# SEDIMENTOLOGICAL FACTORS AFFECTING THE DISTRIBUTION AND GROWTH OF VISÉAN CANINIOID CORALS IN NORTH-WEST IRELAND

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ABSTRACT. The Viséan limestone-shale sequences of north-west Ireland contain a characteristic distribution pattern of alternating coraliferous and 'barren strata' (called 'inter-beds'). The varied geniculation in the assemblages of prone solitary caninioids in both types of strata are interpreted from comparison with observations and experiments on modern corals, as showing a close relationship of coral growth to stability, sedimentation, and penecontemporaneous erosion of the soft lime-mud substrate. Two types of lime-mud are found in the axial region of the corals: fine homogeneous micrite flooring the tabulae is regarded as original infill, while extraneous biomicrite, introduced through openings caused by penecontemporaneous erosion and boring sponges and bryozoa is evidently of subsequent origin. Adverse environmental conditions during skeletogenesis are believed to be responsible for the widely spaced tabulae, conspicuously thin skeleton, and suppression of the dissepimentarium, which are irregularly developed and often associated. The effects of compactional loading and diagenesis are outlined. Each bedding-plane strewn with adult caninioids is regarded as a winnowed death assemblage involving many different generations and accumulating during periods of slow deposition. The difficulties for corals living on an unlithified sea bed are discussed and some wider regional implications considered.

BEDDING-PLANES strewn with large solitary cylindrical Rugose corals (Pl. 41, fig. 1) alternating with comparatively barren strata are common in the Viséan limestone–shale sequences of north-west Ireland. The coralliferous partings are particularly well known from around the shores of Donegal Bay from whence they have been described since the mid nineteenth century (see Wynne 1864, p. 38; Wynne 1885). Until now no ecological interpretation has been attempted, but this would now seem opportune in the light of recent work on ancient and modern carbonate sedimentology and on modern coral habits.

## METHOD

Detailed field observations form the bulk of this work because little of the material is suitable for laboratory study. The Viséan around Donegal Bay from Easky (Irish National Grid Reference G380 385) to Muckros Head (I.N.G.R. G620 375) (see text-fig. 1) is ideally exposed in sections showing deeply weathered, almost horizontal strata. But crucial information has been derived from the comparatively poorly weathered inland escarpments of Benbulben (I.N.G.R. G684 462) and Knocknarea (I.N.G.R. G622 350). Quantitative field analyses which involved more than 3000 caninioids include data incorporated in the 100 one-metre quadrat analysis (see Hubbard 1966, p. 254) of the following localities: Easky (I.N.G.R. G380 385), Aughris (I.N.G.R. G485 350), Serpent Rock (I.N.G.R. G558 460), and Streedagh Point (I.N.G.R. G627 510). Selective laboratory studies which exposed the three-dimensional relationship of the coralla to their matrices and infilling material were implemented by means of polished and etched specimens, thin sections, and acetate peels. In addition 160 thin

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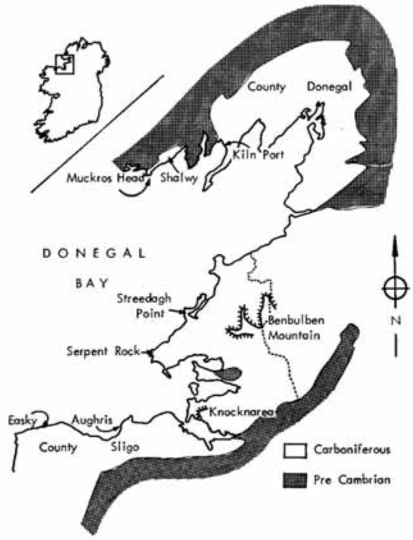
sections and 320 acetate peels of the associated sediments at Streedagh Point and Easky were studied petrographically.

Terminologically the caninioids mentioned include the solitary specimens of *Caninia* spp. and *Siphonophyllia* spp. listed in stratigraphical accounts of the area (see Table 1). Systematic studies show that there is much intraspecific variation at Streedagh Point (Dixon 1970) but all those corals quoted are siphonophyllids, whereas outside this locality occasional caniniids are known notably in Co. Donegal.



TEXT-FIG. 1. Outline map of the Sligo–Donegal coast to show the location of the most informative sections in the Viséan limestone–shale sequences in relation to their regional setting.

## EVIDENCE

### 1. *General distribution*.

Corals occur throughout the limestone–shale sequences of north-west Ireland but are remarkably rich on certain bedding-planes. There is a tendency for one member of the fauna to predominate in each stratum, e.g. caninioid, zaphrentoid, fasciculate, or cerioid lithostrotionoid corals. But of these the caninioids are not only the most spectacular in the variability of their growth forms and distribution patterns, but are also the most ubiquitous in their sedimentary associations. They are found in biosparites and shales as well as all intermediate sediment types. Their distribution, which may be compared with other faunal elements, mirrors subtle lithological variations. Essentially their occurrence can be divided into two categories which have distinct sedimentological associations, (*a*) caninioid-dominated bedding-planes and (*b*) interbeds with sparse caninioids (see Table 2); the main difference being that whereas the former accumulates almost invariably represent condensed composite death assemblages

## EXPLANATION OF PLATE 41

Fig. 1. An adult caninioid-dominated bedding-plane at Serpent Rock showing the comparatively uniform size and variability in growth forms of the partially silicified, randomly oriented, prone coralla of a composite winnowed death assemblage. The deep weathering of the present day intertidal zone has eroded the majority of the epithecae thus exposing many internal structures in longitudinal section. The corals rest on a crinoidal biomicrite, which probably equates with a high energy organic sand substrate, but are overlain by an impure dark trace fossil-riddled micrite matrix, which represents a lower energy rapidly deposited lime-mud. Scale of 1000 mm.

Fig. 2. A vertical polished section of a prone adult caninioid from a block of graded biomicrite at Streedagh Point showing extensive penecontemporaneous erosion of the upward facing surface of the coral. The caninioid's lower surface rests on a more richly organodetrital biomicrite of coral–echinoderm–brozoan debris than the overlying material which has a somewhat higher mud content. Scale of 50 mm.

the latter occasionally incorporate individuals which are thought to be preserved in positions of growth.

