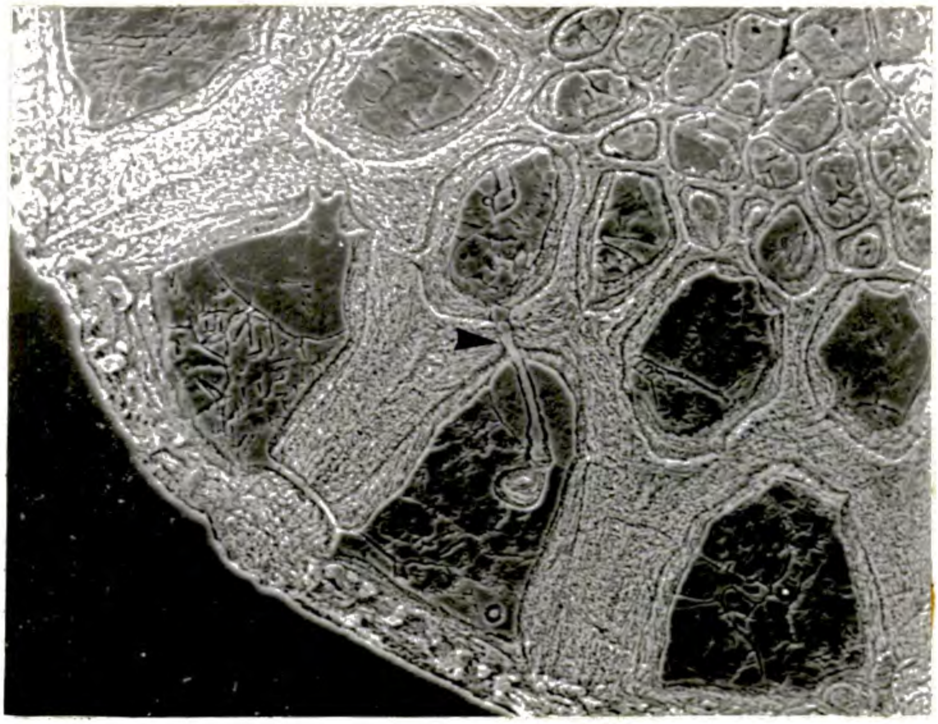
a

b

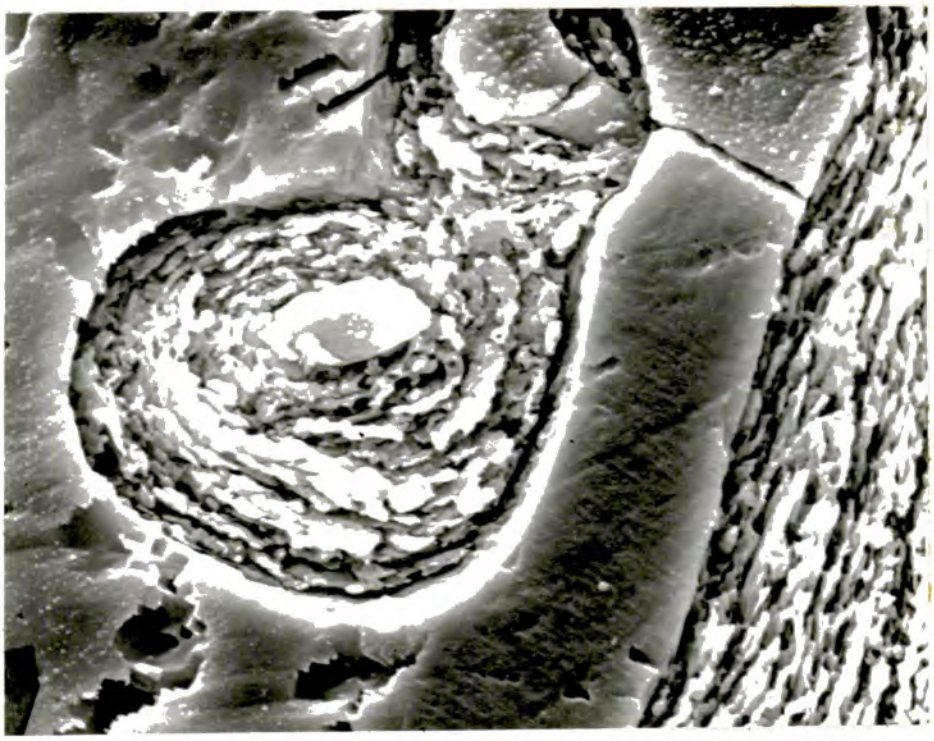
Plate 3. _Collapora_ _straminea_ SEM photomicrographs of polished and etched zoarial sections. PT A3-100 Bajocian, Millepore Bed, Yons Nab, Yorkshire. Transverse zoarial sections showing interzooecial wall ultra-structure and a paradoxical intrazooecial structure apparently eminating from an interzooecial pore (arrowed in fig.a).

Fig.a. X200.

Fig.b. X2000.



a



b

Plate 4. SEM photomicrographs of polished and etched zoarial sections.

Fig.a. Collapora straminea. PT 73 Upper Aalenian, Lower Freestone, Cleeve Hill, Gloucestershire. Ultrastructure of an interzooecial wall and a zooecial frontal wall. Skeletal laminae are deflected towards the exterior (arrowed) at their junction with pseudopores in the zooecial frontal wall. X500.

Fig.b. Collapora microstoma. PT A5-26 Upper Bathonian, Upper Rags, Bathampton, Somerset. Section through a zooecium with a conspicuous pseudopore (arrowed) penetrating the frontal wall which apparently protrudes into the overgrowing zoarial layer at the top of the photomicrograph. X1000.

a

b

Plate 5. SEM photomicrographs of polished and etched zoarial sections.

Fig.a. Mesenteripora undulata PT 573-1 Upper Bathonian, ?Langrune Member, Commeaux, Normandy. Transverse section through a zoarial layer with the basal lamina at the top right. Interzooecial walls possess an apparent thin outer laminar layer (arrowed). X500.

Fig.b. Entalophora annulosa PT 655-2 Upper Bathonian, St. Aubin Member, St. Aubin-sur-mer, Normandy. Interzooecial wall with well-developed outer laminar layer (arrowed) near to its junction with a zooecial frontal wall (f). X200.

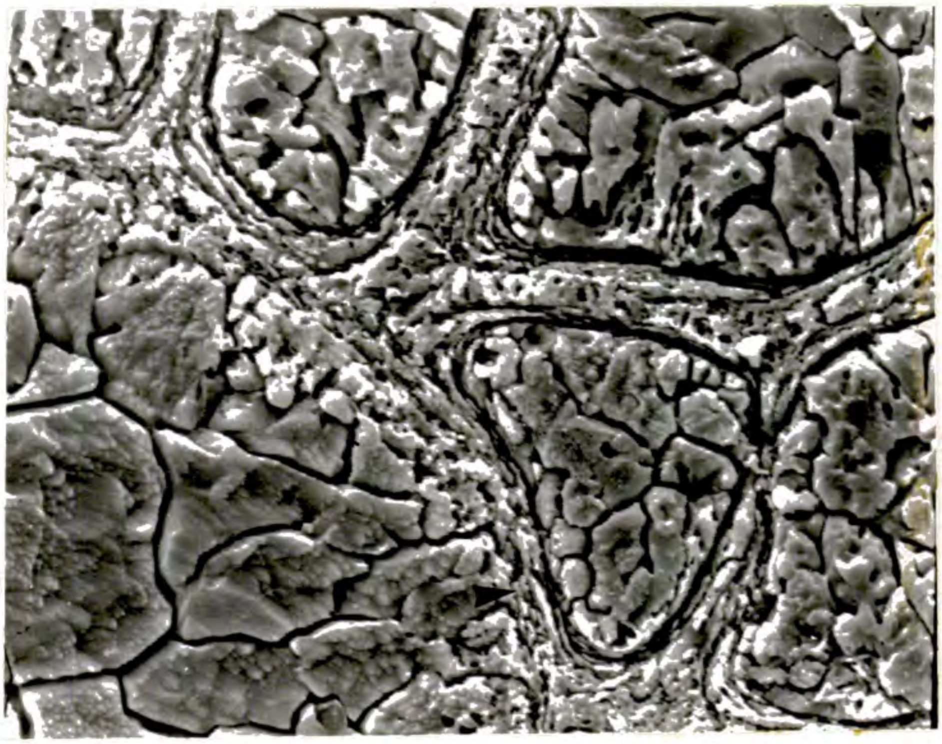
a

b

Plate 6. SEM photomicrographs of polished and etched zoarial sections.

Fig.a. _Entalophora annulosa_ PT 655-2 Upper Bathonian, St. Aubin Member, St. Aubin-sur-mer, Normandy. Portion of the tube-shaped budding lamina (arrowed) showing its very indistinct boundary with secondary calcite filling the branch axial lumen (bottom left). X1000.

Fig.b. '_Mecynoecia_' _bajocina_ PT 765-5A Bajocian, Microzoa Bed, Shipton Gorge, Dorset. Interzooecial wall with thick inner and outer laminar layers and zooecial frontal walls (f). Laminae of the inner laminar layer appear to be orally divergent in the region indicated by the arrowhead. X500.



a

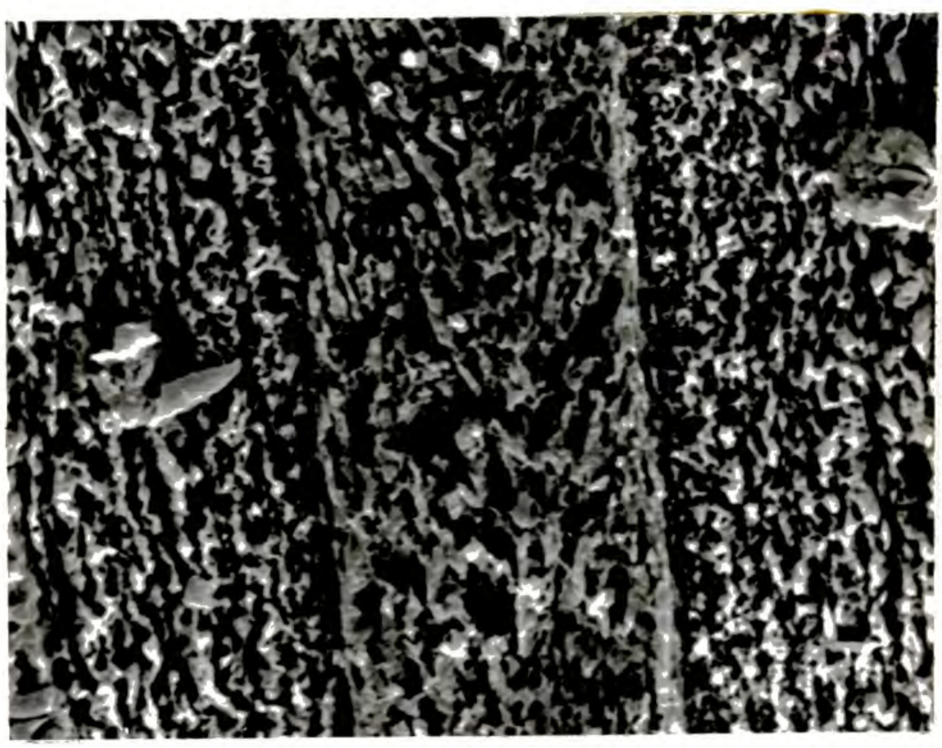
b

Plate 7. 'Mecynoecia' bajocina PT 765-5A
Bajocian, Microzoa Bed, Shipton Gorge, Dorset. SEM photomicrographs of a polished and etched zoarial section.

Fig.a. Transverse section through the axial region of a branch. Zooecia were budded around the branch axis (a). A secondary laminar layer developed during zooidal ontogeny and interzooecial walls separating zooecia of widely differing ages are markedly asymmetrical (arrowed). X500.

Fig.b. Interzooecial wall with a comparatively coarse laminar layer flanked by a fine laminar layer on both sides. Distal is towards the top of the plate. X2000.

a



b

Plate 8. <u>Terebellaria</u> <u>ramosissima</u> BMNH D2111 'Bathonian, Ranville, Normandy' SEM photomicrographs of a polished and etched zoarial section.

Fig.a. Interzooecial wall with a pore (arrowed) dividing into two zooecial frontal walls overgrown by the basal lamina of a succeeding exozonal layer. X400.

Fig.b. Zooecial frontal wall with two pseudopores (centre) covered by the basal lamina (arrowed) of a succeeding exozonal layer. X1300.

a

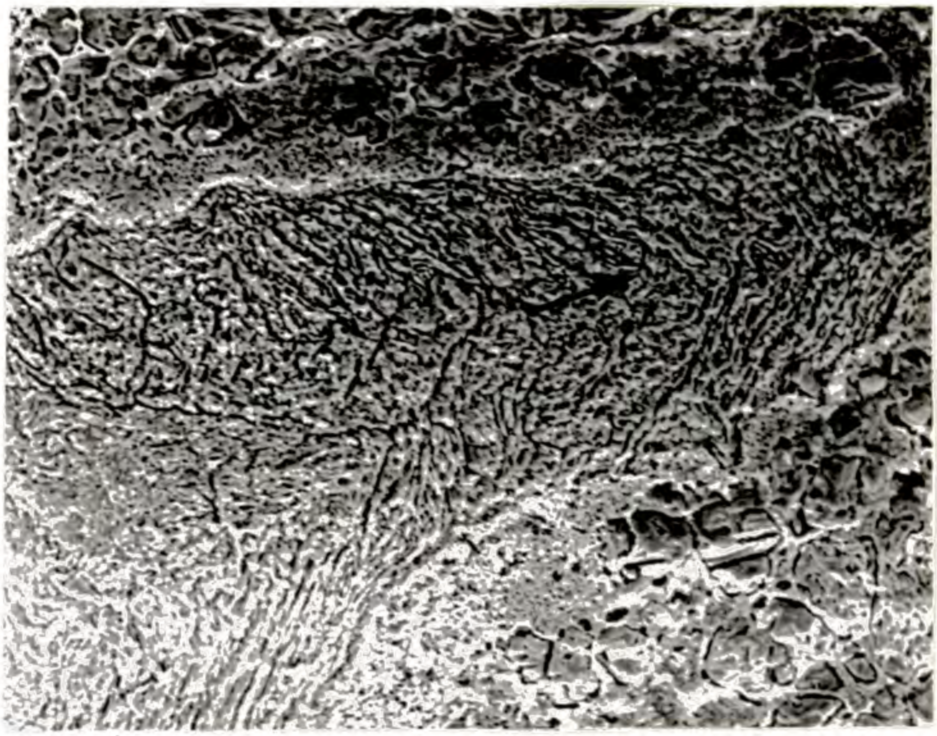
b

Plate 9. Ceriocava corymbosa PT 655-3 Upper Bathonian, St. Aubin Member, St. Aubin-sur-mer, Normandy. SEM photomicrographs of a polished and etched zoarial section.

Fig.a. Oblique section showing interzooecial walls and thin basal diaphragms orally flexed at their junction (arrowed) with interzooecial walls. X200.

Fig.b. Aborally divergent laminae in an interzooecial wall. The arrow indicates the direction of wall growth. X500.

a



b

Plate 10. SEM photomicrographs of polished and etched zoarial sections.

Fig.a. Cava subcompressa PT 549-2 Upper Bathonian, St. Aubin Member, Carriere des Campagnettes, Ranville, Normandy. Longitudinal section through asymmetrical interzooecial walls with thicker outer laminar layers on their proximal sides (arrowed) than on their distal sides. X200.

Fig.b. Crescis dumetosa PT 549-1 Upper Bathonian, St. Aubin Member, Carriere des Campagnettes, Ranville, Normandy. Transverse zoarial section showing a bilamellar budding lamina penetrated by a possible interzooidal pore (arrowed). X200.

a

b

Plate 11. SEM photomicrographs of polished and etched sections.

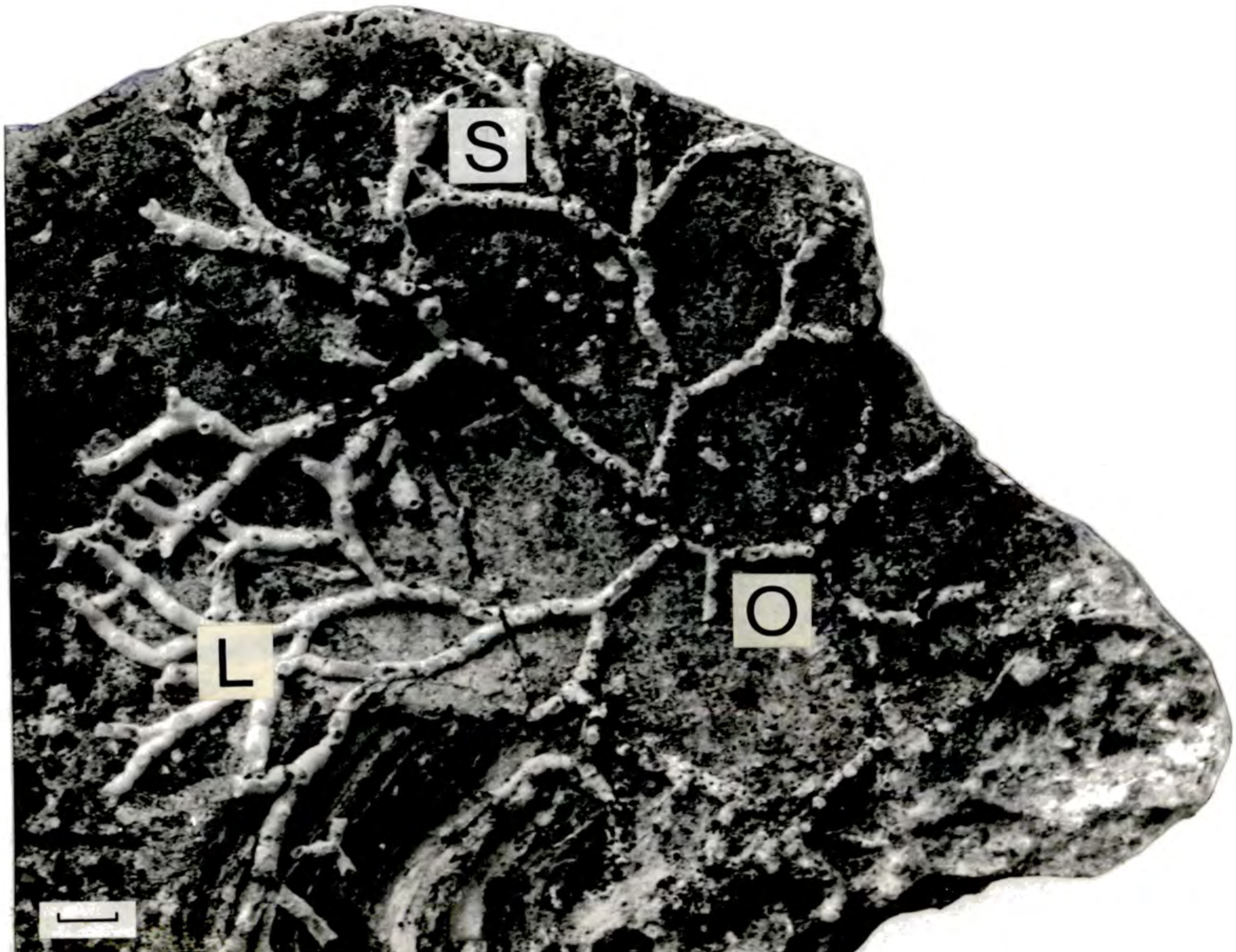
Fig.a. Alveolaria semiovata PT 416. Pliocene, Coralline Crag, Suffolk. Transverse section of an interzooecial wall showing a tripartite structure. X2800.

Fig.b. Neuropora sp. PT 172. Bajocian, Microzoa Bed, Shipton Gorge, Dorset. Transverse section through a cylindrical specimen. The solid skeleton is composed of concentric laminae with regular deflections (arrowed) towards the exterior. X200.

a

b

Plate 12. *Stomatopora dichotomoides* BMNH D52642, Upper Bathonian (probably Kemble Beds), Baunton near Cirencester. The analysis of spatial heterogeneity of zooecial length enabled a patch of long zooecia (L) and a patch of short zooecia (S) to be identified within the zone of astogenetic repetition. The colony originates at O. Bar at the bottom left represents 1mm.



S
L
O

Plate 13. <u>Stomatopora</u> and colony growth-forms

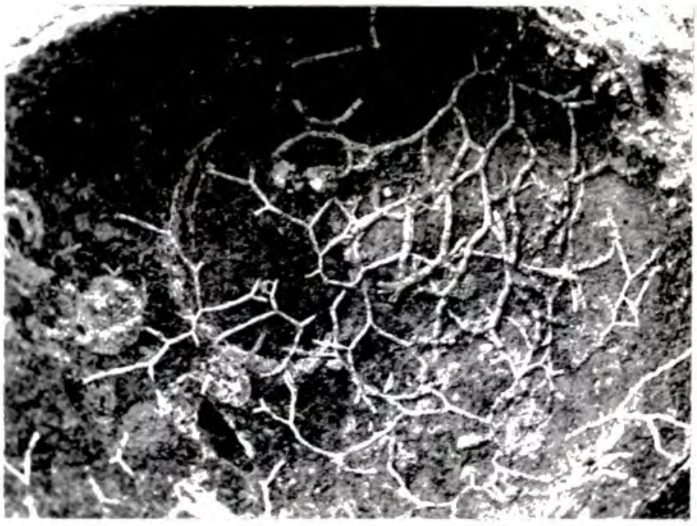
Fig.a. <u>Stomatopora</u> colonies encrusting an oyster valve. PT 497-4 Bathonian, Baunton, Gloucestershire. X3.

Fig.b. Symmetrical colony of <u>S.bajocensis</u>. Colony origin (the protoecium) is marked with a black dot. PT 497-71 Bathonian, Baunton, Gloucestershire. X9.

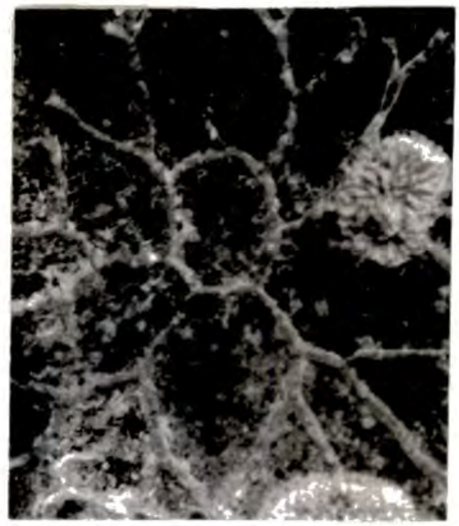
Fig.c. <u>S.bajocensis</u>. After the 2nd branch dichotomy (arrowed) the lower branch buds 1 zooecium and the upper branch 2 zooecia before dichotomising. PT 497-5A Bathonian, Baunton, Gloucestershire. X9.

