VARIATION IN THE VISÉAN CORAL *CANINIA BENBURBENSIS* FROM NORTH-WEST IRELAND

by O. A. DIXON

ABSTRACT. *Caninia benburbensis* Lewis occurs in abundance in upper Viséan marine limestones and shales in north-western Ireland. Study of a single assemblage reveals a range of variation which expands Lewis's concept of the species. The morphological affinity of certain variants to *C. cylindrica* (Scouler) strongly suggests that this Tournaisian or lower Viséan species is ancestral to *C. benburbensis*. The morphological mode clearly distinguishes this species from all earlier caniniid populations.

CERTAIN Lower Carboniferous formations in north-western Ireland contain large, caniniid corals in a profusion that has inspired repeated comment by geologists for more than a century. The coral-rich strata are magnificently exposed at several localities along the coast of County Sligo and have been recognized at inland exposures in several areas of Counties Sligo, Leitrim, and Roscommon. Hubbard (1966, p. 253) summarized the important coastal exposures and, supported by Hubbard and Sheridan (1965, pp. 193–4), strongly substantiated the idea that many of the important caniniid-rich beds in the region are synchronous and of late Viséan age.

However, large caniniid corals occur throughout the Lower Carboniferous in north-western Ireland (generally more than 1150 m. thick) and elsewhere in the British Isles. Attempts in the past to utilize the caniniids for stratigraphical purposes have been inconclusive, probably due in part to misinterpretations of local stratigraphy and in part to intraspecific variation, which impedes the precise identification of isolated specimens. In an attempt to define the limits of variation within a single assemblage, a collection from one of the best-known localities, Streedagh Point in Co. Sligo, was studied.

A narrow strip of gently dipping limestones and shales is exposed along the sea coast at Streedagh Point (text-fig. 1). The strata are cut by several, small, vertical faults with displacements up to 6·5 m. The faults are made obvious by offset of beds containing rich accumulations of species of the compound coral *Lithostrotion*—useful marker beds for stratigraphical control within the area. The caniniid assemblage was collected systematically through the sequence represented by the generalized stratigraphical column in text-fig. 2. All but six specimens came from richly fossiliferous beds between 18 and 22·6 m. More extensive collecting was limited, as many of the corals are intractably set in thick and resistant limestone beds.

The fossils generally are well preserved, although it is common to find the epitheca and a thin layer of the adjacent rock silicified, while the remainder of the fossil is calcitic. In addition, some specimens in outcrop are missing parts of the epitheca and dissepimentarium. Where some of the matrix still adheres to the fossil, it is possible to demonstrate in many instances that these parts of the skeleton were removed by abrasion before final burial in the sediment.

The collected specimens clearly are not contemporaneous but represent several successive palaeobiological populations. Initial attempts to attribute observed morpho-

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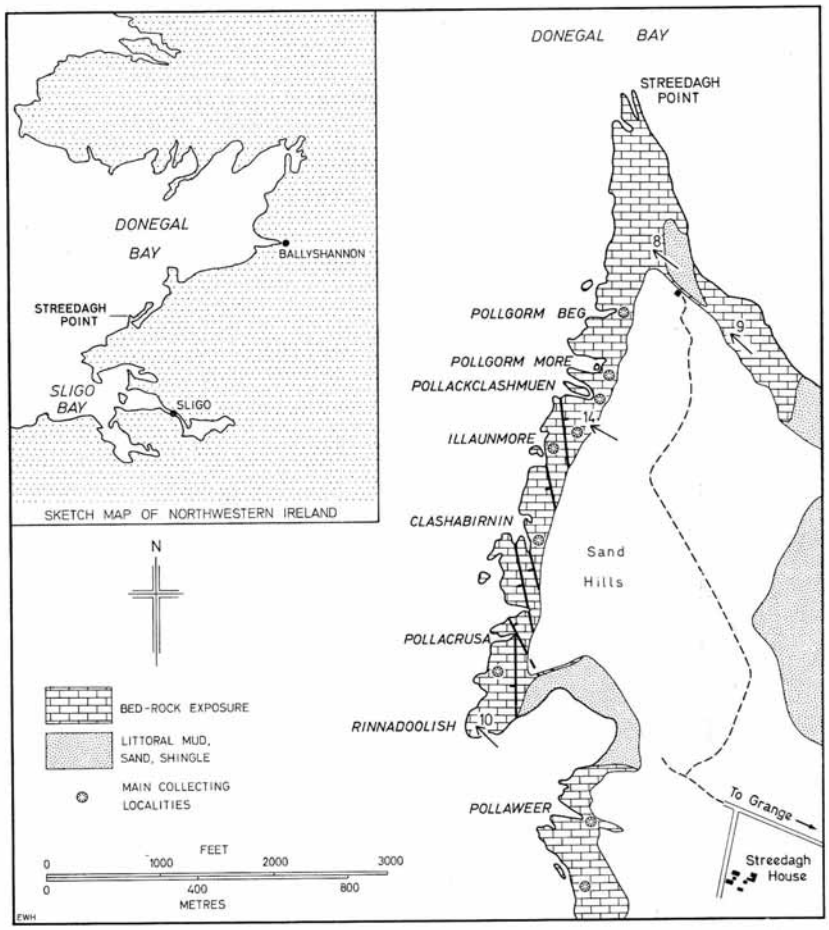
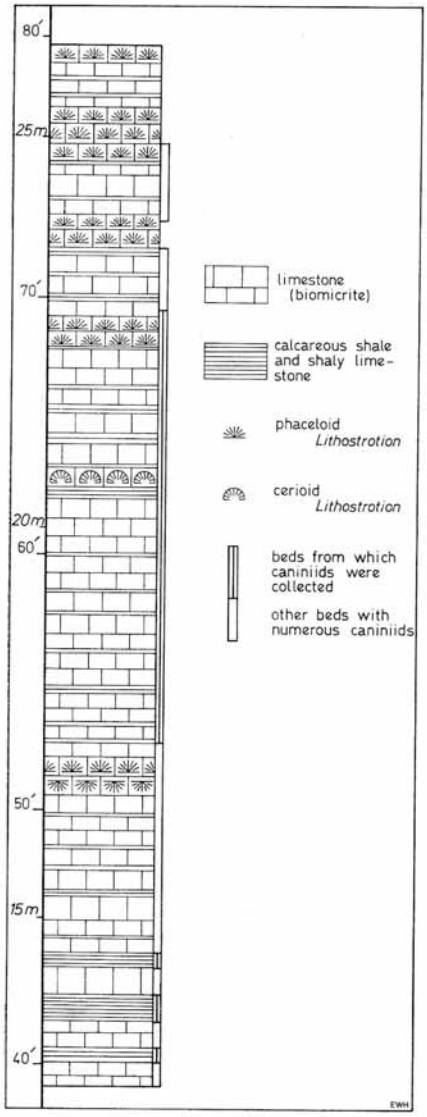
logical variations to changes of facies or to phylogenetic change were unsuccessful, and consequently the specimens were grouped and studied as a single population. The areal distribution of the assemblage is sufficiently limited that each included population may