(*a*) *Caninioid-dominated bedding-planes*. The bedding-planes strewn with large adult prone caninioids (Pl. 41, fig. 1) are particularly conspicuous in the shore sections of Streedagh Point, Serpent Rock, Aughris, and Easky. This style of exposure usually results from differential weathering of weak partings at limestone–shale interfaces. Thus, where thin shale partings overly the corals the overlying limestone is readily undermined and stripped off. The partially silicified coralla resting in or on the underlying silty biomicrites are thus left as upstanding features in the contemporary foreshore. Where the overlying shale parting is absent or limited to an unusually thin veneer the corals do not weather out so readily on the surface of bedding-planes, but are traceable in bands along the cliff. The true lateral extent of these caninioid-dominated planes is difficult to determine. Inland they give the impression of continuity over a matter of kilometres, but coast sections expose much small-scale faulting which complicates correlation. Certainly the evidence available suggests that the minimum continuity is in excess of 30 m. The distribution of caninioids within these planes is more variable and their orientation is apparently random (compare text-figs. 2 and 3). Caninioid population densities vary from four to eleven adults per square metre. Occasionally such concentrated accumulates pass abruptly into 'barren' areas within a metre, and in these cases there is usually evidence of shoaling organic debris on the lee sides of the caninioids.

TABLE 1. The regional distribution and systematic status of the caninioids discussed according to the stratigraphical lists in 1, Oswald (1955), 2, Bowes (1957, unpublished Ph.D. thesis University of Glasgow), and 3, George and Oswald (1957).

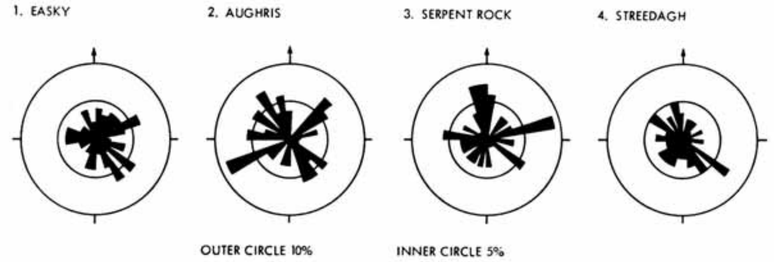
| | *Co. Sligo* | | | *Co. Donegal* | |
|---|---|---|---|---|---|
| *Systematic status* | *Benbulben* | *Aughris* | *Easky* | *West* | *South-east* |
| *Caninia cornucopiae* Michelin | 1 | | | | 3 |
| *C. benburbensis* Lewis | | 2 | 2 | | |
| *C.* cf. *benburbensis* Lewis | | 2 | 2 | | |
| *C.* cf. *cylindrica* (Scouler) | 1 | 2 | 2 | | |
| *Caninia* sp. | | 2 | 2 | | |
| amplexoii caniniids | | | | 3 | |
| *Siphonophillia cylindrica* (Scouler) | | | | 3 | |
| *S.* cf. *cylindrica* (Scouler) | | | | 3 | |
| *S.* cf. *britoliensis* (Vaughan) | | | | 3 | |
| *S.* cf. *benburbensis* (Lewis) | | | | 3 | |
| *Siphonophyllia* sp. (see Lewis 1927, p. 37) | | | | | 3 |

There is a marked tendency for a uniformity of late neanic growth stages to predominate. These range up to 1064 mm. in length and 82 mm. in diameter, but average 505 mm. in length and 76 mm. in diameter. Juveniles are rare or absent. Growth forms, however, are highly variable and random in their associations. Thus straight, gently arcuate, and complexly geniculate forms often occur together. Though the proportion of straight to geniculate caninioids is not constant, the latter tend to be more numerous (text-fig. 4*a*). There is no correlation between the size of the corallum, the number, type, or distribution of geniculations. Thus geniculate caninioids range from simply curved

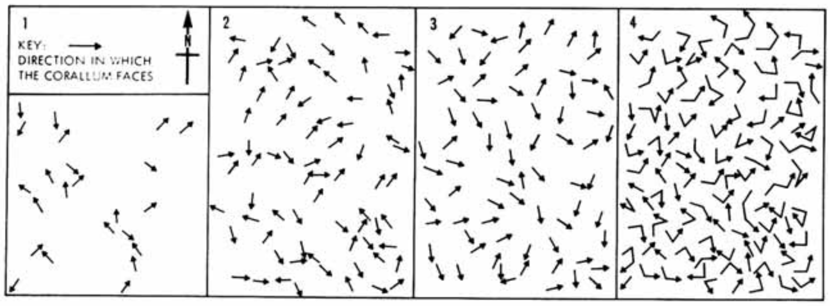
TABLE 2. A synoptic comparison of the caninioid-dominated strata and 'inter-beds' to show their contrasts in population structure, population density, epifauna, thickness, and lithological associations.

| | *Caninioid-dominated bedding-planes* | *'Inter-beds'* |
|---|---|---|
| 1. *Approximate frequency of 'inter-beds' to caninioid-dominated units* | 1 in 16. | 16 to 1. |
| 2. *Average thickness of unit* | Variable—less than 50 mm. | 100–9015 mm. |
| 3. *Population structure* | | |
| (*a*) *Density* | High (up to 11 adults per sq. m.). | Low. |
| (*b*) *Frequency* | Constant. | Sporadic. |
| 4. *Growth stages present* | Mainly adults (*c.* > 90%). | Juveniles dominant, most growth-stages known. |
| 5. *Growth forms recorded* | All styles from complexly geniculate in several planes to simple straight forms. | Straight or simple forms with only small simple geniculations at the apical end. |
| 6. *Orientation* | 90% prone (i.e. long axis of the corallum parallel to bedding).<br>10% low angle oblique to bedding. | 80% prone (mainly adults).<br>10% inverted (mainly ephebic and young neanic).<br>7% in position of growth associated with fasciculate lithostrotionids (all growth stages except gerontic).<br>3% independently in position of growth (usually young neanic). |
| 7. *Evidence of attachment* | | |
| (*a*) *Scars* | None. | None. |
| (*b*) *Holdfasts* | Three neanic individuals attached to one adult specimen at Serpent Rock (text-fig. 5 3). | Rare: (*a*) young neanic individual attached to a spiriferid fragment by rootlets at Serpent Rock (*b*) one adult attached to linoproductid fragment in the Streedagh Shales at Streedagh Point. |
| 8. *Epifauna* | Rare: a local feature at Easky and Pound Point (St. John's Point). | Rare. |
| (*a*) *Aulopora* | Encrusting upward facing surfaces of prone caninioids, linoproductoids, and davisielloids. | Encircling the median region of one upstanding juvenile caninioid in position of growth at Largymore. |
| (*b*) *Boring by sponges and bryozoa* | Both types known. Penetration restricted to theca. Locally common, e.g. Streedagh Point, Easky. | Not recorded. |