Fig.d. Probosciniiform zoarium. PT B250. Boueti Bed, Dorset. X11.

Fig.e. Bereniciform zoarium. BMNH D47329 Oxford Clay, Woodham Brich Pit, Buckinghamshire. X11.



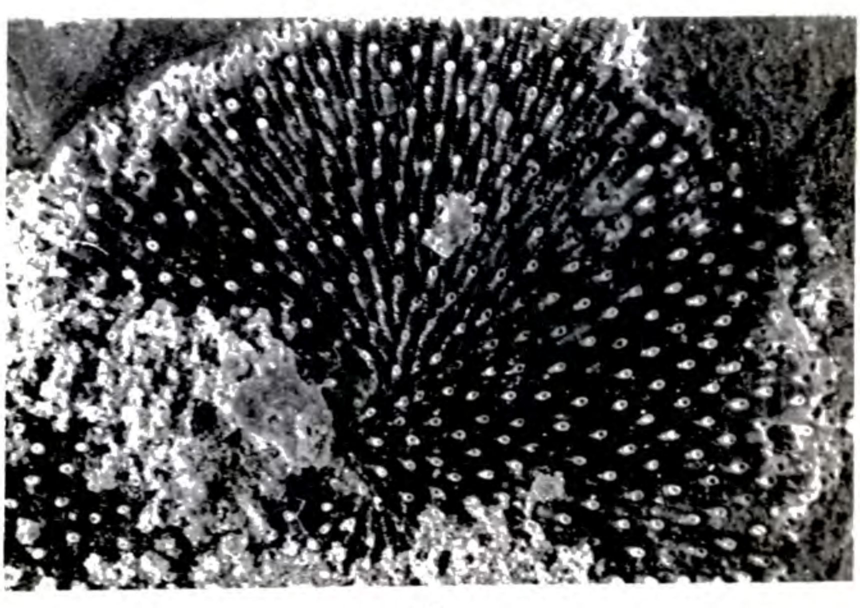
a



b

c

d



e

Plate 14. Colony growth-forms.

Fig.a. Reptomultisparsiform. Abraded zoarium of *Mesenteripora undulata* with layers visible at the right. BMNH 35250 Bradford Clay, Bradford-on-Avon. X2.5.

Fig.b. Vinculariiform. *Collapora straminea*. DGSD P2072 Inferior Oolite, Cleeve Hill, Gloucestershire. X1.5.

Fig.c. Reticuliporiform. *Reticulipora dianthus*. BMNH 60229 Bathonian, Ranville. X1.5.

Fig.d. Terebellariiform. Transverse section of *Collapora microstoma* YM 469-1 ?Lower Cornbrash, Stanton St. Quintin, Wiltshire. X35.

Fig.e. Diastoporidiform. DGSD P207 Inferior Oolite, Cleeve Hill, Gloucestershire. X3.

Fig.f. Diastoporidiform. *Mesenteripora michelini* BMNH 46785 Bathonian, Ranville. X1.5.

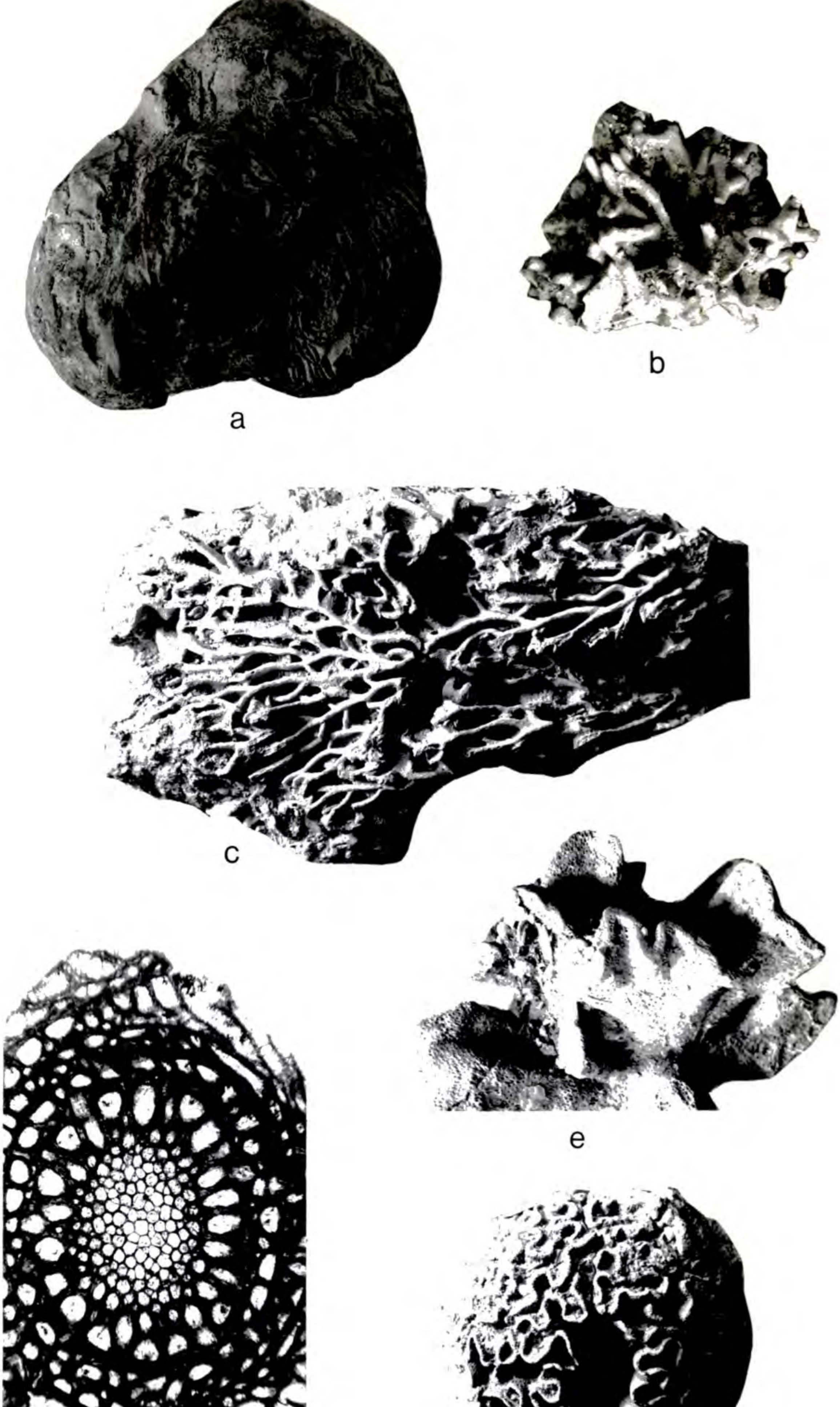

a
b
c
d
e
f

Plate 15.

Fig.a. Ceriocava corymbosa showing contiguous polygonal zooecial apertures which are occluded by terminal diaphragms slightly proximal to the edges of the interzooecial walls. PT 653-4 St. Aubin Member, St.Aubin-sur-mer, Normandy. X9.

Fig.b. C.corymbosa. An ovicell (left centre) has an abraded frontal wall which is pseudoporous. PT 653-8 St. Aubin Member, St.Aubin-sur-mer. X9.

Fig.c. C.corymbosa. Transverse section showing regular interzooecial budding. The zooecium indicated with a star is surrounded by 6 young buds. PT 554-2 Campagnettes Member, Carriere des Campagnettes, Ranville, Normandy. X85.

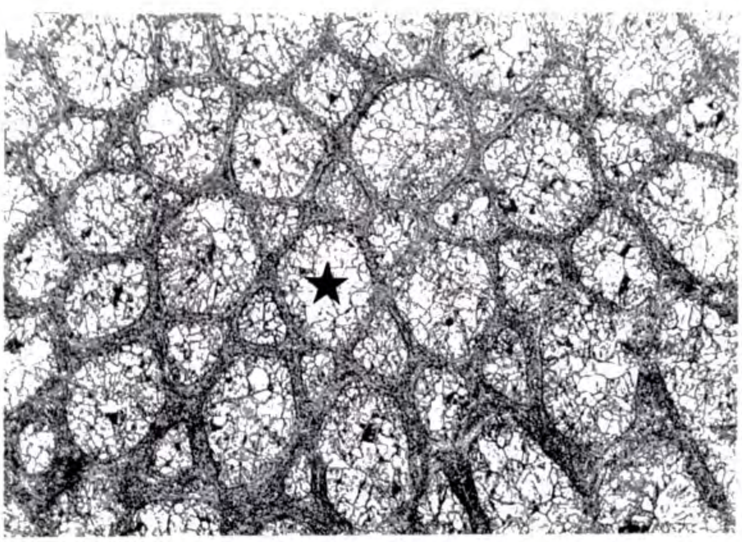
Fig.d. Transverse section through the cavariiform base of a diastoporidiform zoarium. The cylindrical cavity, now calcite-filled, may have been occupied by a marine plant during life. Negative photograph prepared from an acetate peel. PT 207-1 Lower Freestone, Cleeve Hill, Gloucestershire. X10.

Fig.e. Ripisoecia conifera. Zoarial T.S. with zooecia cut longitudinally in the exozone where they possess numerous basal diaphragms often at equivalent heights in adjacent zooecia. PT 608-1A Langrune Member, Luc-sur-mer, Normandy. X38.

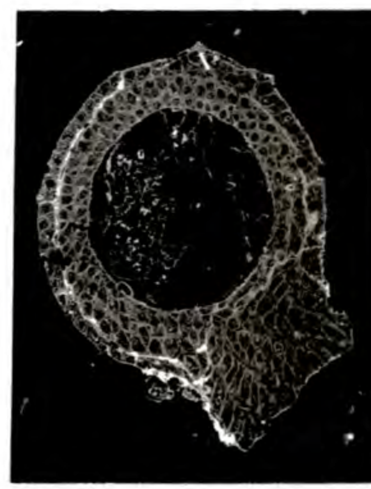
Fig.f. Reptomultisparsa oolitica. 'Stunted' autozooecia in a hollow on the substrate. BMNH D1828 Inferior Oolite, ?locality. X12.

a

b



c



d

e

f

Plate 16.

Fig.a. Bereniciform zoarium with two fan-shaped lateral lobes. BMNH D30035 Pea Grit, Frith Quarry, Gloucestershire. X12.

Fig.b. Assymmetrical fan-shaped bereniciform zoarium. PT A7-1 Pea Grit, Leckhampton Hill, Gloucestershire. X12.

Fig.c. Inferred growth of a bereniciform colony around an unpreserved object represented by a patch of vacant substrate (centre). PT 497-21 Bathonian, Baunton, Gloucestershire. X12.

Fig.d. Immature peripheral fan-shaped subcolony (arrowed). PT 497-26 Bathonian, Baunton, Gloucestershire. X19.

Fig.e. Reversal of growth direction (centre) in a bereniciform zoarium. PT 653-5 St. Aubin Member, St. Aubin-sur-mer, Normandy. X10.

Fig.f. Reversal of growth direction in Reptomultisparsa oolitica (Vine). An autozooecium with apertures at both ends of its frontal wall is arrowed. BMNH D1828 Inferior Oolite, ?locality. X12.

Fig.g. Kenozooecia (e.g. arrowed) at the anastomosis between growth margins of bereniciform colonies. PT 653-2 St. Aubin Member, St. Aubin-sur-mer, Normandy. X20.

Fig.h. Lobate expansion at the margin of a bereniciform zoarium BMNH D41611 Oxford Clay, Woodham Brick Pit, Buckinghamshire. X11.

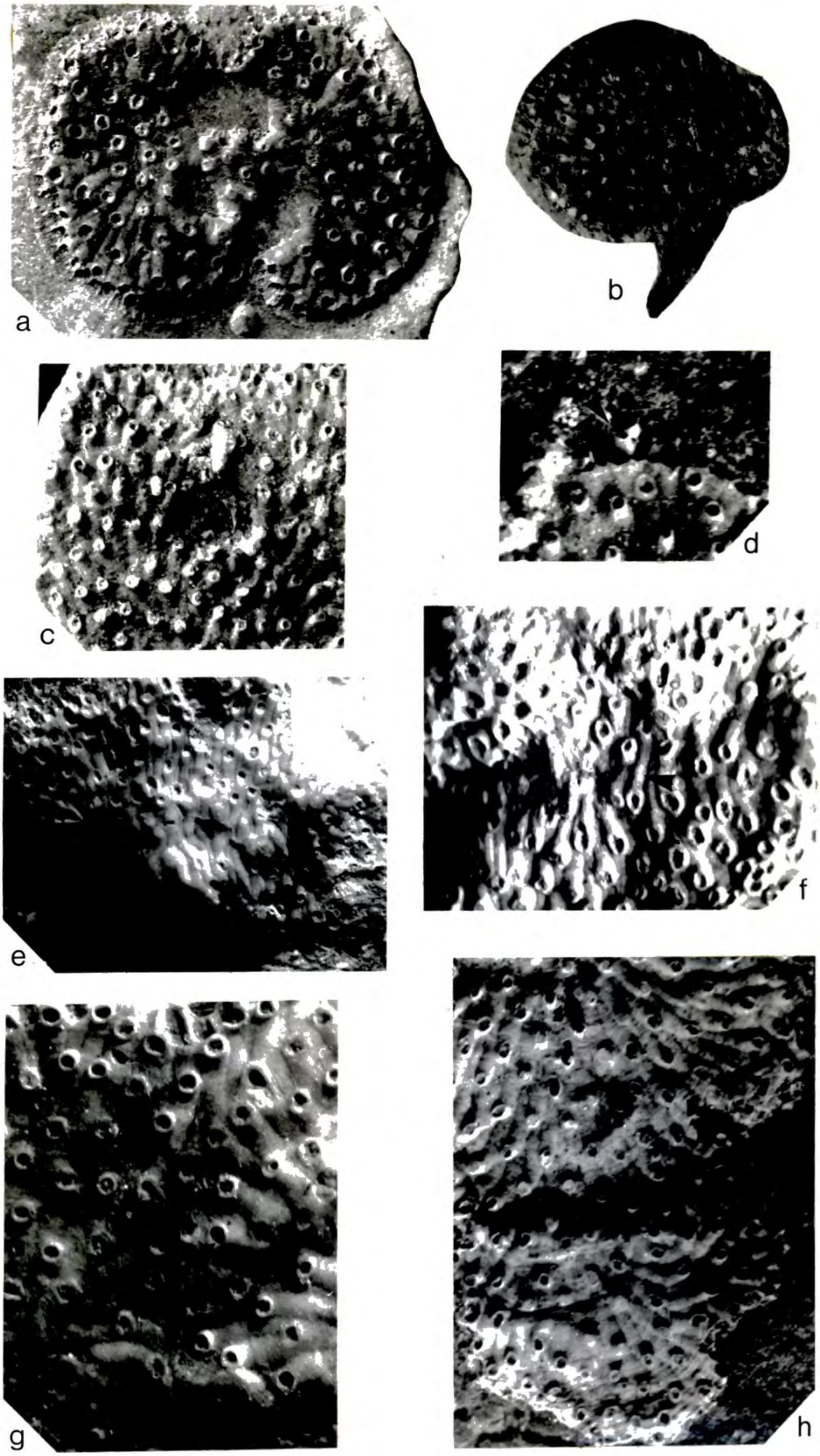


Plate 17. Alveolaria semiovata Busk.

Fig.a. Ridge formed by juxtaposed subcolonies in the erect stage of growth. Fractured specimen. DGSD P2068 Pliocene Coralline Crag, Suffolk. X12.

Fig.b. Erect (e) and tabular (t) stages of growth. DGSD P2068 Corraline Crag, Suffolk. X12.

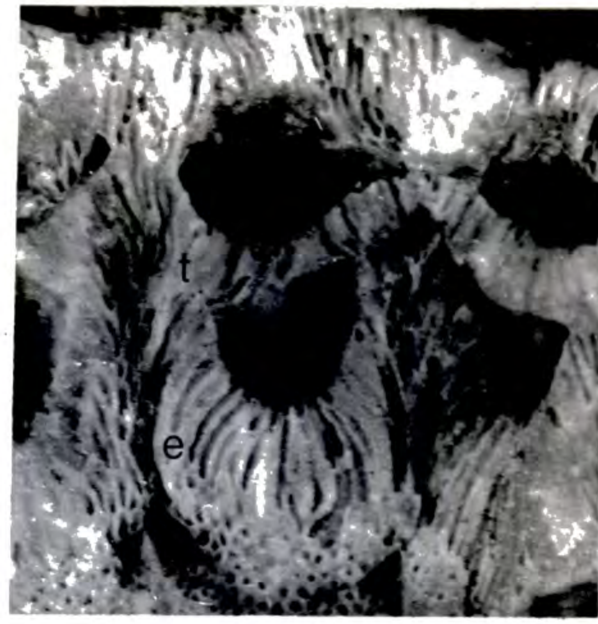
Fig.c. Interdigitating juxtaposed budding laminae (centre) belonging to adjacent subcolonies. PT 213-1 Coralline Crag, Suffolk. X80.

Fig.d. Ridged surface of a zoarium in the erect stage of growth. GL 928 Coralline Crag, Suffolk. X12.

Fig.e. Flat surface of a zoarium in the tabular stage of growth. GL 2113 Aldeburgh Brick Pit, Suffolk. X12.

Fig.f. New subcolonies forming as thick-walled areas (e.g. arrowed) at the centres of existing subcolonies. DGSD P2068 Coralline Crag, Suffolk. X12.

a



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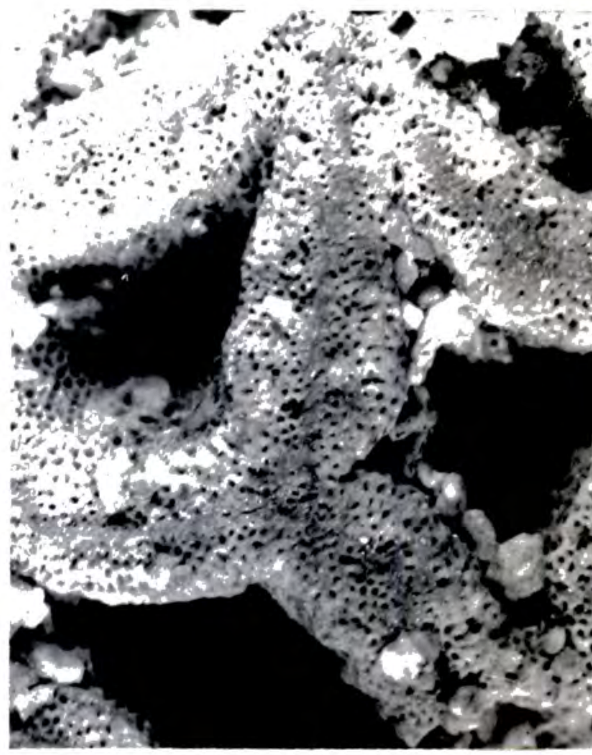

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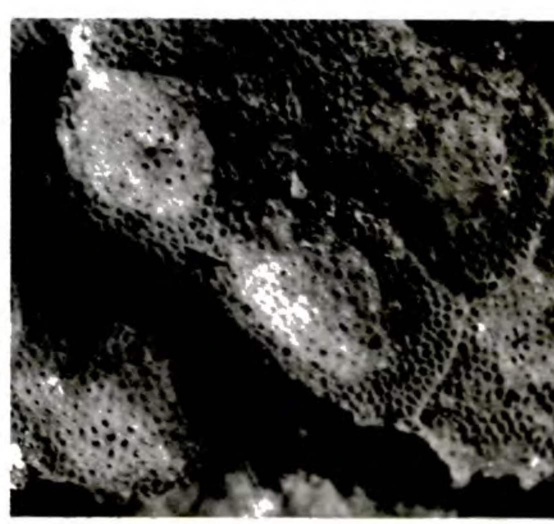

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Plate 18 Differing arrangements of autozooecial apertures from which extrazooidal water current systems may be inferred (Chapter 18).

Fig.a. Near hexagonal close-packing of apertures. *Hyporosopora sauvagei* PT A4-17 Bradford Clay, Bradford-on-Avon. X12.

Fig.b. Apertures on long peristomes in a distal ontogenetic zone '*Entalophora*' *clavata* BMNH (Zool.) 1967.8.6.5 Recent. X8.

Fig.c. Apertures in radial rows. *Plagioecia patina* BMNH 1911.10.1.154 Recent. X8.

Fig.d. Apertures in transverse rows or nodes. *Spiropora elegans* PT 655 St. Aubin Member, St. Aubin-sur-mer. X9.

Fig.e. Apertures in linear fascicles. '*Actinopora*' BMNH D30005 Lower Inferior Oolite, Crickley Hill. X1.7.

Fig.f. Apertures in circular fascicles. *Meandropora tubipora* GL 2112 Pliocene Coralline Crag, Suffolk. X7.

Fig.g. Open apertures in an outer ontogenetic zone (zone 2) Bereniciiform tubuloporinid BMNH D2237 Bathonian, Ranville. X18.

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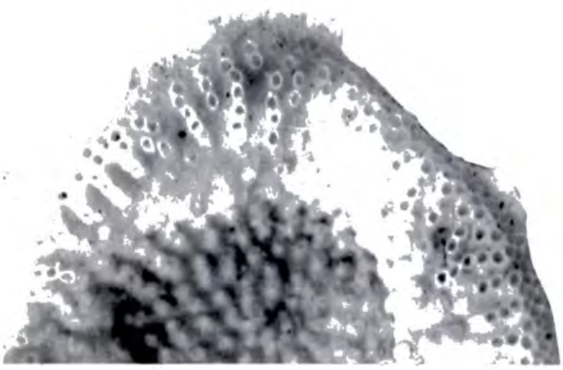

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Plate 19 Zoarial morphologies indicative of extrazooidal water current system development (Chapter 18).

Fig.a. Monticules in a cheilostome (left) and and cyclostome (right) from the Tertiary of New Zealand (BMNH unnumbered). X2.

Fig.b. Monticules in a Lower Carboniferous trepostome from Ashfell Edge, Cumbria. The monticules also functioned as budding loci (arrowed). PT 385. X9.

Fig.c. Monticules in a Recent _Heteropora_ BMNH (Zool.) 1889.1.1.6 . X11.

Fig.d. Dome-shaped _Lichenopora_ BMNH (Zool.) 97.5.1.1154 Recent. X10.

Fig.e. Subtriangular branches of _Idmonea_ _Triquetra_ PT C13 Jurassic, Bradford Clay. X3.

Fig.f. Fenestrate cryptostome. DGSD P2062 Lower Carboniferous. X1.1.

Fig.g. Fenestrate cheilostome (rete porid). GL unnumbered Recent. X0.5.

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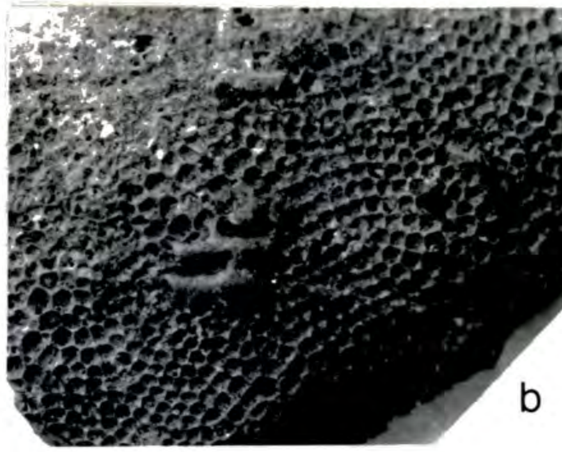

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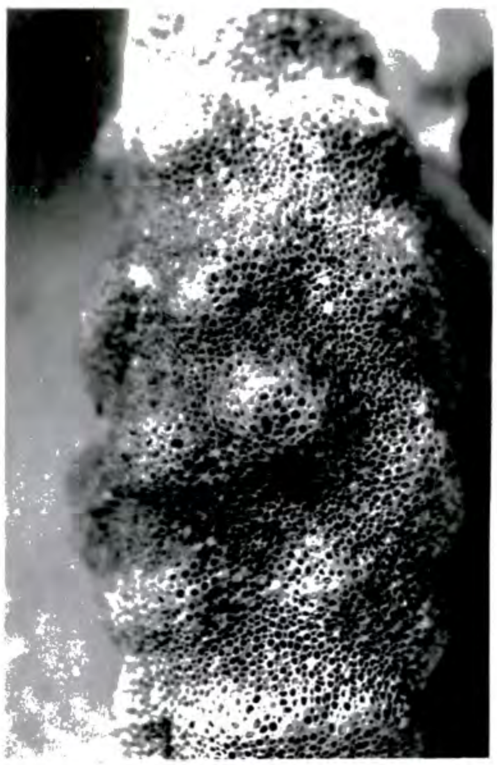

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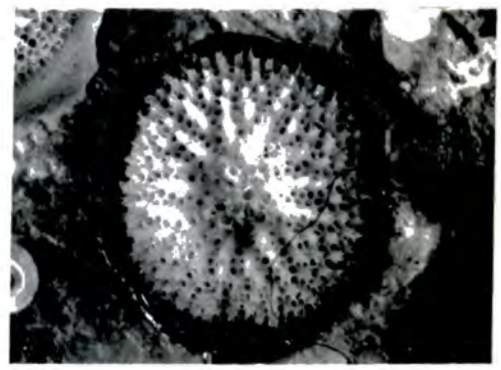

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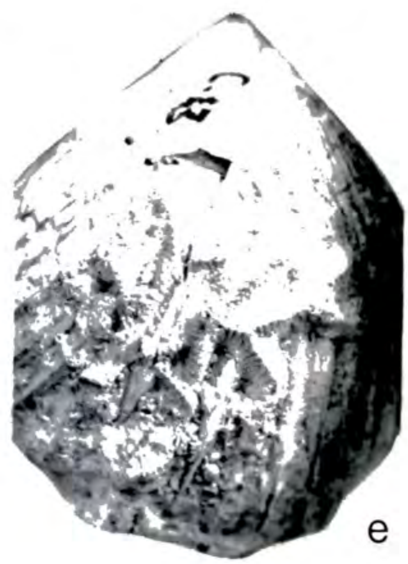

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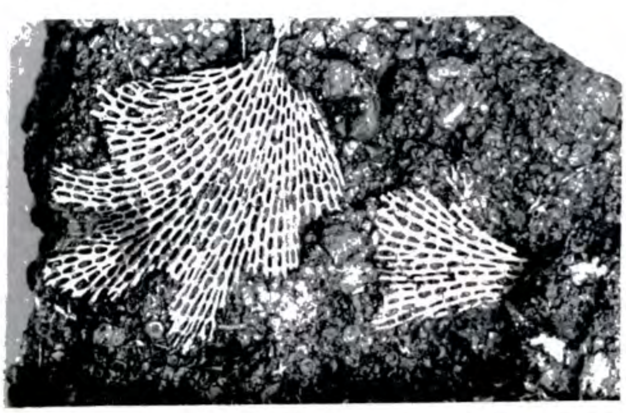

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Plate 20. _Reptomultisparsa_ _incrustans_ (d'Orbigny) except for fig.d _Hippoporidra senegambiensis_.

Fig.a. Transverse section through sediment-filled gastropod shell (g) encrusted by a thick multilamellar zoarium. BMNH 60221 Bathonian, Ranville. X4.

Fig.b. Negative photograph (prepared from an acetate peel) of a longitudinal section through a bryozoan-encrusted gastropod shell. Thinning of zooecial layers close to the shell aperture is visible and the arrow indicates the position of a change in the area of shell encrusted by the bryozoan. PT 541-1A St. Aubin Member, Carriere des Campagnettes, Ranville. X4.5.

Fig.c. The lectotype. MNHN 2981A Upper Bathonian Conlie. X3.

Fig.d. _Hippoporidra_ _senegambiensis_. Branched and pigmented colony. DGSD P6653 Recent. X2.

Fig.e. PT 541-3 Carriere des Campagnettes, Ranville. X2.

Fig.f. Thinning of zooecial layers close to the shell aperture. The thin layers are composed of kenozooecia rather than autozooecia. PT 541-1A St. Aubin Member, Carriere des Campagnettes, Ranville. X32.

Fig.g. A gonozooecium with ooeciopore arrowed. MNHN 2981 A Upper Bathonian, Conlie. X11.

Fig.h. Autozooecia. BMNH 60242 Bathonian, Ranville. X14.

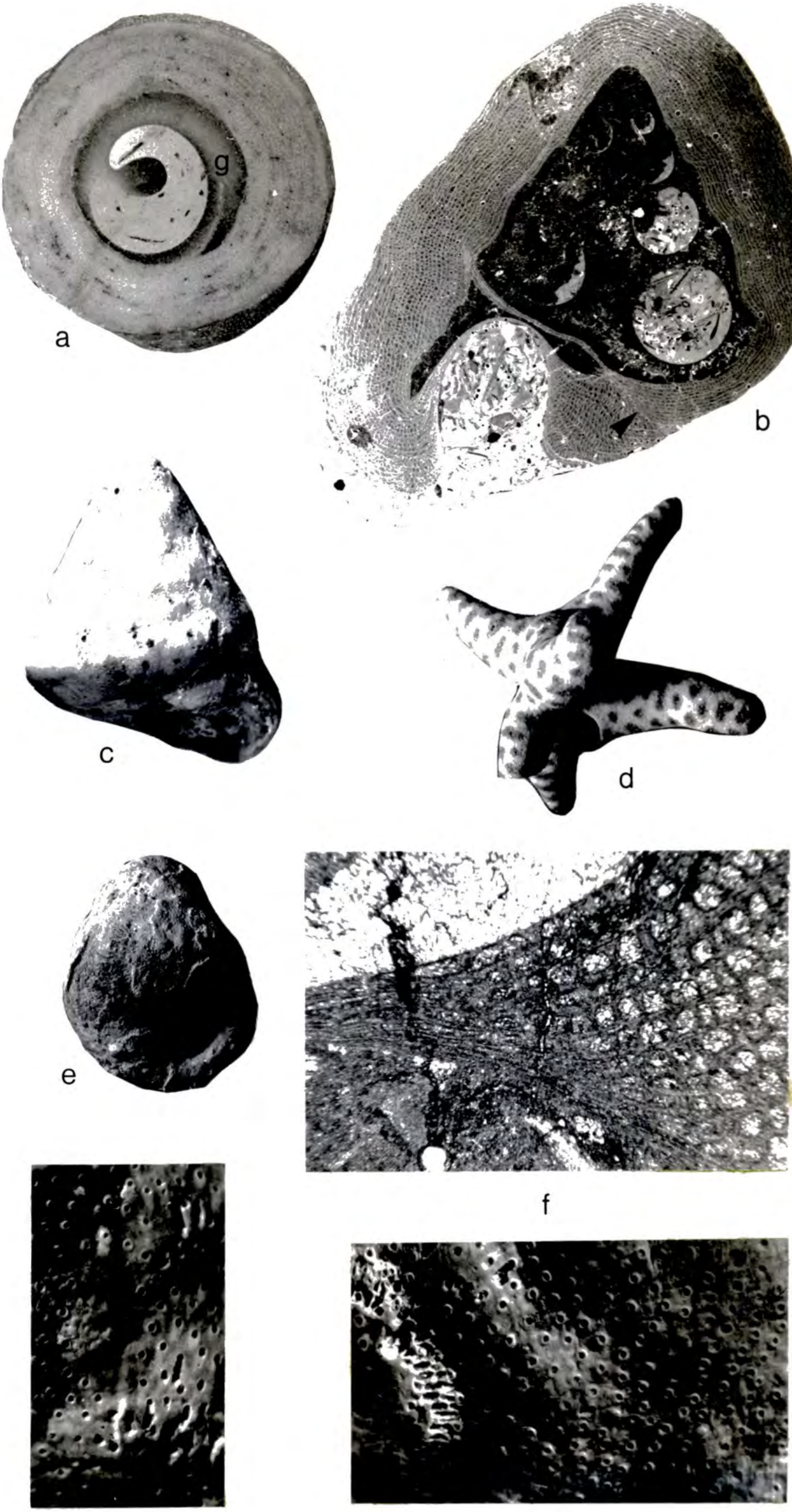

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Plate 21.

Fig.a. <u>Reptomultisparsa</u> <u>tumida</u> sp. nov. The holotype BMNH D13346 Bradford Clay, Bradford-on-Avon. X17.

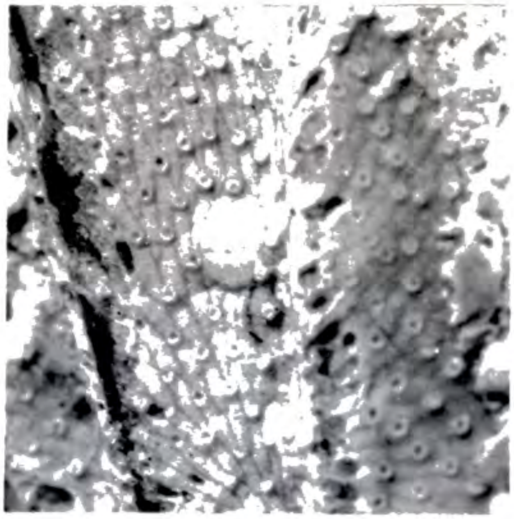
Figs.b-e. <u>Reptoclausa</u> <u>porcata</u> sp. nov.

Fig.b. Multilamellar zoarium with a pivot point (arrowed). Paratype BMNH D8724 Pea Grit, Birdlip. X9.

Fig.c. Abraded zoarium with well developed autozooecial ridges and kenozooecial furrows (e.g. arrowed). Holotype BMNH D31586 Lower Limestone, Crickley Hill. X12.

Fig.d. Abraded gonozooecia (ooeciopore of one is arrowed). Holotype BMNH D31586 Lower Limestone, Crickley Hill. X12.

Fig.e. Young colony in which ridge development has not commenced. BMNH B4855 Lower Ragstone, Cold Comfort. X10.



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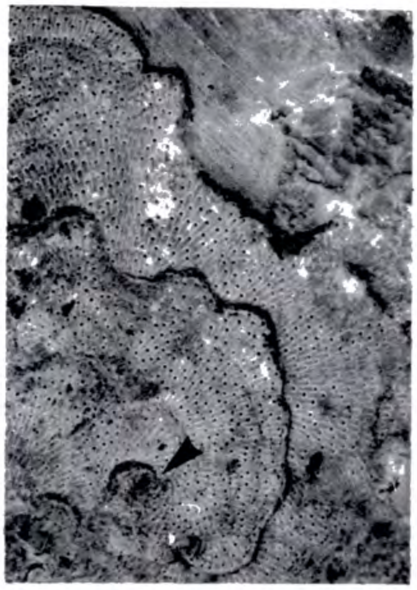

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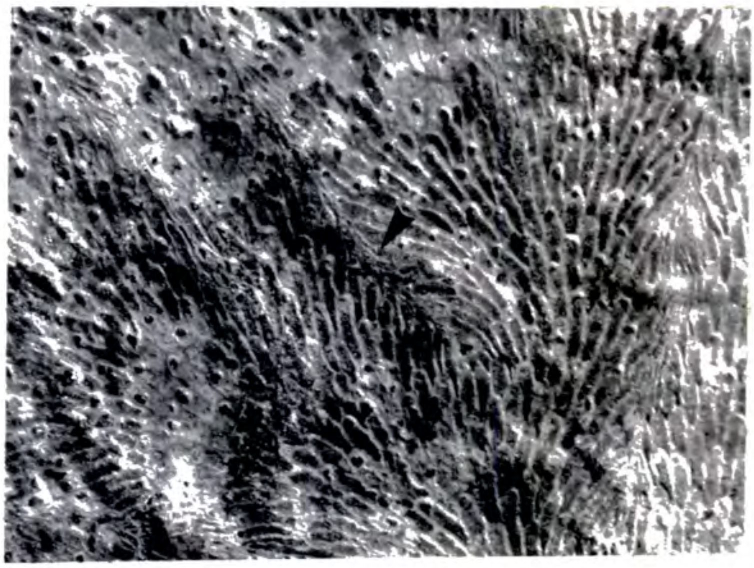

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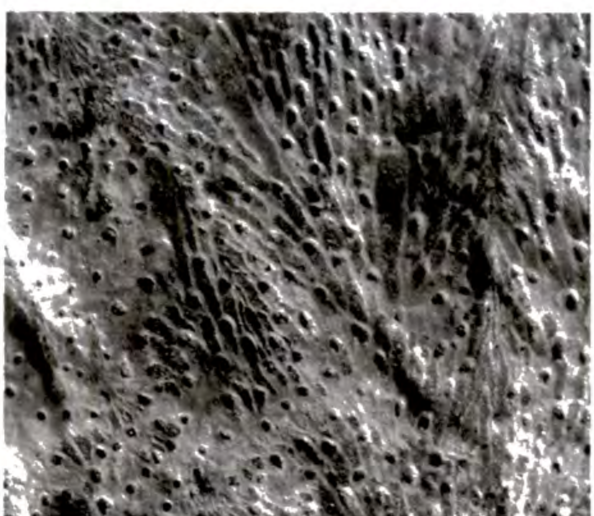

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Plate 22. Collapora straminea (Phillips)

Fig.a. Vinculariiform branches arising from a cavariiform colony base. BMNH D2221 'Bathonian, Ranville'. X10.

Fig.b. PT A3-8 Millepore Bed, Yons Nab, Yorkshire. X9.

Fig.c. Branch with occluded growth tip PT A3-77 Millepore Bed, Yons Nab. X12.

Fig.d. Transverse zoarial section through an attachment scar of the type shown in fig.i. Interzooecial walls divide to give two basal laminae at the attachment (e.g. arrowed). PT A3-15 Millepore Bed, Yons Nab. X44.

Fig.e. Kenozooecia at the anastomosis between lobes of a lamellar branch overgrowth. PT A3-73 Millepore Bed, Yons Nab. X19.

Fig.f. Gonozooecium with a large ooeciopore (arrowed). PT A8-1 Inferior Oolite, Gloucestershire. X11.

Fig.g. Crushed gonozooecium illustrating a typical preservation. PT A3-27 Millepore Bed, Yons Nab. X11.

Fig.h. The type specimen of Haplooecia irregularis Gregory 1896c. BMNH D44 Lincolnshire Limestone, Stamford. X12

Fig.i. Concave attachment scars. PT A3-17 and A3-15 Millepore Bed, Yons Nab. X10.

Fig.j. Framboidal clusters of pyrite (e.g. arrowed) representing 'brown deposits' in a zooecial chamber. Photograph of a polished specimen viewed in reflected light. PT A3-71 Millepore Bed, Yons Nab. X300.

Fig.k. Oblique L.S. showing a thin-walled basal diaphragm (arrowed). PT A3-72 Millepore Bed, Yons Nab. X70.

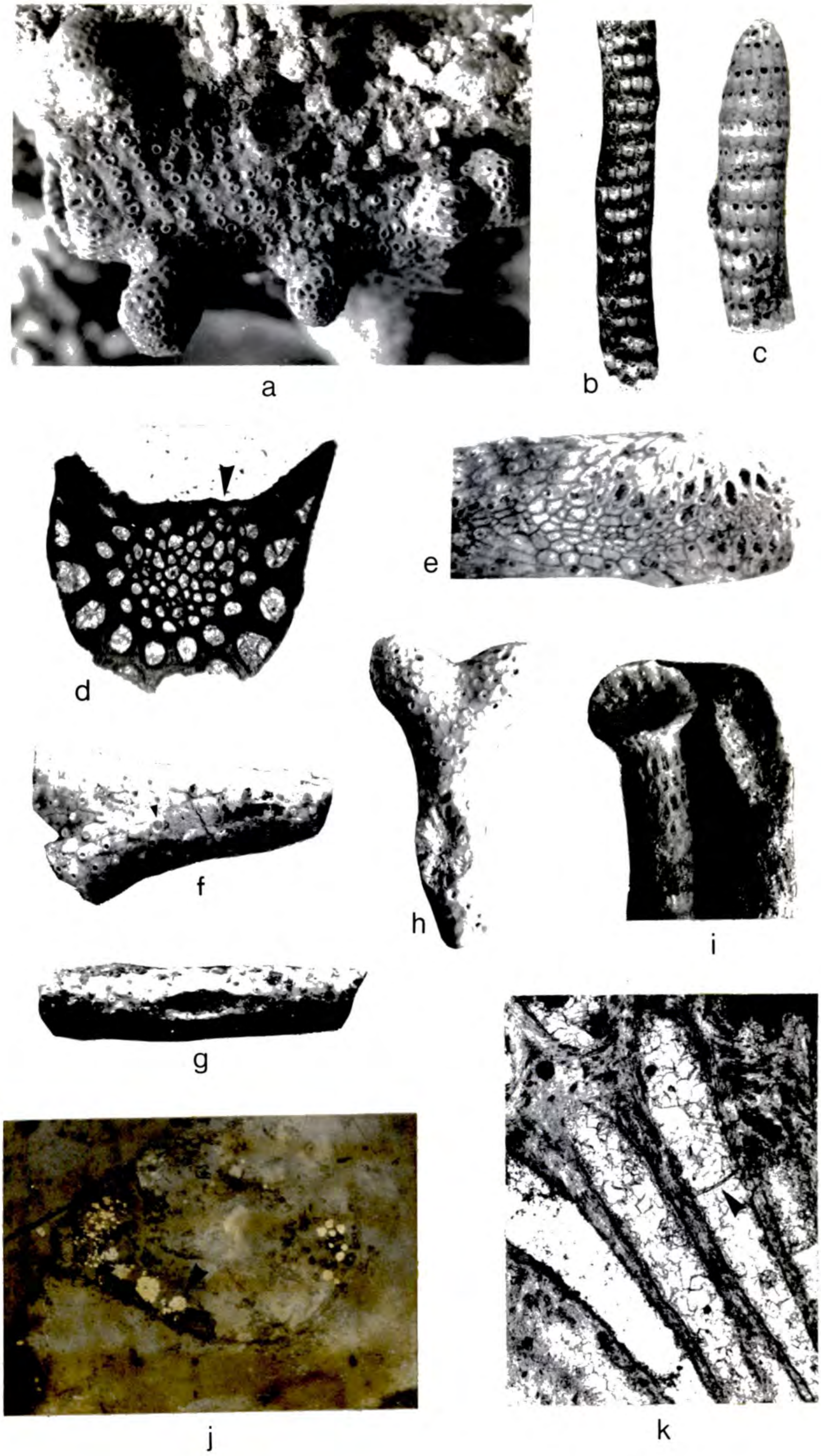
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Plate 23. Collapora straminea (Phillips)

Fig.a. Longitudinal section through a specimen (shown externally in fig.c.) displaying apparent rejuvination of growth. Numerous zooecial buds (e.g. arrowed) originate on a convex surface. PT A3-75 Millepore Bed, Yons Nab, Yorkshire. X42.

Fig.b. Apparent occlusion (arrowed) of a autozooecium by an overlying gonozooecium (crushed distally). PT A3-78 Millepore Bed, Yons Nab. X42.

Fig.c. Trichotomising branch representing an apparent rejuvination of growth. PT A3-75 Millepore Bed, Yons Nab. X12.

Fig.d. Anastomosis between zooecia of a branch growing from the upper left and a branch growing from the lower left. Zooecia fail to develop frontal walls at their junction. L.S. PT A3-20 Millepore Bed, Yons Nab. X79.

Fig.e. Longitudinal section through the distal portion of a branch. PT A3-77B Millepore Bed, Yons Nab. X42.

Fig.f. Transverse section through a dichotomising branch. PT A3-40 Millepore Bed, Yons Nab. X42.

Fig.g. Interzooecial wall with a thick outer laminar layer. PT A3-74 Millepore Bed, Yons Nab. X240.