| | | |
|---|---|---|
| 9. *Damage* | Sporadic epithecal erosion in some adults. | Limited to prone adults. |
| 10. *Associated fauna* | Variable in numbers and kinds: generally not forming a significant proportion of the population. Chiefly corals, long hinged brachiopods and bryozoa, with crinoid and trilobite debris. | Variable in numbers and kinds: often forming a significant proportion of the population: generally mixed with dominance of corals and brachiopods (including short hinged forms). |
| (*a*) *Nos. of families and genera* | Restricted. | Diverse. |
| (*b*) *Nos. of individuals* | Comparatively 'high'. | Sparse. |
| (*c*) *Sizes and growth stages* | Uniform. | Not conspicuously uniform. |
| (*d*) *Preservation* | Generally transported and commonly disarticulated. | Mixed autochthonous and indigenous. |
| (*e*) *Commensal* | None. | Fasciculate lithostrotionids. |
| 11. *Associated sediment* | Variable often with impurities. | Generally uniform. |
| (*a*) *Overlying the corals* | (*a*) Commonly dark shales and shaly biomicrites passing up into biomicrites.<br>(*b*) Occasionally uniform biomicrites. | Uniform, either<br>(*a*) light-coloured barren micrite,<br>(*b*) light-coloured crinoidal biomicrite, or<br>(*c*) shales. |
| (*b*) *Underlying the corals* | Commonly biomicrite: composition variable, usually light-coloured biomicrite, occasionally darker and gradational towards shelly micrite. | |
| 12. *Interpretation* | Almost invariably composite death assemblages. | (*a*) *Mainly transported death assemblages.*<br>(*b*) Occasional individuals in position of growth, e.g. Serpent Rock, Streedagh Point, Knocknarea, and Largymore. |



TEXT-FIG. 2. Rose diagrams to illustrate the random orientation of the geniculate caninioids in the caninioid-dominated bedding-planes. Each diagram represents 100 readings in which the angle of interception of the coral is plotted.



TEXT-FIG. 3. Diagrammatic illustration of an analysis of the orientation of 100 prone, adult caninioids on a single bedding-plane at the top of the Streedagh Point succession. Inset 4 represents the field evidence, in which all stages of the coral growth visible are plotted. The directions in which arrows point indicate the orientation of the calices and their geniculations are plotted to the nearest degree. The diameters of the coralla are constant but unrepresented. The relative lengths of the intergenicular regions are approximately in proportion. Inset 3 represents the final stage of growth only. Inset 2 shows the orientation of the coralla before the last geniculation, while inset 1 records only the first stage of growth visible. Thus there seems to be no apparent preferred orientation either at a particular growth stage or *in toto*.

cylindrical specimens to more complex S– and Z–shapes in which the geniculation(s) occur in one plane or at random. Similarly the genicular angle may be wide and gently arcuate or narrow and sharply V-shaped. Geniculations show no constant relation to the situation of the cardinal quadrant, apex, or calice. The epitheca is often partially removed from the upper surface of the corals as a result of penecontemporaneous

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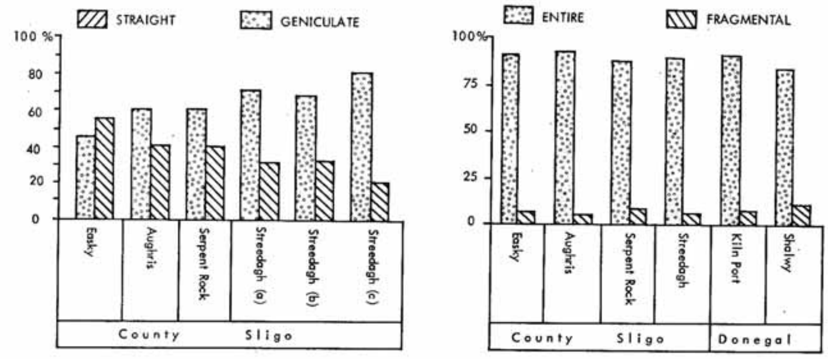
## EXPLANATION OF PLATE 42

Close-up of a prone caninioid in a naturally eroded, longitudinal section resting in a bioturbated coralliferous biomicrite at Serpent Rock. This illustrates the fine detail often visible in the field as compared with laboratory preparations (Pl. 44). The corallum shows repetitive suppressions of the dissepimentarium, local asymmetrical development of the dissepimentarium, local thinning of the septa (halfway up the coral), and a gently arcuate geniculation suggesting that this coral's life was periodically fraught with the dangers of silting up during adverse conditions. Scale of 100 mm.

erosion (Pl. 41, fig. 2), but this damage is seldom extensive and breakages are few numbering less than 10% of any population studied (Text-fig. 4*b*).

(*b*) '*Inter-beds*'. In contrast to the caninioid-dominated strata these are varied in thickness, lithology, and faunal content (Table 2). They contain few whole fossils but are composed of a high organo-detrital content. The population is low in numbers but more varied, containing representatives of various growth stages of a fauna which appears to be locally indigenous and occasionally in position of growth (Text-fig. 5). Whereas the caninioid-dominated bedding-planes are generally marked by an abrupt change in sedimentary style, e.g. silty biomicrite to bioturbated shale, the 'inter-beds' are conspicuous for their uniformity. At most they are graded within the individual stratum. But there is a tendency for these 'inter-beds' to be terminated abruptly at their upper surface by a caninioid-dominated bedding-plane.



TEXT-FIG. 4. Caninioid statistics: Left, histogram to show the ratio of geniculate to straight caninioids within a single bedding-plane. Three horizons are cited at Streedagh Point. A dominance of geniculate forms is generally discernible. Right, percentage histogram of entire and fragmental caninioids calculated from 100 one-metre quadrats at each locality.

## 2. *Caninioid growth*

Longitudinal axial sections exposing the tabularium, many of which are as well etched in the field (Pl. 43) as can be achieved in the laboratory (Pl. 44), are plentiful in the foreshores and yield important information on the growth of the corallum. The arrangement of the tabulae, though variable in detail, is generally parallel to the orientation of the external growth rings. This constancy may be used indirectly as evidence of the probable direction of growth of the live coral.

(*a*) *Geniculation*. A gradual compensational swing of both tabulae and growth rings is usual (Text-figs. 5 1, 2; Pl. 43). Abrupt changes are rare.

(*b*) *Attachment*. Evidence is seldom found as the apical region is either buried or rarely seen preserved. Three juveniles are known on the epitheca of one adult caninioid

(Text-fig. 5 3), while another juvenile attached itself to a spiriferid fragment by supporting 'rootlets'. Only one attached adult is known from Co. Sligo; it is cemented apically to a linoproductid fragment in the basal shales of Streedagh Point. In all four cases the scar is evident, but small. No evidence of attachment scars is found outside the apical region.

(*c*) *Attitude of growth.* Several young caninioids are known in upright positions which would seem to be functionally viable (Text-figs. 5 1, 2, 3; Pl. 44, fig. 1). These are recorded from 'inter-beds' and are known from similar sediments in the escarpments of Knocknarea and Benbulben as well as the shores of Easky, Aughris, Serpent Rock, Streedagh Point, and Shalwy. But they are rare occurrences limited to homogeneous biomicrite and silty biomicrite facies. Several neanic and ephebic caninioids are found in this position where they are intergrown with fasciculate lithostrotionoids as though deriving benefit from their shelter (Pl. 44, fig. 1).

3. *Preservation.*

(*a*) *Axial infill.* The advanced state of diagenesis of both corallum and matrix often obscures the original nature of the axial infill. The coralla are preserved in finely crystalline silica and carbonate, from which, by granular cementation of the carbonate crystals, the intraskeletal voids are filled. Locally coarse drusy carbonate is developed, often at the expense of the skeletal structure. Thus tabulae, septa, and dissepiments terminate abruptly against the mosaic (Pl. 43). The coarse mosaic is commonly developed in bands of less than 50 mm. deep within the tabularium. Occasionally this extends laterally into the dissepimentarium.

In addition to the crystalline infill, lime-mud is found locally in the axial region. This consists of two types, (*a*) very fine homogeneous micrite flooring the tabulae, and (*b*) extraneous silty biomicrite which frequently completely fills the intertabular space but shows no geopetal features. This latter infill often occurs in the genicular region of the corallum, where the skeleton is conspicuously thin, and/or in areas where the tabulae are disorganized.

(*b*) *Penecontemporaneous erosion.* Caninioids are seldom as extensively eroded as the one illustrated in Plate 42, but localized erosion of parts of the corals' outer surface is not uncommon. Damage is usually restricted to the upward facing sector of the corallum. Often the epitheca is breached, but penetration is known to extend as far as the tabularium thus allowing the introduction of extraneous lime-mud into the axial region. This type of damage is readily distinguished from the products of differential loading and diagenesis (compare Tables 3 and 4).

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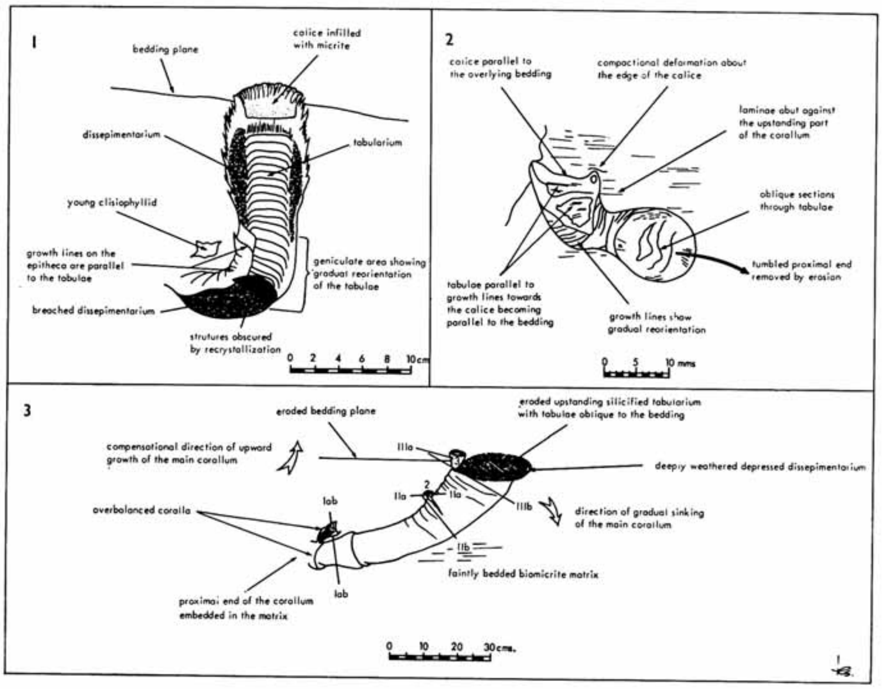
EXPLANATION OF PLATE 43

A longitudinal section of a deeply etched, prone, geniculate caninioid. The dissepimentarium shows pronounced constrictions on the convex side and a certain degree of asymmetry. The tabular region is locally confused by diagenetic rupture, while the intertabular interval is somewhat masked by the uneven distribution of carbonate mosaic and silica. Scale of 10 mm.



TEXT-FIG. 5. Caninioid corals preserved in their probable positions of growth.
(1) Field sketch of an adult geniculate caninioid at Serpent Rock illustrating the relationship of the calice to the axial structures and bedding. There is a conspicuous parallelism of growth-lines, tabulae, and calice, which distally are almost parallel to the bedding. The apical region is inaccessibly buried in the matrix. The geniculate development of the corallum suggests that the young coral became unbalanced and managed to reorient itself successfully with respect to its substrate by gradual upright growth, which is reflected in both growth rings and tabulae.
(2) Sketch from a peel of a young geniculate caninioid from Knocknarea illustrating the relationship between the corallum and matrix. In the upstanding portion of the corallum the bedding terminates abruptly against the epitheca indicating that deposition and coral growth were contemporaneous. The calice is at a low angle, in this case almost parallel to the succeeding sedimentary laminae. The growth history of the coral may be traced from the orientations of the tabulae and growth-lines with respect to the bedding. During its early life the coral overbalanced and came to rest obliquely on the sea bed, but compensation reorientation enabled the polyp to resume its upright position and continue growing until its premature death. This probably resulted from 'suffocation' as there seems to be little evidence of a break in sedimentation between the coral's successful readjustment and its final burial. At the calical margin the overlying bedding, which is affected by compactional deformation, and is of post-mortem origin completely transgresses the corallum.
(3) Field sketch of a caninioid life assemblage comprising an adult supporting three juveniles at Serpent Rock. The inferred directions of settling of the main corallum are indicated by the angular discordance between its growth rings (Ib, IIb, IIIc) and those of the small coralla (Ia, IIa, IIIa) which probably initially attached themselves in an erect position.

TABLE 3. A synopsis of caninioid features which result from post-mortem causes.

| *Feature* | *Area affected* | *Frequency* | *Cause* |
|---|---|---|---|
| SKELETAL DAMAGE | | | |
| 1. Thecal breaching; occasionally superficial sometimes associated with damage of contiguous internal structures, e.g. abruptly truncated tabulae (see Pl. 41, fig. 2). | Commonly confined to upper surfaces of prone adults. Locally coincident with geniculations. | Irregular. | Contemporaneous erosion while strewn over the sea bed. |
| 2. Tabular slivers arranged *en échelon* between complete tabulae. | Random. | Irregular. | Expansional rupture during diagenesis. |
| 3. Tabulae missing and/or represented by slivers with random orientation in biomicrite filled intertabular area. | Random.<br>Sometimes associated with particularly thin skeletal areas. | Irregular. | Introduction of extraneous material resulting from local breaching by contemporaneous erosion. |
| 4. Planar orientation of skeletal fragments parallel to the bedding. | Variable, often extensive or developed throughout the length of the corallum. | Common. | Crushing during compactional loading. |
| INFILLING MEDIUM | | | |
| 1. Homogeneous micrite A. | Locally developed flooring intertabular areas. | Rare. | Original. |
| 2. Homogeneous micrite B. | Local, usually associated with the external margin of the dissepimentarium. | Sporadic. | Diagenesis. |
| 3. Drusy carbonate. | Local, commonly restricted to 50 mm. thick bands in the tabularium, but is also found affecting adjacent areas of the tabularium. | Sporadic (total loss of internal structures). | Diagenesis. |
| 4. Cryptocrystalline silica. | Locally present in intertabular area. | Sporadic. | Diagenesis. |
| PRESERVATION OF CORALLUM | | | |
| 1. Microcrystalline carbonate. | Throughout. | Usual. | Replacement. |
| 2. Cryptocrystalline silica. | Irregular, usually best developed at the theca, from which it selectively penetrates the septa. | Variable. | Permineralization. |