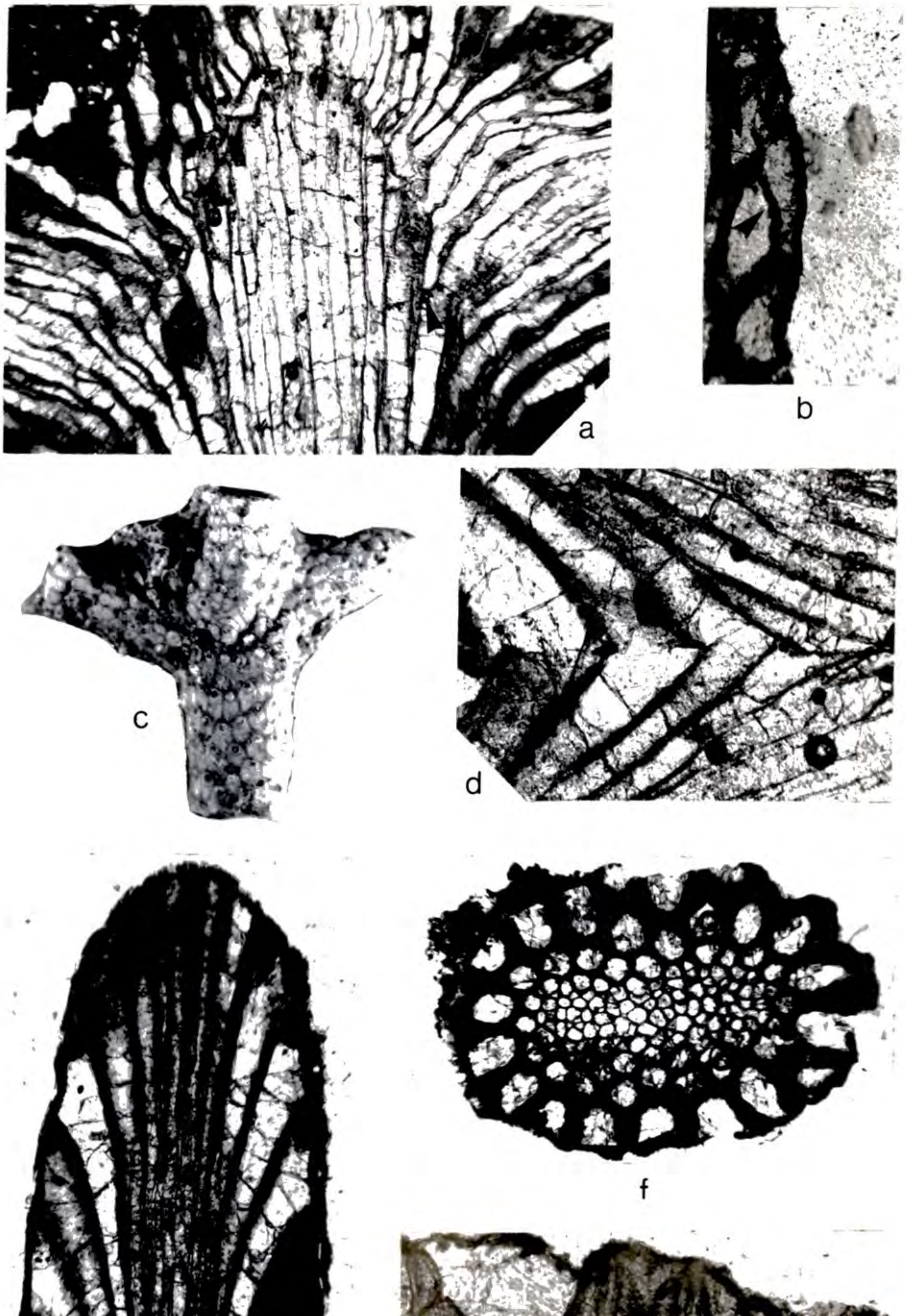
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Plate 24. <u>Collapora</u> <u>microstoma</u> (Michelin)

Fig.a. Terebellariiform zoarium. The lectotype of <u>Multiclausa</u> <u>jellyae</u> Gregory BMNH B4872 Bradford Clay, Box, Wiltshire. X2.

Fig.b. Bulbous kenozooecium-rich area which appears to be an aborted branch dichotomy giving rise to a lamellar overgrowth. BMNH D2212 Bathonian, Ranville. X12.

Fig.c. Lamellar overgrowth ascending an erect branch. BMNH D2212. X18.

Fig.d. Broken bases of two erect branches (arrowed) elongated parallel to the growth direction of zooecia around. BMNH D7614 Bradford Clay, Bradford-on-Avon. X11.

Fig.e. Broken erect branch surrounded by adnate zooecia which include an apparent astogenetic zone of kenozooecia. BMNH D7607c Bradford Clay, Bradford-on-Avon. X11.

Fig.f. Zoarium with branches predominantly in one plane. BMNH D2212. X4.

Fig.g. Peripheral fan-shaped subcolony (arrowed) overgrowing the parent colony. BMNH D51462 Hampen Marly Beds, Enstone, Oxfordshire. X10.

Fig.h. Discoidal frontally-budded subcolonies (arrowed) PT 665 St. Aubin Member, St. Aubin-sur-mer, Normandy. X6.

Fig.i. Adnate zoarium with gonozooecia (an ooeciopore is arrowed). The holotype of <u>Berenicea</u> <u>cobra</u> Pitt and Thomas. BMNH D51459 Hampen Marly Beds, Enstone. X8.

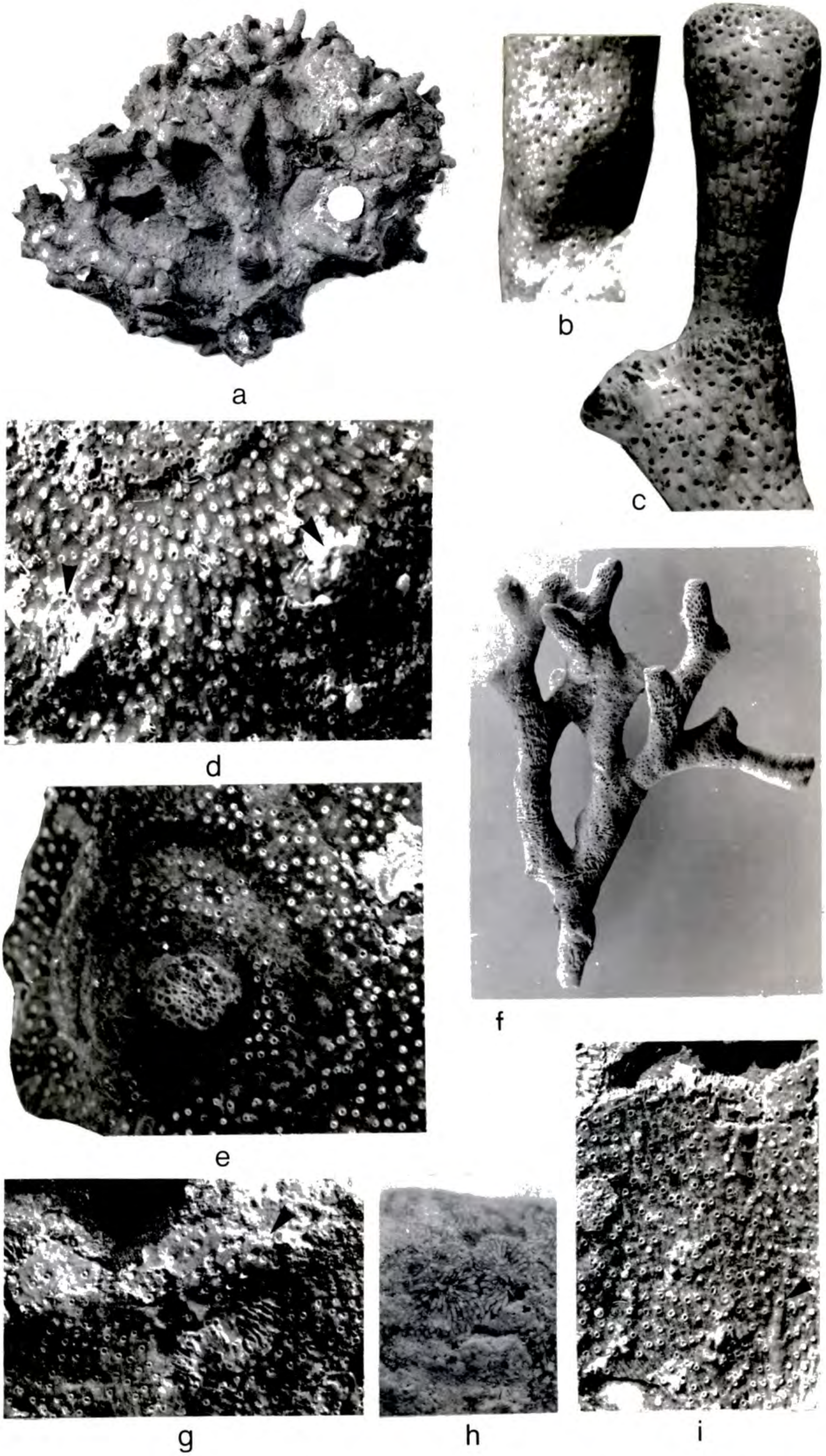
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Plate 25 Collapora microstoma (Michelin)

Figs.a-d. Serial transverse sections at 0.3 mm intervals through an adnate colony giving rise to an erect branch. Non-lamellar zooecial budding (e.g.arrowed) is evident in fig.c. The crossed lamellar microstructure of the Oxytoma costatum substrate can be seen. BMNH D7612 Bradford Clay, Bradford-on-Avon. X38.

Fig.e. Transverse section through a vinculariiform branch with a unilamellar overgrowth. Zooecia with small diameters occur at the endozone/exozone boundary in the erect portion. PT A4-24A Bradford Clay, Bradford-on-Avon. X38.

Fig.f. Immature erect branch (centre) arising directly from a frontal bud. BMNH A4-60B Bradford Clay, Bradford-on-Avon. X12.

Fig.g. The neotype. MNHN unnumbered Ranville. X12.

Fig.h. Depressed region occupied by kenozooecia which is the origin of a frontally-budded overgrowth on an erect branch. BMNH D2156 Bradford Clay, Bradford-on-Avon. X18.

Fig.i. Pivot point (arrowed) terminating an occluded growth margin of a lamellar overgrowth on an erect branch. BMNH D52645-4 Bradford Fossil Bed, Sunhill, Gloucestershire. X18.

Fig.j. Vinculariiform fragment. The type specimen of Entalophora richmondiensis Vine. BMNH D1935 Great Oolite, Richmond. X11.

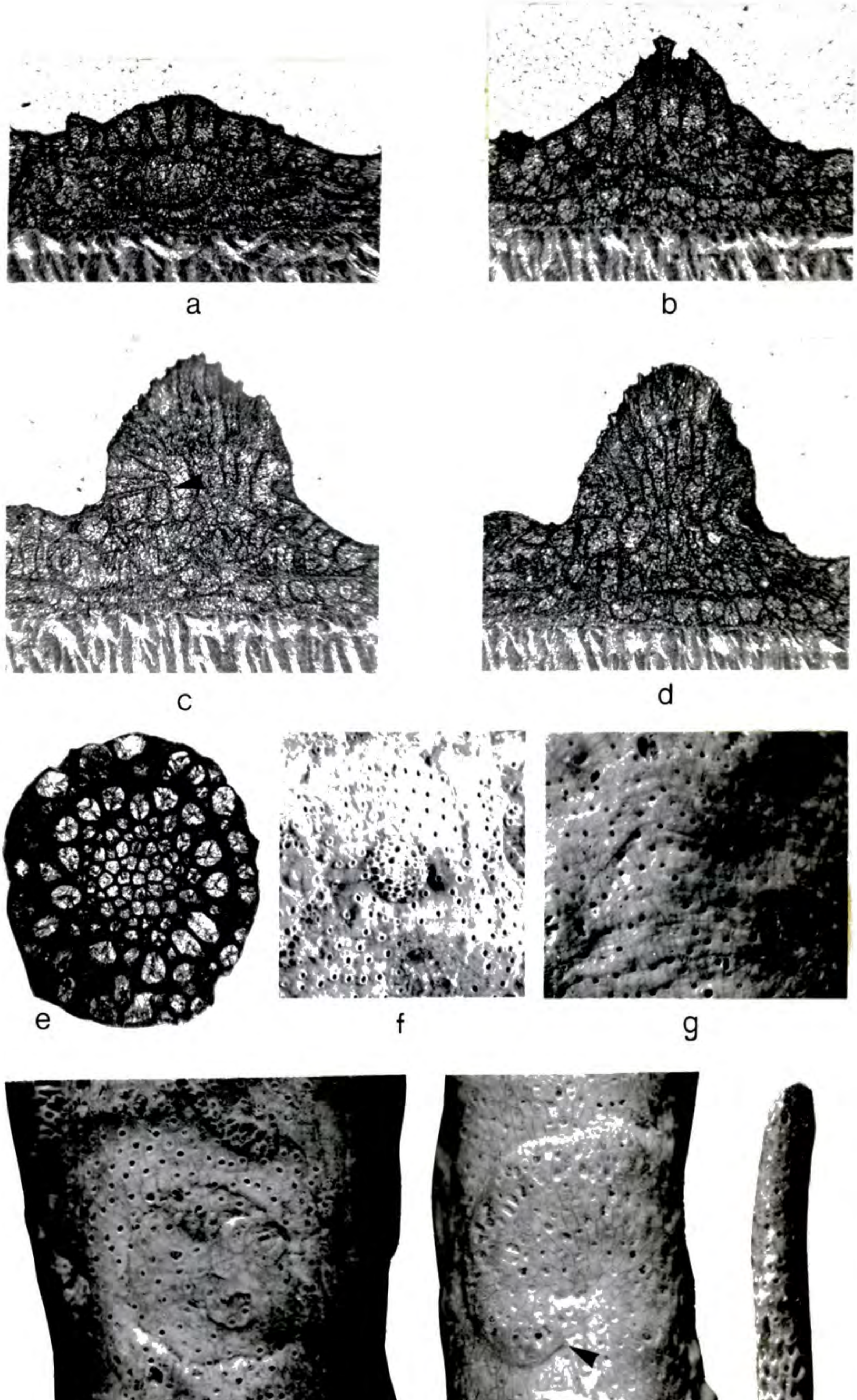
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Plate 26. <u>Collapora tetragona</u> (Lamouroux)

Fig.a. Portion of a zoarial transverse section. PT 549-4 St. Aubin Member, Carriere des Campagnettes, Ranville, Normandy. X35.

Fig.b. Portion of a T.S. of a zoarium which possesses thick interzooecial walls developing an outer laminar skeletal layer. BMNH 60213 Bathonian, Ranville. X35.

Fig.c. BMNH 60212 Bathonian, Ranville. X1.5.

Fig.d. Encrusting base giving rise to a broken erect branch (left). PT 653-7 St. Aubin Member, St. Aubin-sur-mer, Normandy. X9.

Fig.e. PT 657-1 St. Aubin Member, St. Aubin-sur-mer, Normandy. X9.

Fig.f. PT 549-5 St. Aubin Member, Carriere des Campagnettes, Ranville, Normandy. X9.

Fig.g. Branch with unusually prominent peristomes. BMNH 60213 Bathonian, Ranville. X9.

Fig.h. Longitudinal section through a zooecium with 2 intermediate diaphragms (arrowed). PT 549-4 St. Aubin Member, Carriere des Campagnettes, Ranville. X70.

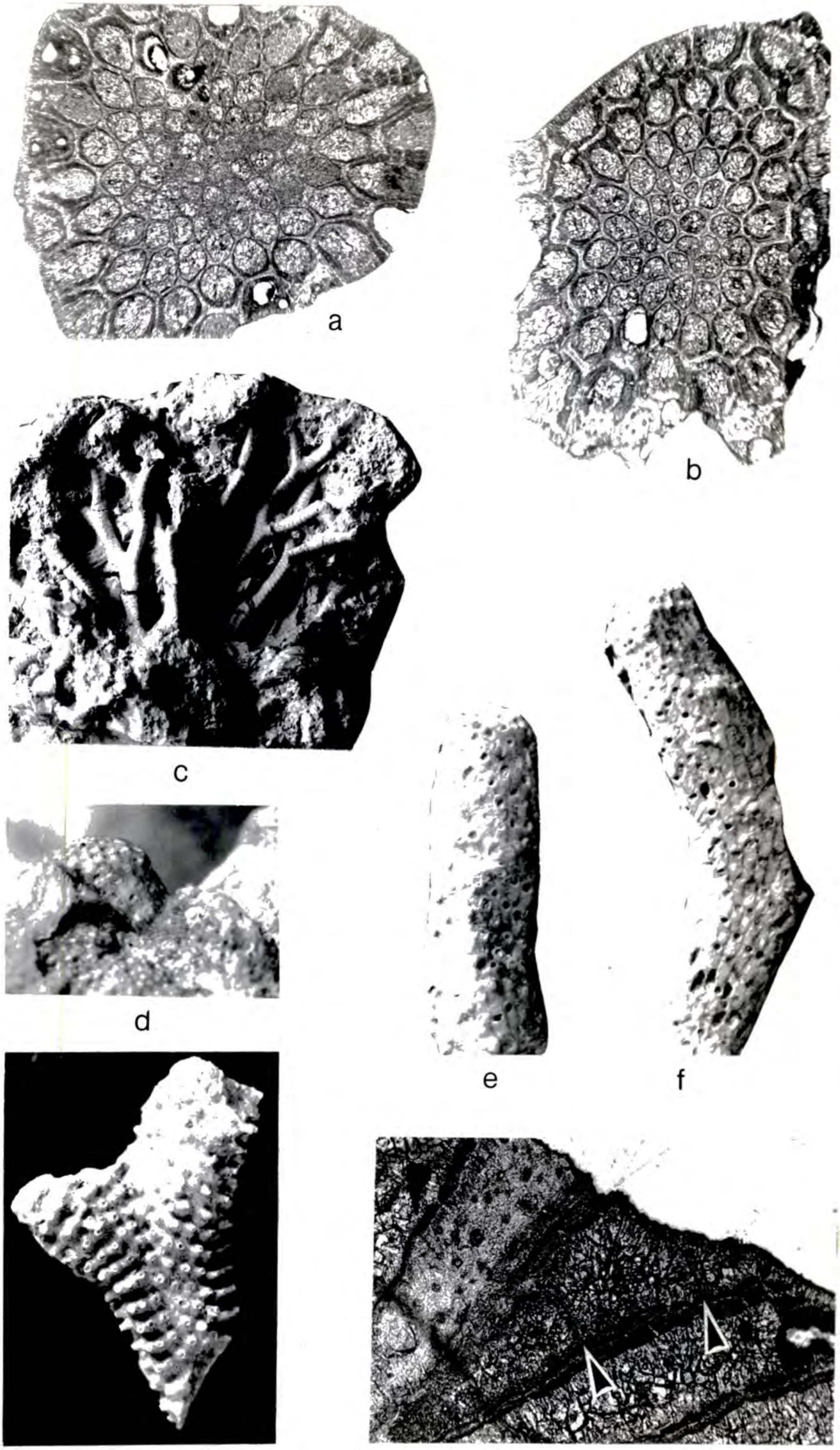
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Plate 27. *Hyporosopora typica* Canu and Bassler, and *Hyporosopora sauvagei* (Gregory)

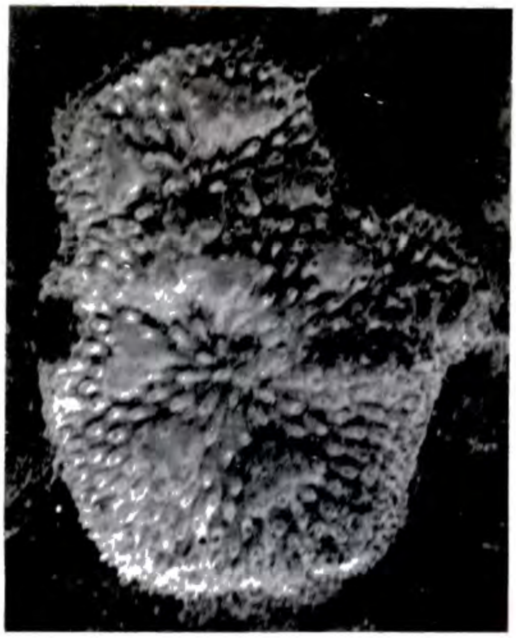
Fig.a. Ovicelled zoaria of *H.typica* figured by Gregory 1896e pl.4, fig.2. BMNH D919 Cornbrash, Thrapston, Northamptonshire. X10.

Fig.b. *H.typica* with gonozooecia which have abraded frontal walls. PT A4-11 Bradford Clay, Bradford-on-Avon, Wiltshire. X11.

Fig.c. *H.sauvagei* with assymmetrical boomerang-shaped gonozooecium (arrowed). BMNH B194d Bradford Clay, Bradford-on-Avon. X11.

Fig.d. *H.sauvagei*. The lectotype. BMNH B194a. X11.

Fig.e. *H.saugavei*. Transverse section of a specimen encrusting a rhynchonellid. The thin zoarium is typically only 1 zooecium in depth. A zooecium sectioned at the level of its aperture is arrowed. PT B456 Boueti Bed, Langton Herring, Dorset. X82.



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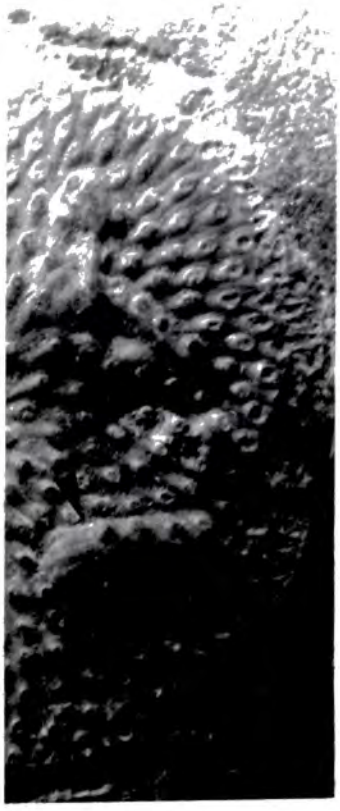

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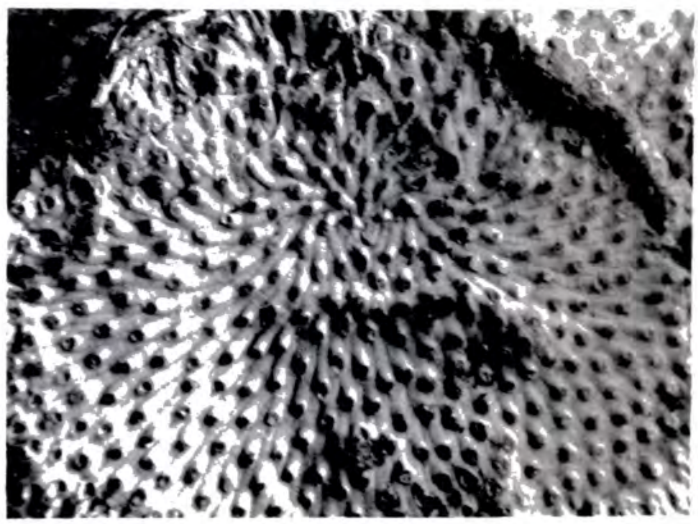

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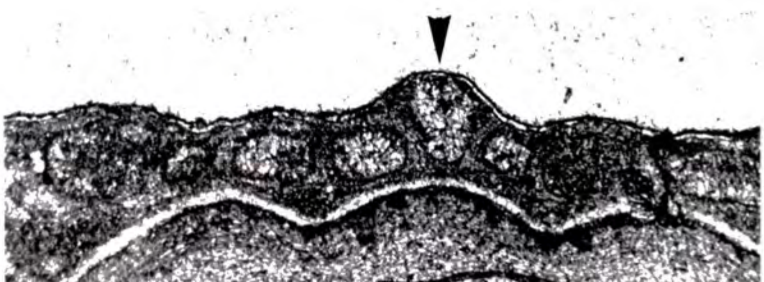

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Plate 28. Hyporosopora parvipora (Canu and Bassler), and Hyporosopora portlandica (Gregory)

Fig.a. Ovicelled zoarium of H.parvipora BMNH D51469 Hampen Marly Beds, Enstone, Oxfordshire. X8.

Fig.b. Abraded zoarium of H.parvipora composed of numerous fan-shaped subcolonies. BMNH D51451-2 Hampen Marly Beds, Enstone. X9.

Fig.c. H.parvipora. Zoaria encrusting vinculariiform Collapora microstoma. Figured by Gregory 1896e pl.4, fig.5 as Berenicea parvitubulata. BMNH D1912 Bathonian, Richmond boring. X9.

Fig.d. H.parvipora. Zoarium composed of successive fan-shaped subcolonies (the origin of the ultimate subcolony is arrowed). PT 67-7B White Limestone, Woodeaton, Oxfordshire. X11.

Fig.e. H.portlandica. Mass of zoaria encrusting Camptonectes lamellosus. BMNH D47325 Portlandian, ?locality. X1.8.

Fig.f. H.portlandica. Ovicelled zoarium. BMNH D47325. X11.

Fig.g. H.portlandica. The holotype with peripheral fan-shaped subcolonies (lower left) and a frontally-budded subcolony (arrowed). BMNH D1853 Portland Oolite, Tisbury, Wiltshire. X10.

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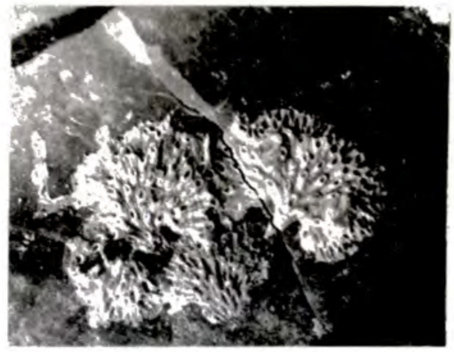

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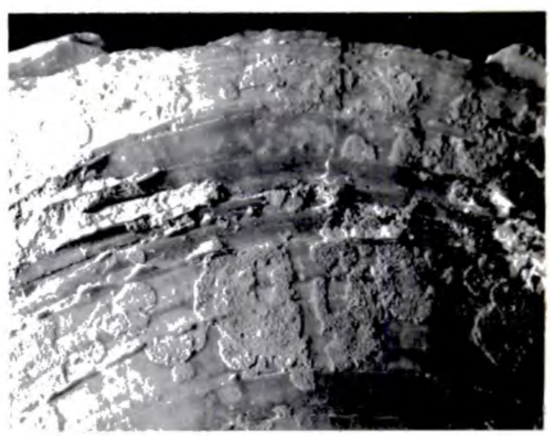

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Plate 29. _Mesenteripora_ _undulata_ (Michelin)

Fig.a. Zoarium encrusting an annelid tube. BMNH D2088 Bathonian, Ranville. X2.

Fig.b. Small fan-shaped colony. BMNH D51449 (figd. by Pitt and Thomas 1969 pl.4, fig.3) Hampen Marly Beds, Enstone. X9.

Fig.c. Thick multilamellar zoarium encrusting the holdfast and stem base of _Apiocrinites_. BMNH 35249 Bradford-on-Avon. X1.7.

Fig.d. Ovicelled colony. BMNH D51451 (the holotype of _Berenicea_ _enstonensis_ Pitt and Thomas 1969) Hampen Marly Beds, Enstone. X8.

Fig.e. Autozooecia and a gonozooecium (ooeciopore arrowed) in the holotype. MNHN unnumbered Luc-sur-mer. X9.

Fig.f. C-shaped growth margin BMNH B4850 ?locality. X19.

Fig.g. Zooecial layer immured (arrowed) between crinoid calcite at the holdfast of _Apiocrinites_. BMNH 35249 Bradford-on-Avon. X12.

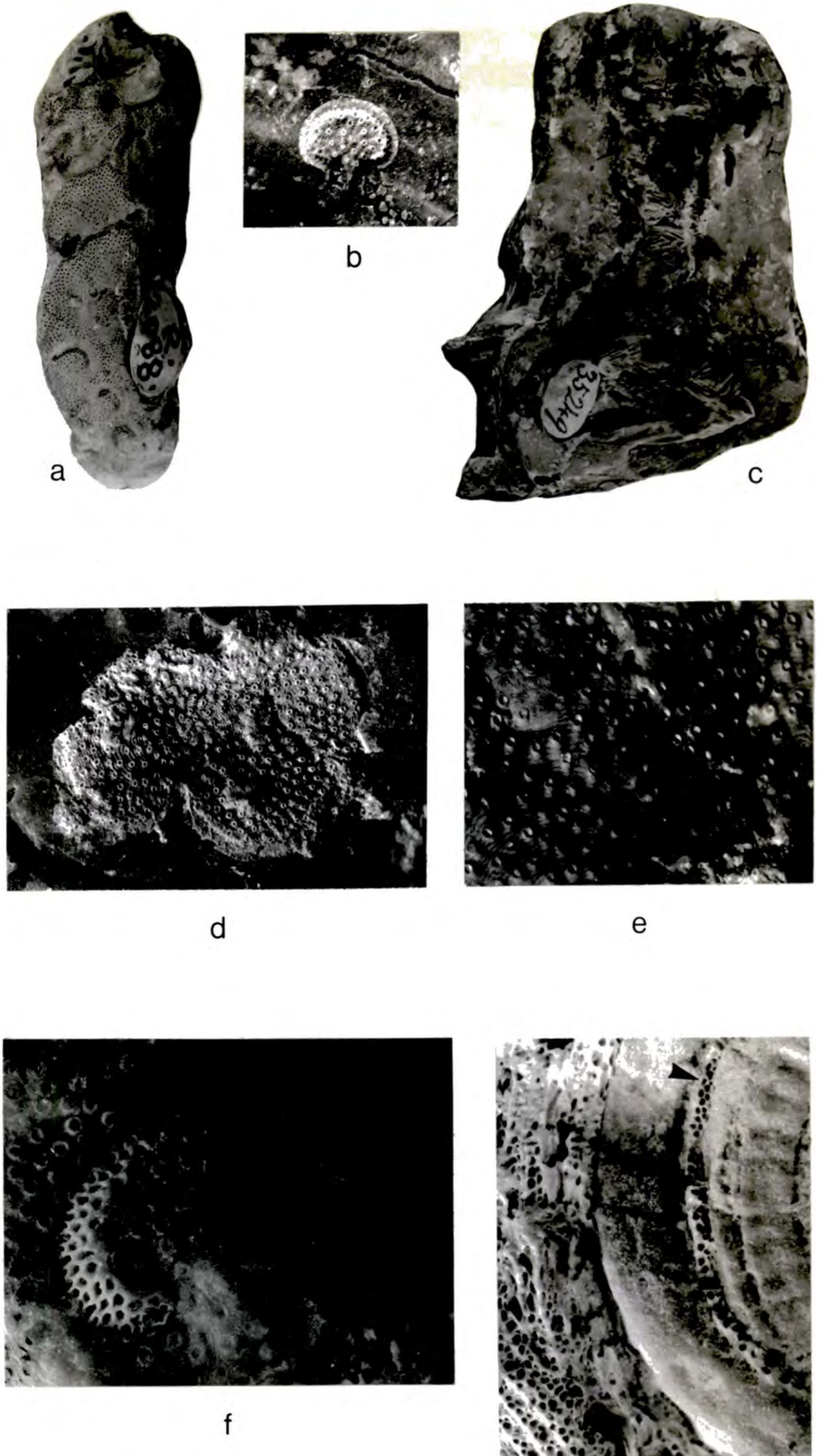

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Plate 30. _Reticulipora_ _dianthus_ (de Blainville) except fig.c '_Reticulipora_' _contingens_ (Lonsdale).

Fig.a. The holotype. MNHN unnumbered Ranville. X1.

Fig.b. Basal surface of a colony. BMNH D2116 Bathonian, Ranville. X6.

Fig.c. '_Reticulipora_' _contingens_ a zoarial homeomorph of _R.dianthus_ BMNH D3073 Upper Chalk, Bromley, Kent. X1.

Fig.d. Central region of a zoarium with small adnate oysters (e.g. arrowed) BMNH D2116. X11.

Fig.e. Basal surface of a colony with an encrusting serpulid (left centre). PT 592 Blainville Member, Blainville, Normandy. X1.

Fig.f. Bilamellar frond contacting a brachiopod shell. The interior wall budding lamina of the frond divides to give two basal laminae at the contact (arrowed). PT 546-1 St. Aubin Member, Carriere des Campagnettes, Ranville. X10.

Fig.g. Occluded autozooecia. BMNH B178 Bathonian, Ranville. X10.

Fig.h. Section of a frond showing the central budding lamina with an interzooidal pore (arrowed). BMNH 60228 Bathonian, Ranville. X79.

Fig.i. Reticulate zoarial upper surface. X10.

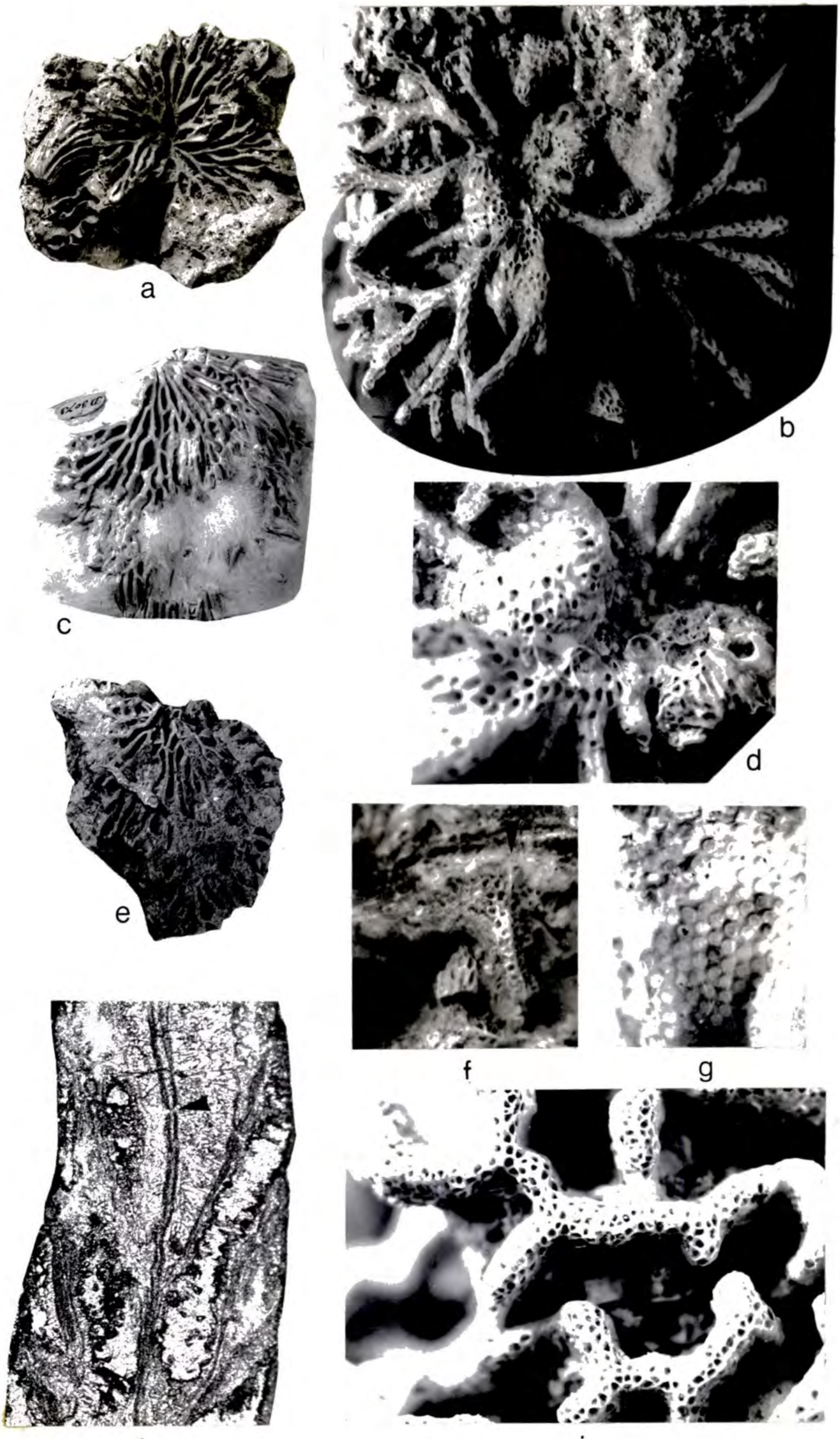
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Plate 31. Entalophora annulosa (Michelin)

Fig.a. Part of a transverse zoarial section showing the branch axial lumen (indicated with a star). PT 655-1 (T.S.) St. Aubin Member, St. Aubin-sur-mer, Normandy. X79.

Fig.b. OUM J21626 Microzoa Beds, Shipton Gorge, Dorset. X12.

Fig.c. Longitudinal section showing zooecia intersecting the zoarial surface at a small angle. PT655-1 (L.S.) St. Aubin Member, St. Aubin-sur-mer. X37.

Fig.d. Dichotomising fragment with long peristomes distally. PT655-5 St. Aubin Member, St. Aubin-sur-mer. X9.

Fig.e. The lectotype. MNHN unnumbered Calvados. X11.

Fig.f. PT 608-3 Langrune Member, Luc-sur-mer, Normandy. X9.

Fig.g. PT 720-2 Langrune Member, Douvres-la Deliverande, Normandy. X9.

Fig.h. Branch with a gonozooecium (ooeciopore arrowed). PT 655-4 St. Aubin Member, St. Aubin-sur-mer, Normandy. X9.

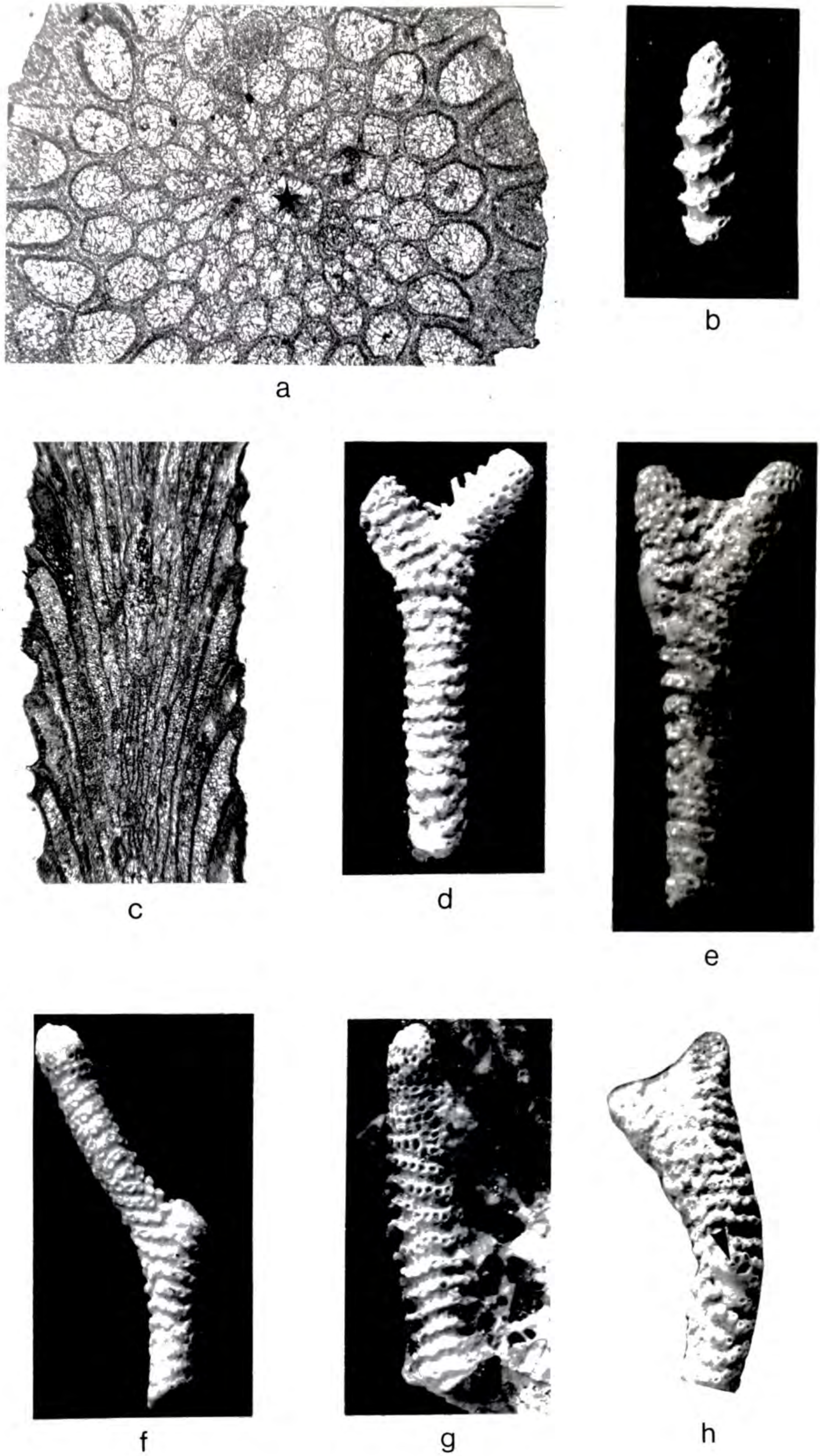
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Plate 32. 'Mecynoecia' bajocina except fig. i. Mecynoecia proboscidea (Milne-Edwards)

Fig.a. Transverse section showing budding around a central zoarial axis. PT 156 A Microzoa Beds, Shipton Gorge, Dorset. X78.

Fig.b. Bulbous gonozooecium with a slit-like ooeciopore (arrowed). OUM J21628 Microzoa Beds, Shipton Gorge. X20.

Fig.c. Aborted gonozooecium (arrowed) lacking an ooeciopore. PT 158 Microzoa Beds, Shipton Gorge. X20.

Fig.d. Three branches showing variation in autozooecial dimensions. OUM J21629 Microzoa Beds, Shipton Gorge. X12.

Fig.e. PT 155 Microzoa Beds, Shipton Gorge. X7.

Fig.f. PT 159 Microzoa Beds, Shipton Gorge. X7.

Fig.g. Apparent frontally budded overgrowth originating (arrowed) from an autozooecial aperture. OUM J21629 Microzoa Beds, Shipton Gorge. X11.

Fig.h. Large overlapping terminal diaphragms (e.g. arrowed). PT 155 Microzoa Beds, Shipton Gorge. X20.

Fig.i. Mecynoecia proboscidea. The probable type specimen. MNHN Risso Collection 5110 Recent. X11.

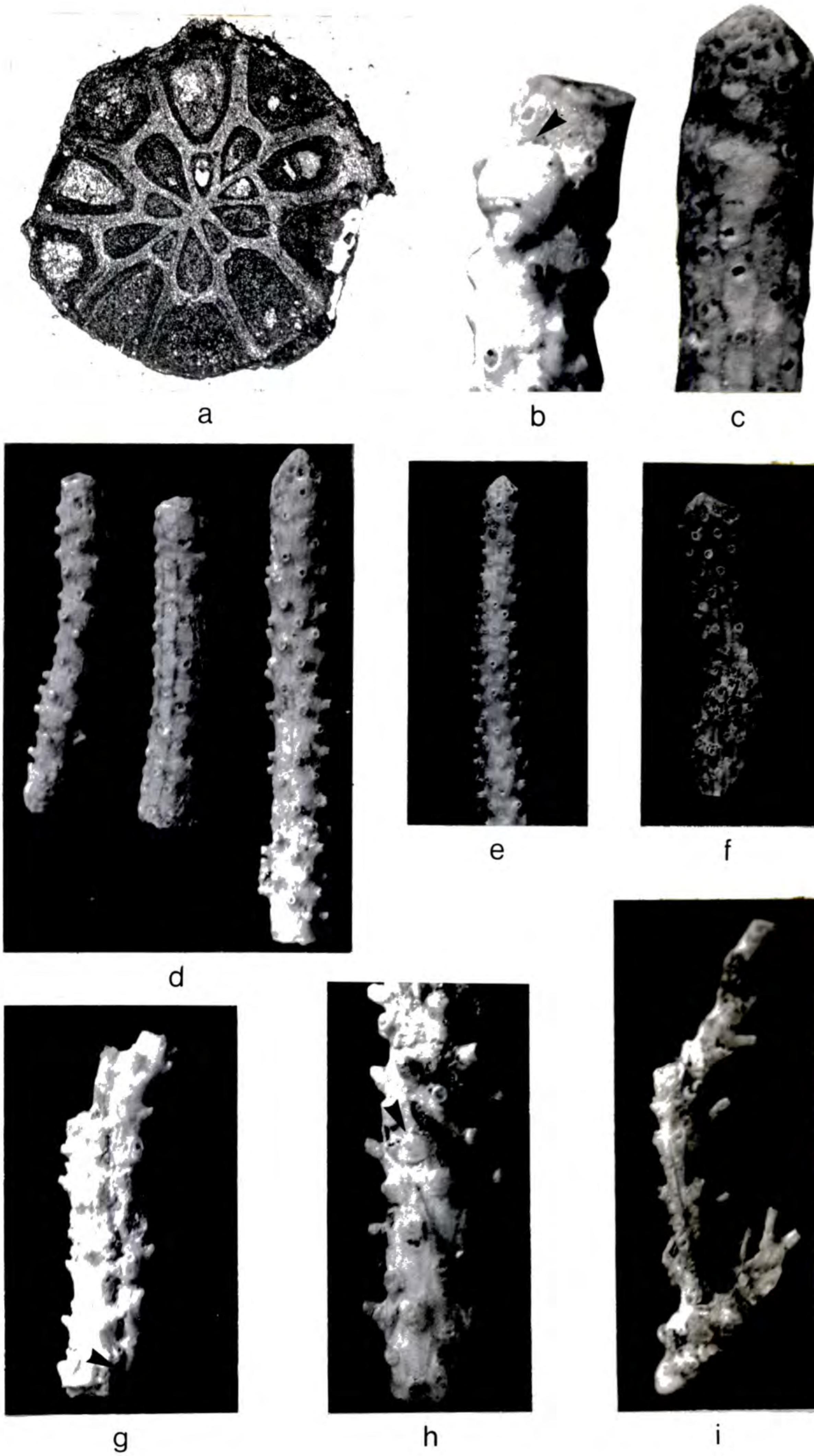
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Plate 33. Terebellaria ramosissima Lamouroux

Fig.a. Growth tip and distal portion of a helico-spiral branch. BMNH 11510c Great Oolite, ?locality. X6.

Fig.b. Zoarium with zooecial frontal walls removed by abrasion. BMNH 60360a Bathonian, Ranville. X6.

Fig.c. Zoarial fragment with a branch dichotomy. BMNH 60215d Bathonian, Ranville. X2.3.

Fig.d. Incipient dichotomy at the tip of a dextral branch. BMNH D1812q Bathonian, Bradford-on-Avon. X7.

Fig.e. Kenozooecia close to the base of a zoarium. PT 652-1 St. Aubin Member, St. Aubin-sur-mer. X12.