TABLE 4. A synopsis of caniniold features which result from the contemporaneous effects of mobile sediment on the growing corallum.

| *Feature* | *Effects or areas affected* | *Location* | *Frequency* | *Likely cause* |
|---|---|---|---|---|
| GENICULATION | (*a*) External form<br>(*b*) Tabularium<br>(*c*) Dissepimentarium. | Random. | Irregular but common. | Negative geotropic readjustment resulting from<br>(*a*) Instability on substrate,<br>(*b*) Unfavourable original attachment,<br>(*c*) Directional growth away from sediment. |
| TABULARIUM | | | | |
| 1. Intertabular distance. | (*a*) Tabulae locally crowded. | Random. | Irregular, usually limited. | Favourable conditions, with sufficient carbonate for additional growth. |
| | (*b*) Tabulae locally widely separated, often coincident with particularly thin tabulae and restricted dissepimentarium. | Random. | Irregular. | Adverse conditions:<br>(*a*) Lack of carbonate for skeletal growth,<br>(*b*) Need of rapid upward extension of the skeleton to avoid choking by mobile sediment. |
| 2. Orientation of tabulae. | (*a*) Oblique to previous tabulae.<br>(*b*) Off-lapping.<br>(*c*) Overlapping.<br>Often associated with parallel directional change in external growth rings. | Variable, most common in genicular areas. | Common. | Compensational growth resulting from readjustment of growth direction. |
| 3. Broken tabulae. | Concentric arrangement of tabulae occupying one intertabular space. Usually associated with thin tabulae. | Irregular. | Rare. | ? contemporaneous collapse of calice during adverse conditions. |
| DISSEPIMENTARIUM | | | | |
| 1. Crowding of dissepiments on concave side of geniculation. | Local, coincident with geniculations. | Variable. | Irregular. | Response to concentric growth about a curve. |
| 2. Locally suppressed:<br>(*a*) symmetrically,<br>(*b*) asymmetrically. | Associated with thin distantly spaced tabulae. | Variable. | Irregular. | Adverse conditions:<br>(*a*) Lack of carbonate for skeletal growth,<br>(*b*) Need added height rather than sturdiness. |

4. *Original skeletal peculiarities.*

Intertabular distance, suppression of the dissepimentarium and skeletal thinning (see Table 4) show random development within the coralla. They are commonly associated with one another and therefore more probably reflect the influence of environment rather then genetic factors.

(*a*) *Tabular distance*. The intertabular distance is variable. Frequently tabulae are grouped into more and less dense areas; these are not quantifiable, and thus are not explicable in terms of Ma's (1937, p. 9) seasonal growth hypothesis. In certain coralla the tabulae are locally widely spaced and unusually thin. This type of development is sometimes coincident with local suppression of the dissepimentarium.

(*b*) *Suppression of the dissepimentarium*. Whereas the tabularium retains a constant diameter, the dissepimentarium frequently shows a marked reduction. In some individuals the suppression may be sufficiently intensive that the dissepimentarium is difficult to recognize. This usually occurs in regions where the tabulae are thin and widely spaced. Often this coincides with the sharper geniculations, but it is also found at random along the length of straight caninioids.

(*c*) *Skeletal thinning*. This is highly variable in its occurrence and is most conspicuous in the tabularium, where it generally coincides with the widely spaced tabulae and restricted dissepimentarium.

These features are thus highly suggestive of temporary adverse conditions in which the coral was unable to sustain its usual rate of skeletal secretion. Hence for survival the coral would be forced to effect a restricted building programme in which it would naturally concentrate on growing upwards and away from the offending sediment, by developing widely spaced tabulae, rather than consolidating its scaffolding by dissepimentarial growth.

5. *Recent analogies.*

Deductions based on analogies between the extinct Rugosa and modern Scleractinia have obvious limitations because of fundamental differences in thecal formation and the development of tabulae. Nevertheless it is still worthwhile reviewing some of the

EXPLANATION OF PLATE 44

Fig. 1. A block of biomicrite at Serpent Rock containing a life assemblage of a slightly geniculate caninioid growing in close proximity to a fasciculate lithostrotionoid corallum suggests that the former derived shelter from the latter. The effect of uneven compactional loading causing 'pinch and flow' structures is seen in the deformed *Chrondrites* rich sedimentary laminae which can be traced from the base of the caninioid obliquely towards the right hand base of the compound coral. Scale of 100 mm.

Fig. 2. A deeply eroded marine platform reveals several different sedimentary environments within a distance of less than 15 cm. in what must have been a soft lime-mud substrate during Viséan times. The section is floored by a linoproductid-coral micrite, which passes up into a dark, bioturbated, biomicrite horizon. The latter is sharply and unevenly overlain by an impersistent uniform impure organodetrital shale, which in turn gives way to another caninioid–lithostrotionoid–linoproductoid micrite which can be traced discontinuously from the top left to the right of centre. Scale of 100 mm.

experimental and observational findings on the habits of modern corals and considering the extent to which these may have controlled growth in caninioids.

(*a*) *Initial attachment*. Experiments with *Pocillopora* larvae indicate that attachment is readily achieved irrespective of the nature of the substrate (Edmondson 1929, p. 8). Algae, broken glass, and the smooth sides of a glass beaker were sufficient for this modern coral; thus the organo-detrital content of the Viséan biomicrites, e.g. comminuted shell, crinoid ossicles, and bryozoan debris, should have been adequate for the caninioids.

(*b*) *Later growth habits*. (i) Upward growth is a direct response of the polyps' need to be above the level where it would be 'suffocated' by moving sediment (Manton and Stephenson 1935, p. 308; Marshall and Orr 1931, pp. 130–1). Phototropism is a subsidiary factor, being an indirect response to the polyps' dependence on light (see Edmondson 1929, Roøs 1967). Thus in life the calice of the caninioid probably faced upwards, and was normally parallel to, or sometimes at a low angle to the sea floor (see text-figs. 5 I, 2, 3; Pl. 44, fig. 1).