Fig.f. Ontogenetically zoned autozooecia BMNH 60215 Bathonian, Ranville. X10.

Fig.g. Ontogenetically zoned zooecia near to a branch dichotomy. BMNH D2111 Bathonian, Ranville. X8.

Fig.h. Young zoarium. PT 569-1 St. Aubin Member, Amfreville. X14.

Fig.i. Gonozooecium (ooeciopore is arrowed) BMNH D52637 St. Aubin Member, St. Aubin-sur-mer. X15.

Fig.j. The opposite end of the horizontal growth margin division shown in figure 63. A zoarial lateral wall extends across the dislocation (arrowed). BMNH 11510d Great Oolite, ?locality. X7.

Fig.k. Portion of a zoarium displaying growth margin occlusion.BMNH D4518 Bathonian, Ranville. X10.

Fig.l. Base of a detached zoarium. BMNH 60215 Bathonian, Ranville. X3.

Fig.m. Adventitious branch (right) arising from a parent branch with occluded growth margins. BMNH 60360b Bathonian, Ranville. X7.

Fig.n. Abraded basal portion of a zoarium with borings ascribed to the activities of acrothoracic cirrepeds. BMNH 60382 Bathonian, Ranville. X10.

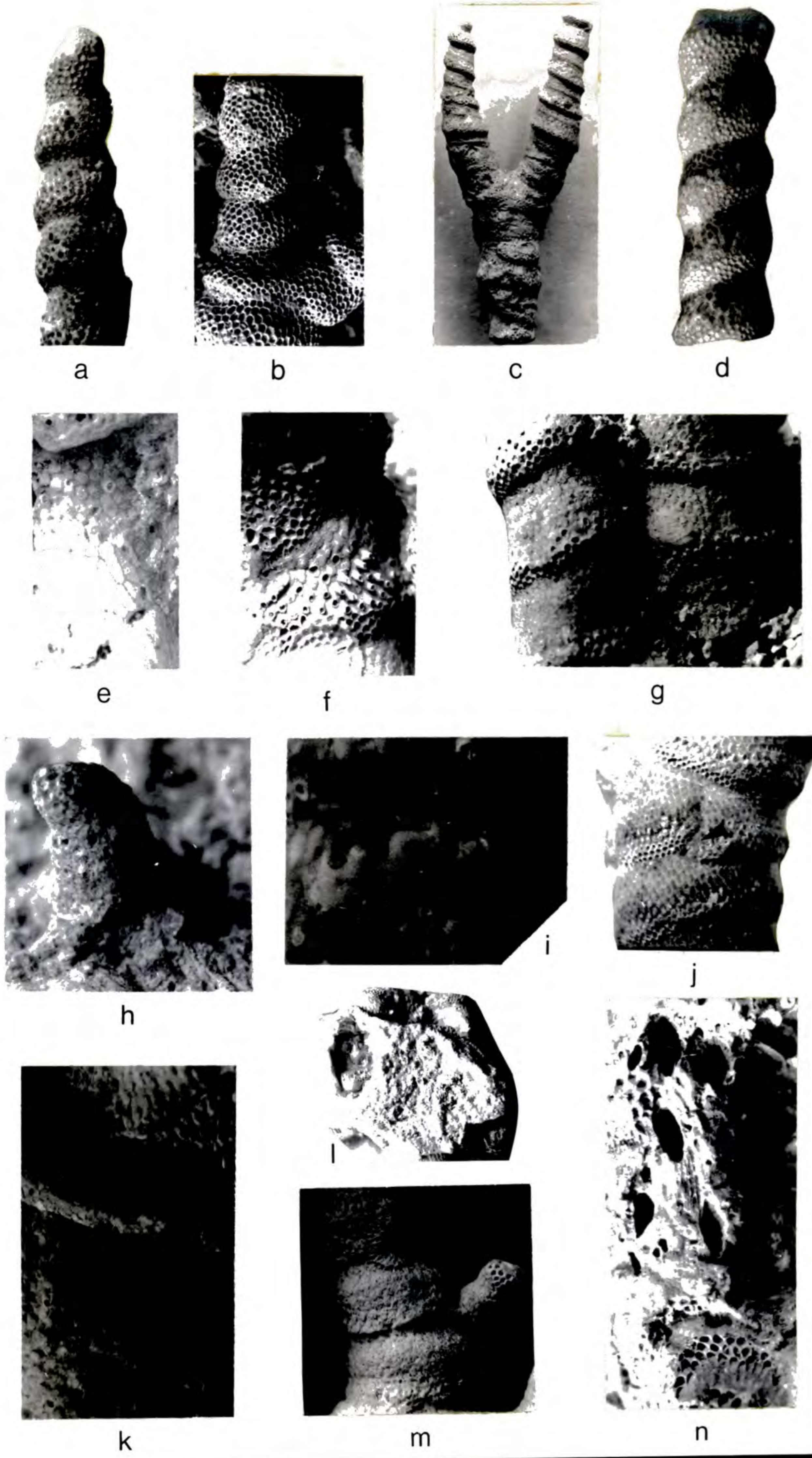
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Plate 34. <u>Terebellaria</u> <u>ramosissima</u> Lamouroux.
Figs. a-d are negative photographs prepared from acetate peels. Figs. e-h are photomicrographs.

Fig.a. Longitudinal zoarial section. BMNH D2111f Bathonian, Ranville. X10.

Fig.b. Transverse section of a branch with a sinistral helico-spiral growth margin. The point of origin of the exozonal budding lamina is arrowed. BMNH 60215c Bathonian, Ranville. X7.

Fig.c. Transverse zoarial section. BMNH D2112 (9.0) Bathonian, Luc-sur-mer. X7.

Fig.d. Transverse zoarial section in the vicinity of a branch dichotomy. BMNH D2111d Bathonian, Ranville. X6.

Fig.e. Oblique transverse section showing endozonal zooecia developing an outer laminar layer (arrowed) to their interzooecial walls. BMNH D2111 Bathonian, Ranville. X60.

Fig.f. Transverse zoarial section showing a long peristome (arrowed) of an endozonal zooecium covered by subsequent exozonal overgrowth. BMNH D2112 (8.5) Bathonian, Luc-sur-mer. X57.

Fig.g. Cyst-like intrazooecial structures. BMNH D2112 (12.6) Bathonian, Luc-sur-mer. X110.

Fig.h. Regular exozonal layers with zooecia budded by the transverse septum method. BMNH D2111k Bathonian, Ranville. X35.

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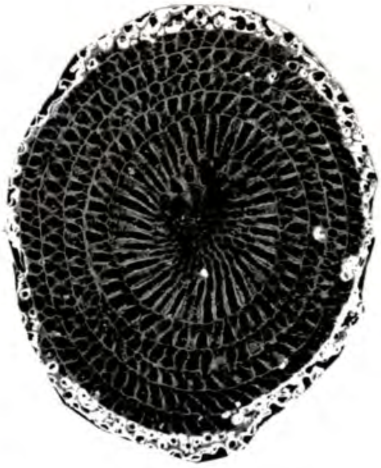

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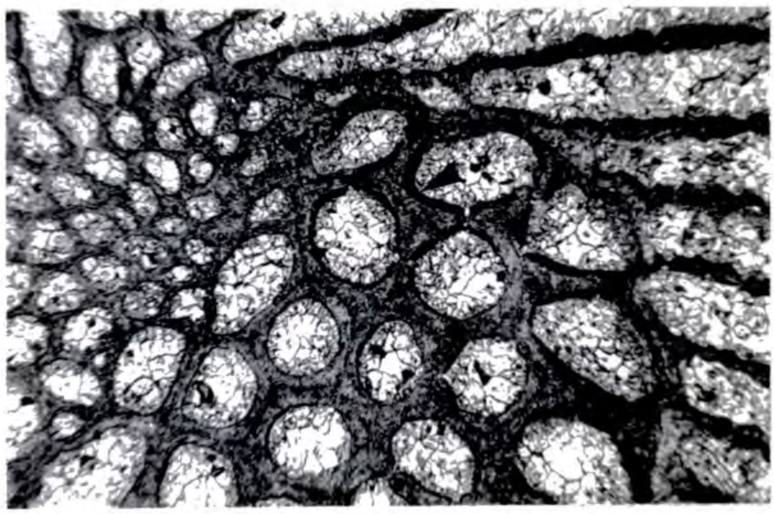

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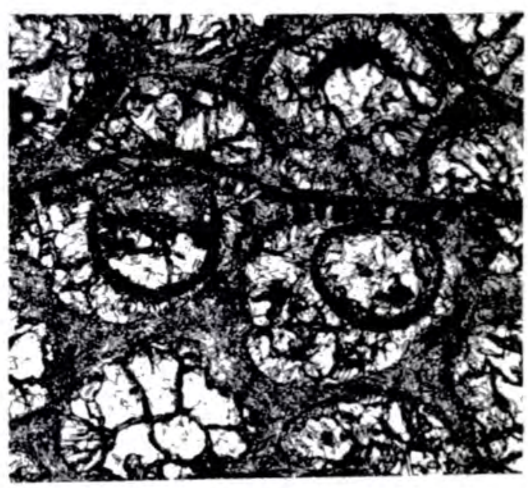

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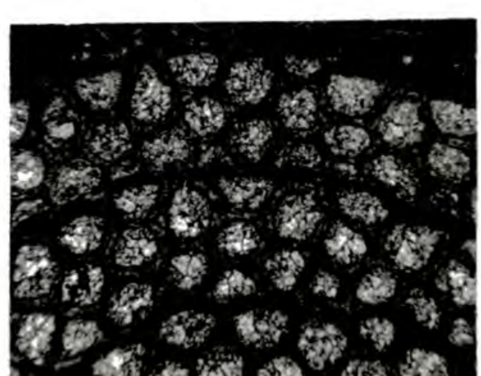

h

Plate 35. The bryozoan-rich sponge reef beds (Upper Bathonian, St. Aubin Member) at St. Aubin-sur-mer, Normandy.

Fig.a. Two sponge patch-reefs broadening upwards. The reef origins are indicated with arrow-heads and the tape measure adjacent to the righthand reef is about 6 cm in diameter.

Fig.b. The origin of the righthand reef shown in fig.a.

Fig.c. Sponge reef dying out towards the east (right on the photograph).

a

b

c

Plate 36.

Fig.a. Upper Bathonian Langrune Member carbonates at Douvres-la-Deliverande, Normandy. A bryozoan-rich bed occurs above the hard-ground on which the hammer is resting.

Fig.b. The Lower Inferior Oolite (Upper Aalenian) at the Limekiln Quarry, Leckhampton Hill, Gloucestershire. The boundary between the Scissum Beds/Lower Limestone and overlying bryozoan bearing Pea Grit is indicated with an arrowhead.

a

b

Plate 37. The Lower Inferior Oolite (Aalenian) at Cleeve Hill, Gloucestershire.

Fig.a. Cross-bedded Lower Freestone (the 'Polyzoa Bed') resting upon flat-bedded Pea Grit.

Fig.b. Limestone clast horizon occurring about 6 metres beneath the top of the Pea Grit. One of the heavily bryozoan-encrusted clasts is arrowed. Frame height = c.60 cm.

a

b

APPENDIX 1

FIELD LOCALITIES

NORMANDY

1. Sully (T761829) near Bayeaux

Middle and Upper Bajocian (*sauzei* to *parkinsoni* Zones) see Arkell (1930, 1956).

The small quarry at Sully near Bayeaux is the type-locality of the Bajocian Stage. It is now very badly overgrown having not been in use since before 1935, according to a local resident. The highly condensed Ironshot Oolite is no longer visible in the quarry itself, but brash on the fields around yielded abundant fossils, predominantly ammonites, from the Ironshot Oolite which is a buff limestone with scattered limonitic ooids. Some of the belemnite guards found had an epifauna of serpulids, small oysters and two bryozoans; *Stomatopora* cf. *dichotoma* and an indeterminate berenici-form plagioecid.

2. Port-en-Bessin (c. T 730885)

Upper Bajocian; White Sponge Oolite (*parkinsoni* Zone) see Arkell (1930), Walter (1969, p.234).

The cliffs at the western end of the harbour expose about 4 metres of the White Sponge Oolite or Oolite blanche overlain by clays of the Lower Bathonian. The White Sponge Oolite is a pale grey, poorly-bedded, hard

Table 17. Chronostratigraphical and lithostratigraphical divisions of the Upper Bajocian and Bathonian in the Calvados region of Normandy. After Walter (1969) and Palmer (1974).

Stage	Zone	Lithostratigraphy
UPPER BATHONIAN	<u>discus</u>	Lower Cornbrash Langrune Member St. Aubin Member Ranville Member
	<u>aspidoides</u> and <u>retrocostatum</u>	Campagnettes Member
MIDDLE BATHONIAN	<u>morrisi</u>	Blainville Member Fontaine-Henry Member
	<u>subcontractus</u>	Revier Member
LOWER BATHONIAN	<u>progracilis</u>	Calcaire de Caen
	<u>zigzag</u>	
UPPER BAJOCIAN	<u>parkinsoni</u>	White Sponge Oolite

limestone containing bivalves, belemnites and sponges. The sclerosponge Neuropora is abundant and, along with poorly-preserved bryozoans, was collected from weathered surfaces. The bryozoan fauna recorded consisted of 'Mecynoecia' bajocina (topotypes), ?Radicipora radiciformis, Ripisoecia conifera, and indeterminate berenic-iform multisparsid species.

3. Fontaine-Henry (T 979786)
Middle Bathonian; Revier Member (subcontractus Zone) and overlying Fontaine-Henry Member (morrisi Zone). see Palmer (1974, p.172).

The quarry at Fontaine-Henry is situated in a wood just outside the village boundary on the road to Colomby-sur-Thaon. About 20 metres of cross-bedded calcarenites of the Revier Member are overlain by 2 to 3 metres of rubbly marly limestone of the Fontaine-Henry Member. Particularly conspicuous in the latter are sponges and characteristically abraded dendroid bryozoans. The recorded bryozoan fauna consists of Terebellaria ramosissima, Ceriocava corymbosa (including flabellotrypiform zoaria), ?Heteropora lorieri, and an indeterminate bilamellar diastoporidiform species.

4. Reviers (T 956818)

Either Middle Bathonian; Revier Member (*subcontractus* Zone) overlain by Fontaine-Henry Member (*morrisi* Zone), or Upper Bathonian; Ranville Member (*retrocostatum*/*aspidoides* Zones) overlain by St. Aubin Member (*aspidoides*/*discus* Zones).

see Guillaume (1929), Palmer (1974, p.172).

Two large disused quarries west of Reviers expose beds originally assigned to the Middle Bathonian by Palmer (1974) but later (Palmer pers. comm. September 1976) assigned to the Upper Bathonian due to the presence of apparent Langrune Member limestones capping the section. The basal beds (Revier or Ranville Member) are comparatively unfossiliferous, massive cross-bedded calcarenites. In the more westerly of the two quarries, the Fontaine-Henry or St. Aubin Member consists of poorly consolidated limestones containing pale grey unbedded sponge masses which are mound-shaped in section. Within these probable reefs fauna other than poriferans is scant, but between the reefs plicate oysters, small sponges (including neuroporids) and bryozoans (some with preserved bases) are common. A particularly conspicuous element of the bryozoan fauna are dendroid zoaria, with zooecia terminated by a thin frontal wall perforated by a central aperture, which were named _Cyclocites primogenitum_ by Canu and Bassler (1922) but referred to _Ceriocava corymbosa_ by Walter (1969). Adnate bryozoans at this locality are much scarcer than in St. Aubin Member exposures sampled elsewhere e.g. Ranville, Amfreville. The bryozoan fauna recorded from the Fontaine-Henry or St. Aubin Member consists of _Multisparsa sp_. (ribbon-shaped bilamellar diastoporidiform zoaria), _Collapora straminea_, _C.microstoma_, _Terebellaria ramosissima_, _Ceriocava corymbosa_ (including '_Cyclocites primogenitum_'), ?_Ripisoecia conifera_, an indeterminate probosciniiform multisparsid species, and indeterminate berenic-iform multisparsid and plagioecid species.

5. _Blainville_ (U080731)
Middle/Upper Bathonian; Blainville Member (_morrisi_/ _retrocostatum_ Zones)
see Bigot (1928, 1949), Walter (1969, p.235), Palmer (1974, p.170).

The Caen to Ouistreham road cuts through the old quarry at Blainville but, although heavily weathered and inaccessible in parts, the quarry face is still preserved. The thick-bedded limestones of the Blainville Member exposed are unevenly cemented and abundant _Reticulipora dianthus_ was obtained from the poorly cemented portions.

Some of the R. dianthus zoaria, inferred to have attached above the sea-bed during life, are encrusted by serpulids and thecidean brachiopods. The bryozoan fauna of the Blainville Member consisted of Stomatopora ?dichotoma, S. ?dichotomoides, Collapora tetragona, Idmonea triquetra, Mesenteripora michelini, M. undulata, Reticulipora dianthus, Terebellaria ramosissima, Ceriocava corymbosa (topotypes), Ripisoecia conifera (globose and dendroid growth-forms), and indeterminate berenic-iform multisparsid and plagioecid species.

6. Carriere des Campagnettes (U114748), Ranville.
Middle to Upper Bathonian; Blainville Member (morrisi/retrocostatum Zones), Campagnettes Member (retrocostatum/aspidoides Zones), Ranville Member (retrocostatum/aspidoides Zones), St. Aubin Member (aspidoides/discus Zones) and Langrune Member (discus zone).
See Guillaume (1925), Bigot (1928), Palmer (1974, p.167).

A large quantity of Jurassic bryozoans held in museum collections bear the label 'Bathonian, Ranville'. Many were obtained from a lenticular deposit known as the caillasse à cephalopodes (Walter 1969, p.236) occurring within the Blainville Member and now apparently completely worked out by the quarrying operations at the large Carriere de Ciments

Francais (Palmer pers. comm. September 1976). Access to this quarry was not granted at the time of visit.

Another quarry in work at Ranville, the Carriere des Campagnettes, exposes a faulted section through the Middle and Upper Bathonian:

a. Blainville Member

The cross-bedded limestones of the Blainville Member contain few complete fossils. A bored hardground terminates the member.

b. Campagnettes Member

Clay-rich bed as the base of the Campagnettes Member yield an extensive fauna dominated by corals, sponges and '*Terebratula*' *circumdata*. Steinkerns of two large gastropods were also obtained. Both had an internal epifauna which developed prior to the dissolution of the gastropod shell, and a later external epifauna encrusting the sediment cast. This, along with the occurrence of heavily abraded and encrusted dendroid bryozoans, suggests that the Campagnettes Member had a long and complex depositional history involving episodes of deposition, lithification and re-working. The following bryozoans were recorded; *Stomatopora* spp., *Multisparsa* spp., *Mesenteripora undulata*, *Terebellaria ramosissima*, *Ceriocava corymbosa* (including '*Cyclocites primogenitum*'),

?Ripisoecia conifera, Crescis dometosa (adnate), an indeterminate probosciniiform species, and indeterminate berenic-iform multisparsid and plagioecid species.

c. Ranville Member

Complete fossils are infrequent in the Ranville Member but fragmentary erect bryozoans were recovered from some of the less consolidated parts. At or near to the base of the member there is a strongly burrowed hardground with an associated fauna of brachiopods, echinoids and bryozoans, dominated by foliaceous forms. The bryozoans found in the Ranville Member consisted of Multisparsa spp., Mesenteripora michelini, Entalophora cellarioides, Spiropora elegans, Reticulipora dianthus, Terebellaria ramosissima, Ceriocava corymbosa, Cava subcompressa, ?Ripisoecia conifera (globose and dendroid), Crescis dumetosa (adnate), and indeterminate berenic-iform tubuloporinids.

d. St. Aubin Member

This member is exposed in the part of the quarry at the downthrown northerly side of the fault. It consists of brown to grey clays and marls, with a prolific fauna of brachiopods, bryozoans, bivalves and bryozoan-encrusted trochoform gastropods. The diverse bryozoan fauna includes a wide variety of growth-forms both erect and encrusting, foliaceous and dendroid. A complex environment containing a variety of habitats stable over a long period of time is therefore suggested. Many of the erect bryozoans are fragmentary, heavily abraded, bored and encrusted. Others are lightly encrusted and their bases may be intact. Some of the erect bryozoan zoaria have branches in one plane only, suggesting colony growth in an environment of unidirectional current flow. The brachiopods lie in many different orientations and also vary in the quantity of epifauna they bear. Some are devoid of epifauna, whilst others are disarticulated and have a thick development of adnate organisms on their abraded surfaces. Abundant large oyster valves may have many layers of epifauna which probably required a number of years to develop. The following bryozoans were recorded; _Stomatopora bajocensis_, _S. dichotoma_, _S. dichotomoides_, _Reptomultisparsa incrustans_, _Multisparsa lamellosa_, _M. sp._, _Collapora microstoma_ (adnate and erect), _C. tetragona_, _Idmonea triquetra_, '_Diastopora_' _foliacea_ (cavariiform), _Hyporosopora typica_, _Mesenteripora michelini_, _M. undulata_, _Entalophora annulosa_, _Spiropora elegans_, _Reticulipora dianthus_, _Terebellaria ramosissima_, _Ceriocava corymbosa_, _Cava subcompressa_, ?_Ripisoecia conifera_ (globose and dendroid) _Crescis dumetosa_ (adnate and erect), _Heteropora lorieri_, indeterminate berenic-iform spp., and indeterminate prob osciniiform spp.

7. Benouville (U097746)

Upper Bathonian; Ranville Member (retrocostatum/aspidoides Zones) and St. Aubin Member (aspidoides/discus Zones).

see Palmer (1974, p.165).

The exposures at Benouville consist of a partly overgrown quarry face on the west bank of the Caen Canal south of Pegasus Bridge, and a small recent exposure by the steps leading up to the Yachting Clubhouse. Resistant limestone of the Ranville Member is terminated by a hardground overlain by marls of the St. Aubin Member. These marls are fossiliferous near to the clubhouse but their fauna becomes less prolific northwards towards Pegasus Bridge. The following bryozoans were recorded from the St. Aubin Member; Stomatopora bajocensis, Multisparsa sp., Mesenteripora michelini, Entalophora annulosa, ? Ripisoecia conifera, and indeterminate berenic-iform tubuloporinids.

8. St. Aubin-sur-mer (T851015)

Upper Bathonian; Ranville Member (retrocostatum/aspidoides Zones)

see Walter (1969, p.237), Palmer (1974, p.161).

The cliffs between St. Aubin-sur-mer and Bernieres-sur-mer expose the upper part of the Ranville Member and the sponge-reef facies of the St. Aubin Member (fig.108). Hard limestones at the base of the St. Aubin Member, immediately above a hardground forming the top of the Ranville Member, contain bored fragments of large dendroid cerioporinids and occasional foliaceous tubuloporinids. Between this resistant limestone and the sponge-reefs are clays and marls containing an abundant fauna dominated by dendroid bryozoans which may lie in inverted positions. Some have a bryozoan epifauna which occasionally spreads over the underside of preserved zoarial bases. Bryozoan encrusted brachiopods also occur in these beds, particularly in clay-rich lenses. Towards the top of the clays and marls there is a broken-up hardground consisting of bored and encrusted limestone clasts. The sponge-reefs appear to nucleate some way above the hardground, although this could result from the cliff-section obliquely intersecting the inverted cone-shaped sponge-reefs. The bracket- to cup-shaped sponges forming the reefs are apparently in life-position and are occasionally bryozoan encrusted. At the eastern end of the cliff-section the reefs originate from discrete nuclei (pl. 35) and spread upwards to coalesce with one another (pl. 35). Further westwards the sponge-reefs are more extensive and lack a definite upward spreading form. The unconsolidated sediment between reefs consists largely of broken vinculariiform bryozoans dominated by Entalophora annulosa (Walter 1969) with occasional Spiropora elegans and some dendroid cerioporinids. Large specimens of Plagiostoma and the sclerosponge Neuropora are the other main faunal elements found between the reefs.

Environmental conditions were probably initially similar to those prevalent during St. Aubin Member deposition further east (at Benouville, Ranville and Amfreville) when the bryozoan-rich beds beneath the sponge-reefs were formed. The environment was probably spatially complex, contained a diversity of habitats, and was stable over a long period of time allowing colonisation by many bryozoan species showing a variety of growth-forms. Dislodged colonies were rolled, bored and encrusted. A hardground eventually formed and became broken-up by the activities of burrowing and boring organisms. The presence of the hardground may have been necessary for nucleation of sponge patch-reefs. The reefs probably had only a slight elevation above the sea-bed, judging by the frailty of their fossilised skeletal framework, but they may have grown upwards and outwards at a fairly rapid rate. The sheltered habitats between reefs were colonised by vinculariiform cyclostomes, notably Entalophora annulosa, whose broken remains formed the bulk of the between reef sediment.

The following bryozoans were collected from the St. Aubin Member; *Stomatopora dichotomoides*, *S. sp.*, *Multisparsa lamellosa*, *M. sp.*, *Collapora microstoma* (adnate and erect), *C. tetragona*, *Idmonea triquetra*, *Hyporosopora typica* (topotypes), *Mesenteripora michelini*, *M. undulata*, *Entalophora cellarioides*, *E. annulosa*, *Spiropora elegans*, *Terebellaria ramosissima* (topotypes), *Ceriocava corymbosa* (including flabellotrypiform and abundant monticuled zoaria), ?*Ripisoecia conifera* (dendroid and globose), *Crescis dumetosa*, indeterminate probosciniiform spp., and indeterminate bereniciform spp.

9. *Amfreville* (U121760)

Upper Bathonian; Ranville Member (*retrocostatum/aspidoides* Zones), St. Aubin Member (*aspidoides/discus* Zones) and Langrune Member (*discus* Zone).
see Bigot (1928), Palmer (1974, p.163).

Bigot (1928) described 8 quarries in the vicinity of Amfreville. Only the two quarries numbered by him III and VIII were visited. The former is a shallow quarry, adjacent to the D514, which exposes about 2.8 metres of friable cross-bedded biosparites of the Langrune Member. The limestones contain abundant abraded bryozoan fragments, predominantly of vinculariiform zoaria. The following species were collected; Collapora microstoma, ?Mesenteripora undulata (erect), Entalophora annulosa, Ceriocava corymbosa, ?Ripisoecia conifera, and an indeterminate diastoporidiiform tubuloporinid.

The large quarry adjacent to the minor road west of the D514 exposes the Ranville and St. Aubin Members. At the top of the quarry fossiliferous St. Aubin Member is developed in a facies similar to that seen in the Carriere des Campagnettes, Ranville. Cerioporinids are, however, less conspicuous here than at Ranville. An extensive adnate bryozoan fauna occurs attached to brachiopods (sometimes disarticulated and covered by an algal coating), large oysters and dendroid bryozoans. The following bryozoans were obtained from the St. Aubin Member; Stomatopora bajocensis, S. dichotoma, Multisparsa lamellosa, Collapora microstoma (adnate), Idmonea triquetra (abundant), Hyporosopora typica, Mesenteripora undulata, Entalophora annulosa, Terebellaria ramosissima, ?Ripisoecia conifera, Crescis dumetosa (adnate and erect), indeterminate prosboscinii form sp., and indeterminate berenic-iform tubuloporinids.

10. Douvres la Deliverande (U032815)
Upper Bathonian; Langrune Member (discus Zone)
see Palmer (1974, p.163)

This large quarry, situated north of the village, was being filled with refuse during September 1976. The typical Langrune Member cross-bedded limestones exposed show conspicuous upwardly-fining units. An oyster-encrusted hardground (pl. 36) occurs about 2.5 metres from the base of the section (Palmer 1974) and the coarse limestone immediately above the hardground yields a diverse fauna, probably originally associated with the hardground, of erect bryozoans, along with some plicate oysters and occasional brachiopods. The bryozoans collected consisted of *Multisparsa lamellosa*, *M.sp.*, *Collapora tetragona*, *Mesenteripora michelini*, *Spiropora elegans*, *Entalophora annulosa*, *Reticulipora dianthus*, *Terebellaria ramosissima*, ?*Apsendesia cristata*, *Ceriocava corymbosa*, *Cava subcompressa*, ?*Ripisoecia conifera*, and an indeterminate berenic-iform sp.

11. *Luc-sur-mer* (U054850)
Upper Bathonian; Langrune Member (*discus* Zone)
see Walter (1969, p.239), Palmer(1974, p.160)

Low cliffs behind the eastern end of the promenade at Luc-sur-mer expose cross-bedded oobiosparites of the Langrune Member. These beds contain an abraded, but generally unencrusted, bryozoan fauna characterised by globose specimens of ?*Ripisoecia conifera*. The bryozoans collected were

Multisparsa lamellosa, *Reptomultisparsa incrustans*, ?*Mesenteripora undulata* (cavariiform), *Entalophora annulosa*, *Terebellaria ramosissima*, *Ceriocava corymbosa*, and ?*Ripisoecia conifera*.

Further east, towards Lion-sur-mer, a bed known as the caillasse à brachiopodes occurs within the Langrune Member at the base of the cliff and on the foreshore. At the time of visit the foreshore exposures, which contain *Avonothyris* in abundance, were not well exposed but the upper part of the caillasse was visible in the wave cut notch at the base of the cliff. The caillasse is composed of large algal-coated shell fragments or oncolites which are set in a matrix of marl. Many of the oncolites bear an adnate bryozoan fauna, particularly of *Mesenteripora undulata*, which apparently developed contemporaneously with algal growth so that some of the bryozoans are partly covered by algally-accreted carbonate. The bryozoans collected consisted of *Stomatopora spp.*, *Reptomultisparsa incrustans*, *Multisparsa lamellosa*, *M. sp.*, *Hyporosopora parvipora* (topotypes), *H. sauvagei*, *Mesonopora concatenata*, *Mesenteripora undulata*, *Ceriocava corymbosa* (monticuled zoaria), ?*Ripisoecia conifera*, indeterminate probosciniiform sp., and indeterminate berenic-iform tubuloporinids.

12. Commeaux (U228233)

Upper Bathonian; ?Langrune Member (discus Zone)

see Walter (1969, p.240).

A shallow overgrown pit to the east of the N158 south of Occagnes, and an adjacent temporary exposure, showed beds probably belonging to the Langrune Member. Bryozoans were abundant in a marly limestone which seemed to be underlain by a burrowed hardground, although the hardground was not seen in situ. Together with the brachiopods *Goniorhynchia boueti*, *Eudesia cardium* and *Digonella*, the following bryozoan fauna was collected; *Stomatopora bajocensis*, *Multisparsa lamellosa*, *M. sp.*, *Collapora microstoma*, *C. tetragona*, *Mesenteripora michelini*, *M. undulata* (adnate and erect cavariiform), *Spiropora elegans*, *Terebellaria ramosissima*, *Ceriocava corymbosa*, ?*Ripisoecia conifera*, *Crescis dumetosa*, indeterminate probosciniiform sp., and indeterminate berenic-iform spp.

13. Occagnes (U232238)

Upper Bathonian; ?Langrune Member (discus Zone)

see Canu (1898), Walter (1969, p.240).

The largely overgrown quarry from which Canu (1898) described the bryozoan fauna is situated in a wood east of the Occagnes to Pommainville road. About 3 metres are exposed of very poorly cemented bryozoan-rich limestones displaying well developed cross-bedding. A diverse transported fauna of fragmentary bryozoans was collected and included Collapora tetragona, Spiropora elegans, Entalophora annulosa, Ceriocava corymbosa, and foliaceous species.

14. Villers-sur-mer (U287827)
Lower Oxfordian; Villers Marls (mariae Zone)
see Bigot (1930), Arkell (1930; 1956, p.47)

The high cliffs between Villers and Houlgate consist of Oxfordian clays capped by Corallian limestones. Loose valves of Gryphaea dilatata, probably from the Villers Marls, are extensively serpulid and foraminiferan encrusted, but also bear occasional small colonies of indeterminate plagioecid berenic-iform tubuloporinids, some of which are comparable with Hyporosopora typica.

DORSET

15. Thorncombe Beacon (SY 435912)

Upper Pleinsbachian and Toarcian; Junction Bed (*spinatum* to *jurense* Zones)

see Jackson (1926), Davies (1935, pp.32-33), Ager and Smith (1965, p.18).

Boulders derived from the highly condensed Junction Bed litter the foreshore beneath the high cliffs of Thorncombe Beacon. Two basic lithologies are present; pink limestone packed with ammonites (often with planed-off surfaces), and a hard grey to brown impure limestone containing a mixed fauna. One of the grammoceratid ammonites collected from the former lithology (probably from the *bifrons* Zone, J.R. Senior pers. comm.) was encrusted by a poorly-preserved berenic-iform tubuloporinid. Jackson (1926, p.510) records 4 species of bryozoan, identified by Mr. A.G. Davis, from the Junction Bed at Thorncombe Beacon.

16. East Cliff (SY 470899), Bridport

Lower Bajocian; Snuff-box Bed (*sauzei* Zone)

see Davies (1935, p.36)

The Bridport Sands form the greater part of East Cliff and are capped by relatively condensed Inferior Oolite carbonates. One particular horizon within the Inferior Oolite contains large limonitic algal concretions known as snuff-boxes. Fallen blocks from the Snuff-box Bed were collected from the beach beneath the cliff. The snuff-boxes are heavily serpulid encrusted but some bryozoans also occur and an indeterminate bereniciform multisparsid was recorded.

17. Shipton Gorge (SY 500915)
Upper Bajocian; Microzoa Beds (parkinsoni Zone)
see Walford (1889, 1894a), Walter (1967), Lord and Senior (1973).

The old quarry opposite the New Inn at Shipton Gorge is one of the classic Jurassic bryozoan localities in England. Fortunately, the quarry face is still preserved at the rear of a private garden. The following section was measured during August 1975:

Limestone, containing ammonites, belemnites, large serpulids, brachiopods and adnate bryozoans	seen for 0.70 m.
Upper Marl with poriferans and bryozoans	0.15 m.
Limestone	0.18 m.
Lower Marl with abundant poriferans and bryozoans	0.20 m.
Limestone	seen for 0.30 m.

The marl horizons, in particular, contain abundant fragments of delicate vinculariiform species, notably '*Mecynoecia*' bajocina. Their presence suggested to Walter (1967) that deposition took place in very calm waters perhaps abounding with marine plants. The conspicuous absence of large dendroid cerioporinids in a deposit so rich in Bryozoa probably indicates comparatively rapid deposition in a temporally unstable environment. This inference is supported by the fact that the bryozoans are unabraded and epifauna on erect species is scarce. The Microzoa Beds contain limestone surfaces and pebbles encrusted by bryozoans indicating submarine lithification and further supporting the calm water theory. An unusual feature of the Microzoa Beds is the occurrence of abundant bryozoans and ammonites in the same deposit. Some of the ammonites from the uppermost limestone are bryozoan encrusted; although, rather than being a life association, the bryozoans more probably colonised shells of dead ammonites lying on the sea-bed.

The following cyclostomes were collected from the Microzoa Beds; Stomatopora bajocensis, S. dichotoma, S. dichotomoides, Stomatoporina spirata, 'Microecia' belemnitarum, Reptomultisparsa oolitica, Collapora straminea, 'Idmonea' sp. (erect curved branches which have a convex side composed of autozooecia and a concave side of kenozooecia), Hyporosopora orbiculata, 'Mecynoecia' bajocina, indeterminate prosciniiform sp., and numerous indeterminate bereniciform spp.

18. Coastguard Station (SY 607813), Langton Herring
Upper Bathonian; Oyster Bed in the Upper Fullers Earth Clay (retrocostatum/aspidoides Zone)
see Arkell (1934), Davies (1935, p.50), House (1958, p.18).

The low cliff behind the coastguard station on the shores of the Fleet backwater exposes about 5 m. of an oyster bed within the Upper Fullers Earth Clay. The bed consists almost exclusively of elongated individuals of Praeexogyra [Liostrea] hebridica contained in a small amount of clay matrix. A large collection of these oysters was made but only 2 specimens had adnate bryozoans. Two species of indeterminate bereniciform tubuloporinid, both with small zoaria and minute zooecia, were found encrusting the inner concave surface of P. hebridica, probably occupying a cryptic habitat protected from muddy sediment.

19. Fault Corner (SY 453908), Watton Cliff, Bridport
Upper Bathonian; Upper Fullers Earth Clay (retrocostatum/aspidoides Zones), Boueti Bed (aspidoides Zone) and Forest Marble (aspidoides/discus Zones)
see Davies (1935, p.33).

Fault Corner is a gully in the cliff which runs along the line of a palaeofault described by Jenkyns and Senior (1977). The cliffs to the east of the fault are formed of Bathonian deposits. The Boueti Bed was not exposed at the time of visit but the Forest Marble could be seen and consisted of shelly limestones containing fragments of abraded erect bryozoans and some zoaria adnate on shell debris. The transported bryozoan fauna consisted of Collapora microstoma, Hyporosopora typica, Terebellaria ramosissima, and an indeterminate bereniciform tubuloporinid.

20. Herbury Peninsula (SY 611810), Langton Herring
Upper Bathonian; Boueti Bed (aspidoides Zone)
see Richardson(1909), Davies (1935, p.50), House (1958, p.18).

The Herbury Peninsula, situated on the Fleet backwater, is the classic locality for the Boueti Bed. Although the bed could not be seen in-situ at the time of visit, its characteristic brachiopod fauna was collected from the foreshore. The adnate bryozoans on the brachiopod shells are described more fully on p. 314 ; the following bryozoans were collected at Herbury; Stomatopora spp., Hyporosopora typica, H. sauvagei, indeterminate proboscinii-form sp., and numerous indeterminate berenic-iform tubuloporinids.

Table 18. Bathonian stratigraphy of southern England. The Forest Marble of the Mid Cotswolds consists of the Kemble and Wychwood Beds separated by Bradford Clay. The Bradford Clay occurs at the base of the Forest Marble in the Bath region. After Torrens (1968, 1969), Palmer (1974).

Zone	Dorset	Bath	Mid Cotswolds
discus	Lower Cornbrash Forest Marble	Lower Cornbrash Forest Marble	Lower Cornbrash Wychwood Beds
aspidoides	*Boueti* Bed Upper Fullers Earth Clay	Great Oolite Limestones	Kemble Beds
retrocostatum	*Wattonensis* Bed	Upper Fullers Earth Clay	White Limestone Formation
morrisi	Lower Fullers Earth Clay	Fullers Earth Rock	
subcontractus			
progracilis		*Acuminata* Beds Lower Fullers Earth Clay	Hampen Marly Fm. Taynton Limestone Fm. Sharps Hill Fm.
zigzag	*Zigzag* Bed	*Anabacia* and *Fullonicus* Limestones	Chipping Norton Formation

21. Furzy Cliff (SY 700818), Weymouth
Oxfordian; Upper Oxford Clay
see Davies (1935, pp.61-62).

The slipped Oxford Clay at Furzy Cliff contains septarian nodules, crushed ammonites and abundant large *Gryphaea dilatata*. Some of the *G. dilatata* shells are heavily encrusted by foraminiferans, serpulids and oysters, and one specimen found had numerous adnate zoaria of a cyclostome comparable with *Hyporosopora typica*.

22. Bran Point (SY 742814), Osmington
Oxfordian; Osmington Oolite (probably *transversarium* Zone)
see Arkell (1933, 1947), Davies (1935, p.65), House (1958, p.16).

Superb sections of the Corallian are exposed between Osmington and Ringstead. A half day's search failed to yield any bryozoans in these beds with the exception of two small zoaria of an indeterminate berenic-iform plagioecid encrusting the inside of an oyster valve from an oyster-rich bed within the Osmington Oolite.

23. West Weare Cliffs (SY 681725), Isle of Portland
Volgian; Portland Stone (*giganteus* Zone, probably equivalent to the *fulgens* Zone, Hallam 1975).

see Davies (1935, pp.54-56), House (1958, p.10), Townson (1975).

Boulders which have fallen from the Portland Stone Quarries above line the path beneath West Weare Cliffs. These boulders are mostly from the Cherty Series of the Portland Stone and many contain the large bivalve *Camptonectes lamellosus*. *Hyporosopora portlandica* is a moderately common encruster of this bivalve, principally on interior surfaces of the shells.

The following Dorset Jurassic localities failed to yield any bryozoans:

A. Stonebarrow Cliffs (c. SY 380927)

The Belemnite Marls (Lower Pleinsbachian, *jamesoni* and *ibex* Zones) contain abundant belemnites whose guards, encrusted by serpulids and foraminiferans, would seemingly constitute a potential substrate for cyclostomes. However, belemnites collected during half a day in the field, and hundreds of specimens collected and examined by J.T.F.S. Bolton, are all devoid of encrusting bryozoans.

B. Fleet Common (c. SY 630798)

Subsoil exposures of the Lower and Upper Cornbrash on the shores of the Fleet River contain a rich fauna of bivalves and brachiopods. Adnate cyclostomes were absent from the numerous specimens collected.

C. Jubilee Coppice (SY 576856), Abbotsbury

The Lower Kimmeridgian (<u>cymodoce</u> Zone) oolitic Abbotsbury Ironstone at this locality failed to yield any cyclostomes despite containing abundant brachiopods which may have served as potential substrates.

WILTSHIRE

24. Canal Quarry (ST 826600), Bradford-on-Avon

Upper Bathonian; Upper Rags (*aspidoides* Zone), Bradford Clay (*discus* Zone) and Forest Marble (*discus* Zone). see Palmer and Fürsich (1974).

At the time of visit, January 1975, the Old Canal Quarry was in the process of being filled in. The extremely fossiliferous Bradford Clay, which overlies a hardground formed at the top of the Upper Rags and with which much of the Bradford Clay fauna was associated during life (Palmer and Fürsich 1974), was not exposed but material derived from it was collected from the quarry floor. The bryozoan fauna of the Bradford Clay is extremely prolific and diverse . The following species were collected at the Canal Quarry; *Stomatopora* spp., *Collapora microstoma* (erect and adnate), *Idmonea triquetra*, *Hyporosopora typica*, *H. sauvagei*, *Mesonopora concatenata*, *Terebellaria ramosissima*, ?*Ripisoecia conifera* (one heavily abraded zoarium), and indeterminate berenic-iform tubuloporinids.

Loose fragments of the Upper Rags contained erect *Collapora microstoma*, but the Forest Marble appeared to be devoid of cyclostomes.

25. <u>Stanton St. Quintin</u> (ST 947813)

Upper Bathonian; Lower Cornbrash (<u>discus</u> Zone)

see Douglas and Arkell (1928, p.141).

This old quarry is situated in a wood on the Stanton St. Quintin to Upper Seagry road. The quarry is badly overgrown and according to a local resident it has remained unworked for about 70 years. However, it was possible to collect large numbers of fossils, particularly <u>Cererithyris intermedia</u>, from the quarry floor and these mostly derive from the basal blue day and 'brash' of the Lower Cornbrash (Douglas and Arkell's Beds 1 and 2). Museum collections frequently contain large erect and multilamellar zoaria of <u>Collapora microstoma</u>, in a matrix comparable to that of these basal beds, said to have originated from Stanton St. Quintin and district. No <u>C. microstoma</u> specimens were found during the visit but two of the brachiopods collected were encrusted by ?<u>Hyporosopora typica</u>.

SOMERSET

26. Bathampton Down (c.ST 776653)

Upper Bathonian; Upper Rags (*aspidoides* Zone)

see McKerrow, Ager and Donovan (1964, p.24), Elliott (1974).

Bryozoans were collected from the Upper Rags at two localities on Bathampton Down; adjacent to the reservoir at the summit of the golf course, and in an overgrown quarry at the north-east corner of the Down. The Upper Rags consist of white to buff oobiosparites, at times brittle but occasionally hard and indurated. Shell fragments abound and small whole brachiopods, poriferans and oysters are common. Evidence suggests that the Upper Rags were deposited in high energy conditions (Elliot 1974). Abundant terebellariiform *Collapora microstoma* zoaria, strengthened by the addition of lamellar overgrowths, occur predominantly as abraded transported fragments, although some comparatively unbroken colonies are also found. Occasional unworn encrusting bryozoans occur in sheltered habitats, such as concave surfaces of shells, and these may have grown in-situ on the accumulating shell debris. The following bryozoan fauna was recorded; *Stomatopora bajocensis*, *Reptomultisparsa cobergonensis*, *Collapora microstoma*, *Hyporosopora parvipora*, *Terebellaria ramosissima*, *Crescis dumetosa*, and an indeterminate berenic-iform plagioecid.

GLOUCESTERSHIRE

27. Cleeve Hill (SO 984260)

Aalenian; Pea Grit and Lower Freestone (*murchisonae* Zone) see Richardson (1929).

The old quarry face on Cleeve Cloud (pl. 37) shows a fossiliferous section through the Lower Inferior Oolite. Two principal horizons yield bryozoans; a bed of rounded limestone pebbles within the Pea Grit (Richardsons bed 20), and the Polyzoa Bed at the base of the Lower Freestone.

About 6 metres beneath the top of the Pea Grit there occurs an unusual horizon (pl. 37) consisting of limestone clasts set in a poorly consolidated marly matrix containing occasional fragmentary erect bryozoan zoaria and *Pentacrinites*. The rounded, slightly reddened, limestone clasts decrease in size upwards through the clast horizon away from the broken upper surface of the underlying bed. Some of the smaller clasts are evidently algal oncolites whilst the larger ones may also have an apparent algal carbonate coating. Serpulids, oysters, small solitary corals and bryozoans constitute a diverse encrusting fauna attached to the clasts. Bivalve borings also abound and the morphologies of many clasts suggest that they have had a complex history of abrasion, boring and

Table 19 . Chronostratigraphical and lithostratigraphical divisions of the Inferior Oolite in the Cotswold Hills. After Arkell (1933), Murray (1969) and Parsons (1974). Double lines indicate major stratigraphical breaks.