(ii) Permanent attachment throughout the coral's life is not necessary. The modern Bahaman solitary coral *Manicena aureolata* Linnaeus (Yonge 1935, p. 187; Squires 1958, p. 258) frequently frees itself and loses all trace of its former attachment on unlithified sediments. Similarly the caninioids appear to have required anchorage only in extreme youth.

(iii) Stability is a common problem in modern unlithified lime-muds. Present-day coral populations in the West Indies tend to have slightly lower specific densities than the surrounding sediments, and it is suggested that this adaptation allows *Manicena areolata* Linnaeus in Bimini Lagoon (Squires 1958, Yonge 1935) to keep a constant proportion of the corallum above the sea water–sediment interface irrespective of the rate of sedimentation. Experimental calculations on the relative densities of caninioids and their associated sediments suggest that this was operative in the Viséan. In the Bahamas as much as 9144 mm. of unconsolidated lime-mud is recorded (Squires 1958, p. 236), a thickness which is more than adequate for the support of any known caninioid. But what proportion of the caninioid remained buried during life is speculative. It could not have survived the effects of mobile sediment in the prone condition. The stability of the coral would have been dependent on the length of the buried portion, the fluidity of the matrix, and current velocities in the surrounding sea water. Even in the ideal situation, perpendicular to the sea bed, it seems unlikely that the caninioid would be stable were more than a third of the corallum exposed above the sediment–sea water interface, and this upstanding part might be considerably smaller.

Subsidiary factors affecting the stability of the corallum include minute textural differences in the matrix and these together with the effects of penecontemporaneous crystallization and early diagenesis could have had a profound effect on the permeability, porosity and compaction of the surrounding sediment (Trask 1931, p. 275).

(iv) The effect of mobile sediment on Recent corals is crucial. In modern seas the effects of rate, type, and direction of mobile sediment is of considerable importance in coral growth and survival. Marshall and Orr (1931, pp. 130–1) show that the larger the calice, the greater is the polyps' ability to withstand temporary muddy influxes. This is paralleled by the ubiquitous caninioids in contrast to the more selective distribution of lithostrotionoid corals in the Irish Viséan. Marshall and Orr also note a close correlation between particle size and 'suffocation' i.e. the finer the particle size the more rapid the 'suffocation'. Similarly they note that the direction of sedimentation can be crucial in *Pocillopora*, *Gallaxea*, *Symphyllia*, *Fungia*, and *Acropora*. These corals can withstand almost unlimited amounts of sediment from above, but where sediment built up around the lower reaches of the calice death followed within forty-eight hours. This apparently results from the polyps' inability to move its tentacles laterally in such circumstances. Thus during windy weather the polyps' chances of survival are somewhat hazardous as the level of the sea bed keeps changing in relation to the polyp. Hence by comparison the movement of only a small amount of Viséan lime-mud could have effectively 'suffocated' a large number of caninioids on what is now represented by a single bedding-plane. But more recently Goreau and Goreau (1959, p. 247) note that the polyps of *Porites* and *Millepora* can withstand starvation during conditions of extreme muddiness. In these conditions the polyps free themselves from the coralla and live for several weeks without a sign of skeletal building. By analogy the thin skeletal structures in some caninioids are attributed to similar, though slightly better conditions than those to which Goreau and Goreau refer.

(v) Sedimentary rates. Even in modern sediments where exact records may be taken it is difficult to distinguish sedimentary rates of consequence. Thus, where two days yield an average of 1 mm. per day, the same locality can also record an average of only 3 mm. in 15–35 days (see Bakus 1967, p. 45). Viséan sedimentary rates are thus speculative, but in comparative terms their variations are significant. Thus argillaceous bands rich in trace fossils represent periods of rapid accumulation, while well-winnowed, organo-detrital calcarenites probably represent slower accumulation, and graded silty biomocrites probably represent an intermediate and gradational rate of accumulation. Variations in the vertical combinations of these lithologies (see Pl. 44, fig. 2) leave little doubt that there were variations in depositional rate during the Viséan. The caninioid-dominated bedding-planes commonly rest on well-winnowed calcarenites and are overlain by bioturbated shales which are in turn overlain by further limestones. Some of these caninioids contain relics of extraneous biomicrite within the intertabular areas which can be matched with the overlying sediments. This suggests penecontemporaneous erosion of the sea bed between the deposition of the underlying and overlying sediments. But there is no evidence of channelling, probably because the sediments were still unlithified and highly mobile. Further indications of breaks in the sedimentary record are provided by truncated trace fossils (see Goldring 1962) and localized epifaunal developments.

The absolute rate of sedimentation during Viséan times is unknown, but indirect estimates may be hazarded using Wells's (1963) geochronometrical analysis of fine growth rings, which in modern corals are added diurnally. According to Wells there were 393 days in the Mississippian year. If this figure is accepted several counts of caninioid diurnal growth increments would suggest that their average growth rate was 65 mm. per annum which is identical to the Devonian *Cystiphyllum americanum* (Wells 1937, p. 17). Thus an age of thirteen years can be ascribed to the longest straight caninioid at Serpent Rock. Hence it is assumed that if vertical growth kept pace with sedimentation a rate of accumulation of less than 65 mm. per annum is indicated. During the life of this caninioid sediment accumulation was uninterrupted, but ultimately the supporting sediment was winnowed away and the corallum left in a prone resting position. But though shoaling of organic debris is not uncommon few coral case histories are as simple as this.

A rate of accumulation of 65 mm. per annum is regarded as high by modern lime-mud standards and compares with lagoonal environments. But in that this rate is shown to be a temporary feature in the Viséan the comparison is plausible.

(vi) Epifauna. The distribution is characteristically local. One bedding-plane may be more affected than another at the same locality. But Easky, Serpent Rock, and Pound Point (St. John's Peninsula) sustain the highest caninioid-based epifauna. *Aupolora* is the most common encrusting creature. It generally attaches itself to the upper surface of prone caninioids on caninioid-dominated bedding-planes and inverted linoproductids and davisiellids on brachiopod-dominated bedding-planes. It is also found attached to one caninioid calice which would suggest that it is usually a post-mortem colonization to combat the adverse effects of life on the lime-mud sea bed. One upstanding caninioid, believed to be in position of growth, at Shalwy is encircled by an auloporid, in this case suggesting a commensal relationship.

Penetration by boring sponges and bryozoa (see Brunton 1966) is locally common, affecting the upper surfaces of prone caninioid thecae at Easky and Streedagh Point. But there is no evidence of contemporaneous infestation. In section the effective depth of penetration by boring creatures is obscured by diagenesis, but it is possible that these passages provided another route for the introduction of extraneous micrite into the axial region.