Stage	Zone	Lithostratigraphical divisions	
BAJOCIAN	<u>parkinsoni</u>	Clypeus Grit	UPPER INFERIOR OOLITE
	<u>garantiana</u>	Upper Trigonia Grit	
	<u>sauzei</u>	Phillipsiana and Bourguetia Beds	MIDDLE INFERIOR OOLITE (RAGSTONES)
	<u>laeviuscula</u>	Witchellia Grit Notgrove Freestone	
	<u>discites</u>	Lower Trigonia Grit Buckmani Grit Gryphite Grit	
AALENIAN	<u>concavum</u>	Tilestone Snowshill Clay Harford Sands	LOWER INFERIOR OOLITE
	<u>murchisonae</u>	Upper Freestone Oolite Marl Lower Freestone Pea Grit Lower Limestone	
	<u>opalinum</u>	Scissum Bed Upper Cephalopod Bed	

encrusting, further abrasion etc. Extensive submarine lithification was almost certainly involved in the formation of this horizon and the lithified limestone was probably broken up partly by biogenic processes. Upward decrease in clast size suggests an overall decrease in environmental energy with time culminating in the onset of accretionary processes (algal carbonate coating). The following bryozoan species were collected; Stomatopora bajocensis, S. dichotoma, S. dichotomoides, 'Proboscina' sp. (this abundantly occurring species is the one described incorrectly by Gregory in his Catalogue of Jurassic Bryozoa as Proboscina morinica (Sauvage)), Reptomultisparsa cobergonensis, R. oolitica, Multisparsa ventricosa (bilamellar diastoporidiiform zoaria), Collapora straminea, Theonoa chlatrata, Ceriocava corymbosa (flabellotrypiform zoaria), Ripisoecia conifera, and indeterminate berenic-iform spp.

The cross-bedded oolitic limestone at the base of the Lower Freestone is known as the Polyzoa Bed from its abundance of bryozoans. Foliaceous species dominate but vinculariiform zoaria abound as well, and thick-branched dendroid colonies also occur. The bryozoan colonies are frequently unbroken and most show no signs of abrasion and lack an epifauna. The fronds of the foliaceous diastoporidiiform zoaria commonly originate from a cavariiform zoarial base in which the axial lumen is a few mm. in diameter and is surrounded by a basal lamina of exterior body wall. This type of structure suggests that, during life, these bryozoans were attached to cylindrical perishable organisms, perhaps marine plants. The Polyzoa Bed fauna probably represents the remains of a flourishing but fairly short-lived community (or succession of communities) which developed above temporarily stabilised sediment and which became buried relatively rapidly by an advancing oolith shoal. Bryozoans of the following species were recorded; _Stomatopora ?bajocensis_, _Multisparsa lamellosa_, _Multisparsa_ cf. _scobinula_, _Multisparsa ventricosa_, _Collapora straminea_, _Mesenteripora_ sp., and _Ripisoecia conifera_.

28. _Crickley Hill_ (SO 930160)
Aalenian; Pea Grit (_murchisonae_ Zone)
see McKerrow, Ager and Donovan (1964, p.11), Murray (1969, p.542).

Scissum Beds and Lower Limestone form the basal parts of the cliffs at Crickley Hill and are overlain by a thick development of pisolitic Pea Grit capped by a bed of transported corals (the Fourth Coral Bed). Bryozoans were found encrusting pisoliths and bored limestone hardgrounds and clasts in the Pea Grit. Abundant zoaria of _Ripisoecia_ _conifera_, some with monticules, occur in the coral bed. The following species were collected; _Stomatopora bajocensis_, _S. dichotoma_, _S. dichotomoides_, '_Microecia_' cf. _matisconensis_, _Reptomultisparsa cobergonensis_, _R. cricopora_, _Reptoclausa porcata_, _Multisparsa lamellosa_, _M. ventricosa_ (topotypes), _Collapora straminea_, _Theonoa chlatrata_, _Ceriocava corymbosa_ (flabellotrypiform zoaria), _Ripisoecia conifera_ (abundant as dendroid colonies with comparatively narrow branches, c. 4 mm diameter), indeterminate probosciniiform spp., and indeterminate berenic-iform tubuloporinids.

29. _Leckhampton Hill_ (c. SO 939185)

Aalenian; Lower Limestone, Pea Grit, Lower Freestone, Oolite Marl and Upper Freestone (all _murchisonae_ Zone)

Bajocian; Lower Trigonia Grit and Gryphite Grit (_discites_ Zone). 'Ragstones'.

see McKerrow, Ager and Donovan (1964), Murray (1969).

The classic sections of the Inferior Oolite at Leckhampton Hill are now deteriorating due to the cessation of quarrying operations combined with excessive collecting. Loose blocks, derived from the Lower Inferior Oolite, lying on the floors of the Lime-kiln quarry (pl. 36) and adjacent South quarry still, however, provide an opportunity for collecting bryozoans, particularly from the Lower Limestone and Pea Grit. A shelly horizon at the base of the Lower Freestone also yields abraded fragmentary zoaria of Collapora straminea. Some bedding planes within the Lower Freestone are bryozoan and oyster encrusted. The following species were obtained from the Lower Inferior Oolite at Leckhampton; Stomatopora dichotoma, S. dichotomoides, Reptomultisparsa cobergonensis, R. cricopora, Reptoclausa porcata, Collapora straminea, Theonoa chlatrata, Ceriocava corymbosa (flabellotrypiform zoaria), Ripisoecia conifera, indeterminate plagioecid and multisparsid bereniciform spp., and an indeterminate diastoporidiform tubuloporinid.

A small exposure of Middle Inferior Oolite 'Ragstones' occurs higher up the hill. Earthy marls and limestones of the 'Ragstones' (probably Gryphite Grit) contained terebratulids, modiolid bivalves and the bryozoans Reptomultisparsa cricopora and Collapora straminea. Numerous well-preserved zoaria of C. straminea, often associated with salmacinid serpulids, contained in the BMNH collections probably originate from this bed.

30. Standish Wood (SO 083069)

Aalenian; Lower Limestone, Pea Grit and Lower Freestone (murchisonae Zone)

see Mudge (1973)

This quarry, situated in the centre of the wood, exposes the Lower Limestone, developed as a white oolitic limestone, the Pea Grit and the Lower Freestone, occurring as rubble at the top of the quarry. The quarry face is high and inaccessible but an almost complete zoarium of *Collapora straminea* was collected from a fallen block of Pea Grit lying on the quarry floor.

31. *Frith Quarry* (SO 867082), Juniper Hill, Painswick
Aalenian; ?Oolite Marl (*murchisonae* Zone)
see Buckman (1895, pp.399-400)

Situated off the Painswick to Wickstreet road, the Frith Quarry is now almost totally grassed over. It once exposed beds between the Lower Freestone and Buckmani Grit, and is the type-locality of *Mecynoecia thomasi* Walter 1969. A small scar visible during July 1976 showed rubbly and marly limestones with terebratulids, bivalves and corals. The presence of loose *Plectothyris fimbria* suggests that the exposure was Oolite Marl. A few poorly-preserved indeterminute berenic-iform tubuloporinids were collected.

32. *Swifts Hill Quarry* (SO 877068)
Aalenian; Oolite Marl and Upper Freestone (*murchisonae* Zone)
Bajocian; Lower Trigonia, Buckmani and Gryphite Grits

(_discites_ Zone), Notgrove Freestone (_laeviuscula_ Zone), Upper Trigonia Grit (_garantiana_ Zone)
see Buckman (1895, pp.397-398), Marker (1972/3).

The Lower Inferior Oolite is not well exposed at Swifts Hill Quarry but is represented by rubble containing _Plectothyris fimbria_ on quarry tracks and heaps; no bryozoans were found in it. A loose bivalve fragment collected from the Middle Inferior Oolite (_discites_ and _laeviuscula_ Zones) is encrusted by an indeterminate berenic-iform tubuloporinid and a discoidal zoarium probably of _Ceriocava corymbosa_. Marker (1972/3) cites Swifts Hill as one of the rare localities at which the hardground terminating the Middle Inferior Oolite is serpulid and bryozoan encrusted. Specimens of the hardground collected during this visit lacked encrusting bryozoans. A rubbly limestone with trigonid bivalves and _Stiphrothyris tumida_, probably Upper Trigonia Grit, overlies the hardground. Some of the brachiopods are encrusted by indeterminate berenic-iform tubuloporinids.

33. _Fiddlers Elbow Quarries_ (SO 887142)
Aalenian; Pea Grit (_murchisonae_ Zone)
Bajocian; 'Ragstones' (_discites_ Zone), Upper Trigonia Grit (_garantiana_ Zone) and Clypeus Grit (_parkinsoni_ Zone)
see Channon (1950).

Now no longer in work, the large quarries at Fiddlers Elbow on the Cheltenham to Painswick road display slipped sections of the Inferior Oolite (and basal Great Oolite).

Fiddlers Elbow Quarry I is adjacent to the road and exposes a thick succession of Pea Grit capped by the Fourth Coral Bed. The Pea Grit contains pisolitic horizons, some with bryozoan encrusted pisolites, and a fauna including small rhynchonellid brachiopods, salmacinid serpulids, encrusting cyclostomes, and small or fragmentary erect cyclostomes. The following bryozoans were collected: *Stomatopora sp.*, *Multisparsa lamellosa*, *M. ventricosa*, *Collapora straminea*, *Theonoa chlatrata*, *Multitubigera bowerbanki*, *Ceriocava corymbosa* (flabellotrypiform zoaria), *Ripisoecia conifera*, and indeterminate multisparsid and plagioecid berenic-iform tubuloporinids.

The beds exposed in Fiddlers Elbow Quarry II are extensively disturbed and their stratigraphical relationships are in places difficult to ascertain. Indeterminate berenic-iform zoaria encrusting *Stiphrothyris tumida* shells were obtained from an exposure of oolitic limestone, probably Clypeus Grit, containing fragments of *Clypeus ploti*.

34. *Snowshill Hill Quarry* (SP 132325)

Upper Bajocian; Clypeus Grit (*parkinsoni* Zone)

Upper Bajocian/Lower Bathonian; Hook Norton Limestone

(*parkinsoni*/*zigzag* Zones)

Lower Bathonian; Chipping Norton Limestone (*zigzag* Zone)

Middle Bathonian; Sharps Hill Beds (?*progracilis* Zone), Taynton Stone (*progracilis* Zone)

see Channon (1950), McKerrow, Ager and Donovan (1964), Torrens (1968, p.253).

The quarry at Snowshill Hill near Broadway shows a well-preserved section through late Bajocian and early Bathonian sediments. Bryozoans were obtained from two horizons; the Clypeus Grit and the Sharps Hill Beds.

Oolitic limestones of the Clypeus Grit contain abundant *Stiphrothyris tumida*, many lightly encrusted by berenic-iform zoaria of indeterminate multisparsid and plagioecid tubuloporinids.

Within the Sharps Hill Beds there is a coral bed formed mainly from branching colonies of *Microsolena excelsa* contained in a dark coloured matrix of clay and marl. Coral calicular surfaces are encrusted by an epifauna of oysters, serpulids and bryozoans which probably developed on the dead coral skeletons prior to their complete burial by muddy sediment. Bryozoans collected personally and those collected by Dr. J.R. Senior include *Collapora microstoma* (adnate zoaria), ?*Hyporosopora typica*, indeterminate probosciniiform sp., and an indeterminate plagioecid berenic-iform sp.

35. Iles Quarry (SP 002061), Daglingworth
Middle and/or Upper Bathonian; White Limestone
(?subcontractus to ?retrocostatum Zones)
see Richardson (1933, p.68), Channon (1950), Torrens
(1967, p.86), Fürsich and Palmer (1975).

The large worked quarry at Daglingworth shows a thick section through the White Limestone. Oolitic limestones forming the lower part of the quarry contain nucleolitid echinoids and Plagiostoma subcardiiformis, one specimen of which was encrusted by a small abraded indeterminate bereniciform tubuloporinid. An extensive platform near the top of the quarry is formed by a planed-off surface terminating a bed riddled with crustacean burrows (Dagham Stone). The walls of these burrows, which are elsewhere bryozoan encrusted (e.g. Foss Cross Quarry, Fürsich and Palmer 1975), do not appear to bear an epifauna at this locality.

36. Lodge Park Quarry (SP 136119), Eastington
Middle and/or Upper Bathonian; White Limestone (?subcontractus to ?retrocostatum Zones)
see Taylor 1974 (unpublished B.Sc. dissertation, Department of Geological Sciences, University of Durham).

The shallow, much overgrown quarry at Lodge Park includes a poorly-developed Dagham Stone horizon. One of the burrows included in this bed was found to be encrusted by numerous serpulids and a small indeterminate bereniciform bryozoan with long peristomes. The burrow, probably vacated by the crustacean, would have provided a cryptic habitat for the bryozoan. Elsewhere in the quarry bryozoans were obtained encrusting corals from a bed above the Dagham Stone, and on shells lying on the quarry floor. The following species were collected; *Stomatopora dichotoma*, '*Proboscina*' *sp*., *Hyporosopora typica*, *Mesenteripora undulata* (adnate), and indeterminate multisparsid and plagioecid berenic-iform tubuloporinids.

37. *Jarvis New Quarry* (SO 994998)
Upper Bathonian; ?Kemble Beds (*aspidoides* Zone)
see Woodward (1894), Channon (1950)

This quarry is situated on the west side of the Cirencester to Tetbury road and is now partly occupied by a clay pigeon shooting club. Channon (1950) records Kemble Beds and Forest Marble in this quarry, but the white oolitic and shelly limestones exposed may alternatively be White Limestone. Oysters, epithyrid terebratulids and *Plagiostoma subcardiiformis* were obtained from weathered faces. A moderately common bryozoan epifauna occurs on the shells and includes *Crescis dumetosa* which is rare in England. The other species collected were *Stomatopora bajocensis*, *Hyporosopora parvipora*, *H. typica*, indeterminate probosciniiform sp., and an indeterminate plagioecid berenic-iform tubuloporinid.

38. *Cirencester road-cutting* (c. SP 025010)
Upper Bathonian; probably Kemble Beds (*aspidoides* Zone) and Forest Marble (*discus* Zone)

New exposures bordering the Cirencester bypass roads are as yet undescribed. One particular road-cutting shows a white oolitic and shell fragment limestone, probably Kemble Beds, overlain by a bluish-grey clay, probably Forest Marble. At the limestone-clay boundary a poorly-preserved 'bradfordian fauna' (Palmer 1974) is developed consisting of rhynchonellids, oysters and rolled bryozoan fragments along with some carbonaceous material. The bryozoan collected were an indeterminate berenic-iform tubuloporinid and ?*Collapora microstoma*. A bed described as the Bradford Clay has in the past (e.g. Richardson 1933, pp.49-51) been described from the Cirencester area where it has been taken to mark the boundary between Kemble Beds and Forest Marble s.s. (Wychwood Beds). Palmer (1974) has shown that the Bradford Clay and its associated fauna is a facies-deposit which developed under particular environmental conditions and which consequently does not necessarily occur at a constant stratigraphical level throughout southern England. The environmental conditions necessary for its formation usually coincided with the change from limestone to clay deposition, as in the Cirencester road-cutting, especially when the limestone upper surface was a hardground.

In the Middle Jurassic of Gloucestershire the only locality visited which failed to yield a bryozoan fauna was the quarry at Farmington (SP 031169) near Northleach. It exposes Lower Bathonian (*progracilis* Zone) carbonates of the Stonesfield Slate Series and Taynton Stone (Richardson 1933, p.42) both containing oysters as potential bryozoan substrates.

OXFORDSHIRE

39. Woodeaton (SP 535122)

Lower to Upper Bathonian; Hampen Marly Beds (*progracilis* Zone), White Limestone (*subcontractus* to *aspidoides* Zones), Forest Marble (*discus* Zone) see Palmer (1973).

The worked quarry at Woodeaton north of Oxford shows a fossiliferous section through tilted Great Oolite strata. *Epithyris oxonica* is extremely abundant in chalky micrites of the White Limestone. Many shells bear an epifauna of small-sized bryozoan zoaria of *Hyporosopora parvipora* and *Collapora microstoma* (discussed more fully on p.317). The bryozoans have minute zooecia with small apertures, probably an adaptation to the low energy environment of deposition. A large number of oysters were collected from the Forest Marble but they lacked a bryozoan epifauna. The Forest Marble also contains no other stenohaline taxa which suggested to Palmer (1973) its deposition in an environment of reduced circulation.

NORTHAMPTONSHIRE

40. Thrapston Station Quarry (SP 998779)

Upper Bathonian; Great Oolite Limestone, Blisworth Clay and Lower Cornbrash (*discus* Zone)

Lower Callovian; Upper Cornbrash (*macrocephalus* Zone)

see Torrens (1968, pp.249-250).

Unfortunately, the section at Thrapston, apparently well-exposed at the time of Torrens' account (1968), was almost completely inaccessible during August 1975. It was possible to collect in-situ material from only one small overgrown and weathered face probably exposing Lower Cornbrash. Specimens lying on the quarry floor were probably derived from an adjacent building site. They included serpulid and oyster encrusted rounded limestone clasts, and an encrusted nerineid gastropod steinkern, undoubtedly from the Upper Cornbrash, which were also encrusted by *Stomatopora* and indeterminate probosciniiform and berenic-iform tubuloporinids. A large oyster, probably from the Upper Cornbrash, was found to be encrusted by *Mesenteripora undulata* and an apparently undescribed probosciniiform multisparsid (fig. 14). Other loose material included *Cererithyris intermedia* (Lower Cornbrash) and small oysters bearing adnate *Collapora microstoma*.

The BMNH collections contain a large number of bryozoan specimens labelled 'Cornbrash, Thrapston'. Many encrust Nucleolites and are probably from the Lower Cornbrash.

YORKSHIRE

41. Eastfield Quarry (SE 915325), South Cave
Bajocian; Cave Oolite (probably *discites* Zone)
see Bisat, Penny and Neale (1962), Bate (1967).

The Cave Oolite, the lateral equivalent of the Whitwell Oolite and parts of the Lincolnshire Limestone, occurs in this now disused quarry to the north of South Cave. The Cave Oolite consists of cross-bedded oobiosparites with a fauna dominated by bivalves. Broken fragments of *Collapora straminea* are relatively abundant and are particularly conspicuous on weathered bedding planes. Thin sections reveal considerable pre-depositional abrasion of zoaria. The bryozoans are probably exclusively allochthonous and also include an indeterminate worn diastoporidiform tubuloporinid.

42. Whitwell Quarry (SE 734642)
Bajocian; Whitwell Oolite (probably *discites* Zone)
and overlying Upper Limestone
see Bate (1967).

The Whitwell Oolite is developed in the same facies as the Cave Oolite but outcrops in the Yorkshire Basin to the north of the Market Weighton Schwelle. Although the

Whitwell Quarry at Mount Pleasant is now occupied by a caravan site, the quarry face is still accessible and shows about 1.5 metres of Whitwell Oolite overlain by sands and clays referable to the Upper Limestone. Collapora straminea is moderately common in the Whitwell Oolite.

43. Cloughton Wyke (TA 021958)
Bajocian; Millepore Bed (probably discites Zone)
see Bate (1967), Hemingway et al. (1968), Hemingway (1974).

The Millepore Bed takes its name from the abundance of Collapora straminea, originally described as Millepora straminea by Phillips (1829). The presence of this bryozoan caused earlier authors to correlate the Millepore Bed with the Lower Inferior Oolite (murchisonae Zone) of the Cotswolds. However, Richardson (1911) drew attention to the occurrence of C. straminea in the Middle Inferior Oolite 'Ragstones' as well, and other faunal evidence favours a discites age for the Millepore Bed. Hemingway and Knox (1973) in a lithostratigraphical revision of the Yorkshire Middle Jurassic, include the Millepore Bed in their Lebberston Member of the Cloughton Formation.

The cliffs at Cloughton Wyke expose Millepore Bed developed in a sandy ferruginous marine facies. Hard red and grey calcareous sandstones, containing bivalves and lignite, are interbedded with pale grey limestones composed of shell debris including C. straminea and crinoids. The shell debris with transported fauna may have been sporadically deposited, perhaps during storms (J.R. Senior pers. comm. 1975) in a marginal marine environment of sand sedimentation.

44. Suffield (SE 979901)
Loose material, probably Upper Oxfordian; Coral Rag (transversarium Zone)
see Hemingway et al. (1968), Wright (1972).

The Suffield Lime Quarry exposes cream oolitic limestones of the Hambleton Oolite containing Gervillella but apparently devoid of bryozoans. However, a pile of field brash deposited in the quarry consisted of large corals which were almost certainly of Coral Rag known to outcrop elsewhere in Suffield. The corals, predominantly Isastrea explanata, are extensively bored by bivalves and encrusted by poriferans, but a few also have adnate bryozoans encrusting their epithecal surfaces. The overhanging epitheca of these corals probably offered cryptic habitats for the indeterminate probosciniiform and berenic-iform bryozoans in the high-energy reef environment. A large bivalve was also collected and found to be encrusted by poorly-preserved cyclostomes including discoidal ?Ceriocava corymbosa and indeterminate multisparsid and plagioecid berenic-iform tubuloporinids.

Other marine Jurassic localities in Yorkshire which were visited but from which no bryozoans were obtained include the Upper Cornbrash (containing abundant Microthyris lagenalis and plicate oysters) of Gristhorpe Bay (TA 085838) and the following Corallian localities:

A. Cropton Quarry (SE 760887). Cropton Shell Bed of the Hambleton Oolite (see Wright 1972, p.238)

B. Rievaulx Quarry (SE 581852). Hambleton Oolite including the Urchin Marl (ibid, p.245)

C. Newbridge Quarry (SE 800862). Includes pisolitic Malton Oolite (ibid, p.240)

D. Ness Quarry (SE 691785). Including the pisolitic Ness Shell Bed of the Malton Oolite (ibid, p.252).

E. Whitewall Corner Quarry (SE 791697). Malton Oolite overlain by fossiliferous Coral Rag (ibid, pp.252, 254).

F. Wrelton Quarry (SE 760869). Malton Oolite overlain by Coral Rag containing abundant small terebratulids (ibid, pp.240, 242).

APPENDIX 2

PUBLICATIONS

a. 1975. Monticules in a Jurassic Cyclostomatous Bryozoan
Geological Magazine 112, 601-606.

b. 1976. Multilamellar growth in two Jurassic cyclostomatous
Bryozoa. Palaeontology 19, 293-306.