## CONCLUSIONS

A crude, somewhat oversimplified flow diagram of the caninioids' probable life histories indicates the main factors affecting caninioid growth and distribution (Text-fig. 6) and ultimate accumulation as composite death assemblages in caninioid–dominated bedding-planes alternating with 'inter-beds'. Mobile sediment is the key inorganic factor.

1. Caninioids grew upright for preference (Text-fig. 6, 3ia–3ic; text-fig. 5; Pl. 44, fig. 1).

2. Caninioids could not live long in the prone condition as even small amounts of mobile sediment would have soon 'suffocated' them (Text-fig. 6, 3iiig–3iiih).

3. Geniculation developed wherever a righting reaction was necessary as for instance:

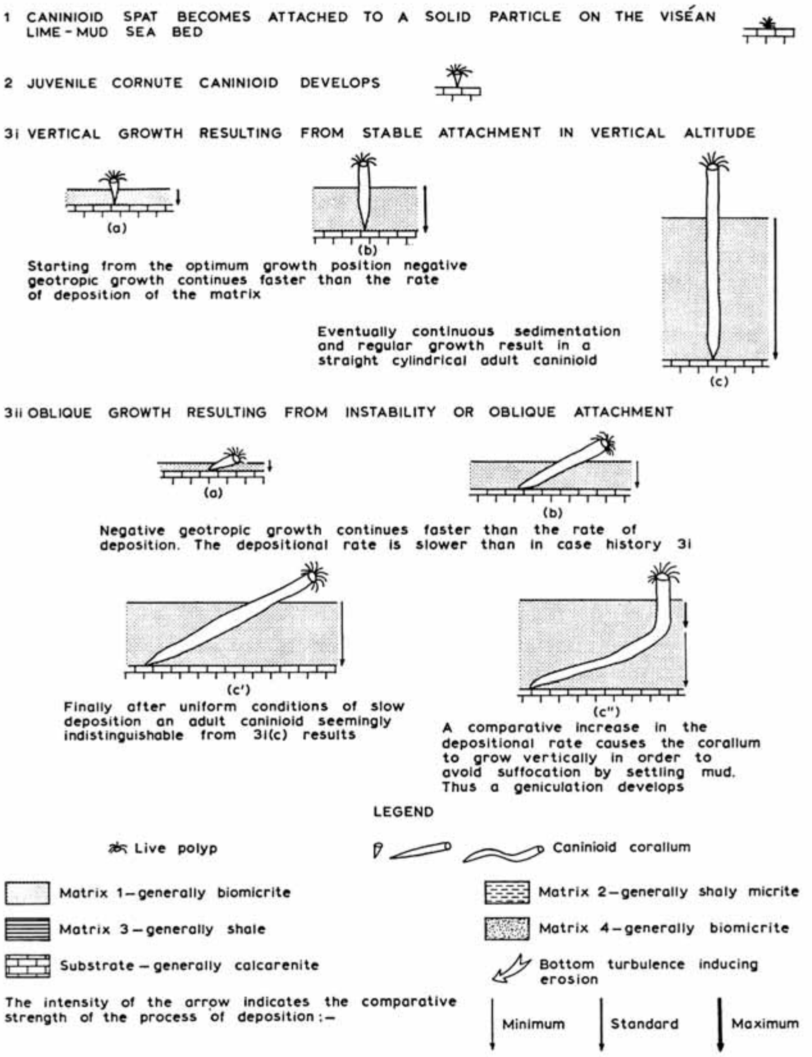
(*a*) Resulting from instability induced by contemporaneous winnowing of the soft lime-mud sea bed (Text-fig. 6, 3iiib–3iiic–3iiid–3iiie).

(*b*) Resulting from instability induced by oblique attachment (Text-fig. 6, 3iia–3iib–3iic).

(*c*) Resulting from instability induced by other causes not witnessed in the fossil record, e.g. behaviour of the substrate during early diagenesis, variations in current strengths due to salinity changes.

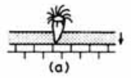
4. The wide caninioid calice renders them more tolerant of mobile sediment than the associated, mainly lithostrotionoid, corals and thus accounts for the ubiquity of the caninioids in contrast to the more environmentally restricted lithostrotionoids.

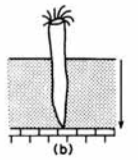
5. The corals' susceptibility to mobile sediment renders the caninioids more complex than other groups which reflect similar variations in Viséan sedimentological conditions. They indicate both the individual's responses throughout life and the effects on the mass

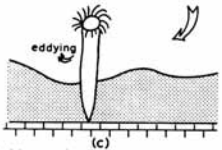


TEXT-FIG. 6. A simplified highly idealized flow diagram which accounts for some of the possible origins of the relationship of the various caninioid growth forms, their orientations, and their matrices. The relative rates of coral growth, stability, sedimentation, and penecontemporaneous erosion as reflected in individual coralla and cannot be represented accurately. A general minimal sedimentary rate is inferred and variations in sedimentary rate are thought to be variable but not in excess of 65 mm. per annum. Periodically, after the repetition of several of these phases, the winnowed accumulates of diverse growth forms of adult caninioids, now preserved in caninioid dominated bedding-planes, were buried by a renewed increase in sedimentation.

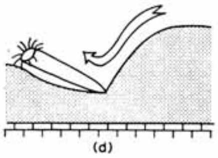
3iii VARIATION IN GENICULAR STYLE RESULTING FROM MOBILITY OF THE SUBSTRATE COMBINED WITH THE ALTERNATION OF DEPOSITION AND PENECONTEMPORANEOUS EROSION

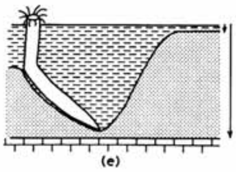






Bottom turbulence involving penecontemporaneous erosion of the matrix

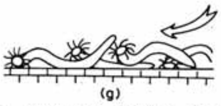




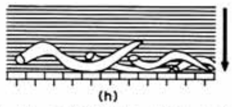
(f) The processes involving 3iii (c)-(e) may be repeated innumerable times thus accounting for an indefinite number of geniculations and variations in curvature

Penecontemporaneous erosion and current activity overbalance the corallum

Renewed influx of sedimentation with the caninioid resuming its negative geotropic tendencies

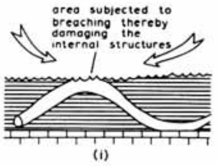


Renewed winnowing. Bottom turbulence removes all the original matrix tumbling and rolling the coralla

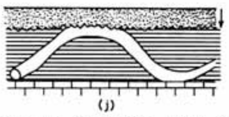


Influx of extraneous mud with rapid deposition causes final suffocation of any but the most recalcitrant caninioid

THECAL BREACHING

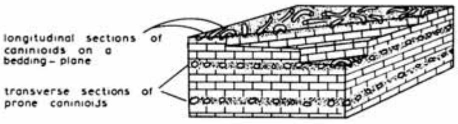


Partial burial and/or subsequent erosion may cause the upstanding geniculate area to be breached



Subsequent deposition infills the buried topography of the eroded caninioid

4 RESULT



Segregations of "prone" adult caninioid-dominated bedding-planes alternate with almost "barren" units of the population at the time of burial. These patterns of organic and sedimentological variation are mirrored in the distribution of brachiopods which occur interbedded in these sequences, of which linoproductids, pustulids, and davisellids are the most common. They are seldom seen in position of growth but often occur as dense masses of adults strewn inverted over shaly bedding-planes.

## GENERAL DISCUSSION

Having reviewed the local factors, i.e. those pertaining to each caninioid assemblage now found on single bedding-planes, other major or regional factors influencing survival and distribution of all recurrent assemblages may be considered briefly. First, there are the palaeogeographical factors which control such peculiarities as the recurrent changes in sedimentary regime which are of a crude rhythmic nature. However, the absence of positive evidence of an inshore facies and adjacent shoreline precludes any definite statement as to this as a control. Further, with the exception of some limited evidence of boring algae, no algal mats, dessication cracks, or carbonate pseudomorphs after anhydrite, which would indicate extreme shallow water conditions are known. This negative evidence together with the study of the caninioids previously presented, indicates conclusively that the caninioid populations were not marginal to any shoreline but may have occupied the dysphotic zones. Other factors which have ultimately to be taken into account are those of a climatic nature whose effects can only be indirectly inferred. It is probable that the Viséan carbonate sediments of north-west Ireland accumulated under climatic conditions similar to those found in the tropical climatic belts of the present time and to be observed in such classic carbonate areas as the Bahamas. In this area seasonal effects occur when an increase in rainfall causes a sedimentary influx coupled with a decrease in salinity (cf. Squires 1958, pp. 234–5) and it is conceivable that similar effects occurred in Viséan times. However, absence of marked concentrations of growth-rings in the north-west Irish Viséan caninioids seems to indicate no seasonal control of growth although the effects of exceptionally severe tropical storms cannot be eliminated entirely.

There are wider implications to be drawn from the abundant development of Viséan caninioid assemblages in north-west Ireland. Thus favourable conditions in Ireland seem to reflect favourable conditions globally in tropical climatic belts as comparable caninioid developments occur in similar horizons not only in north-west Europe but also in the U.S.S.R. and North America. So apart from the local factors which influenced initial colonization and survival there were wider controls whose nature can only be very indirectly inferred at the present time. It is evident that caninioid growth in one and in all the recurrent assemblages was an extremely complex process which is not unique to Viséan times. In other systems, e.g. Middle Devonian of New York (Oliver 1951) and the Eifel (Birenheide 1962*a*, *b*, *c*, 1963) and the Silurian of Norway (Kiaer 1906) earlier but similar complexities governing the distribution of solitary corals seem to have been present.

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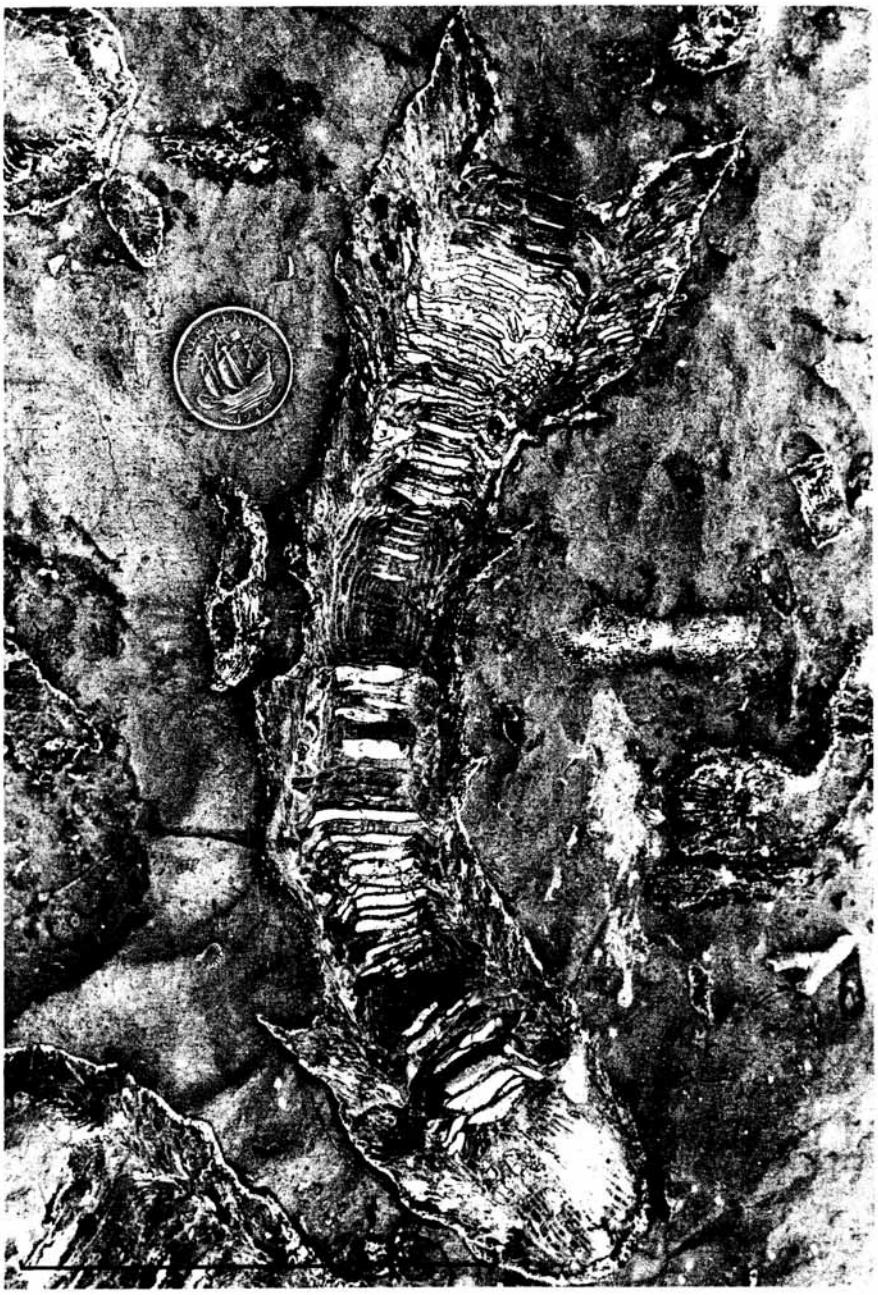
HUBBARD, Caninioid corals



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