TEXT-FIG. 1. Streedagh Point, north-western Ireland. Hachured open circles mark the principal collecting localities. Base map courtesy of the Ordnance Survey, Phoenix Park, Dublin.

be assumed to have experienced free panmixis. The profusion of caniniids in limestones and shales throughout this limited succession suggests, too, that the area was continually populated, and favours the treatment of the assemblage as a unit having a very restricted time range within the entire caniniid lineage.

Foraminiferan evidence places the rocks at Streedagh Point in the lower D_1 subzone



TEXT-FIG. 2. Diagrammatic section representing the top 13 m. of strata exposed on Streedagh Point. The column incorporates (and extends about 3 m. below) the 'coral limestone horizon' of Hubbard (1966, fig. 11).

of late Viséan age (Oldroyd 1965, p. 195), and specimens of *Dibunophyllum* found with the caniniids support this. The suggested correlation is with the Benbulben Shale–Glencar Limestone transition (Hubbard 1966, pp. 267–8; Oswald 1955, pp. 175–6).

SYSTEMATIC DESCRIPTION

Superfamily ZAPHRENTICAE Milne-Edwards and Haime 1850
Family CYATHOPSIDAE Dybowski 1873
Genus CANINIA Michelin 1840

Caninia benburbensis Lewis

Text-figs. 3–11

1925 *Caninia* cf. *samsonensis* Salée; Lewis, in L. B. Smyth, pp. 145–6.
1927 *Caninia benburbensis* Lewis, pp. 378–80, pl. 16, figs. 5–6; pl. 17, figs. 1–4.
1930 *Caninia benburbensis* Lewis; Lewis, p. 267, pl. 20, figs. 2*a–c*.
1939 *Caninia benburbensis* Lewis; Hill, p. 112.

Material. Adult portions of 149 coralla, the majority lacking juvenile apical portions.

Diagnosis. Large solitary rugosans. Diameter of tabularium 28–46 mm. Major septa commonly number 56–78, extend well into tabularium, mostly continuous extrathecally, may be sinuous and split along axial planes to various extents; transition to a few forms with septal crests on dissepiments. Minor septa commonly semi-continuous extrathecally (continuous near theca), few project intrathecally; transition to a few forms lacking minor septa and a few with many minor septa projecting intrathecally. Dissepiments mainly concentric or herringboned; transition to a few forms with predominantly lonsdaleoid dissepiments. Large, well-defined cardinal fossula.

Description. The specimens are large, solitary rugosans, mainly 50–70 mm. in diameter (maximum more than 80 mm.), and as much as 0·9 m. long. The corallum may be straight,

uniformly curved, sharply geniculated (one or more times), or developed in a loose spiral. In the initial conical stage, the corallum expands at angles between 13 and 25°. The adult corallum may continue to increase in diameter very gradually, may maintain a fairly uniform diameter (except for rugae), or may be marked by constrictions of varying magnitude.

The coral polyps rested in a deep, beaker-shaped calice, the vertical inner wall of which is formed by the theca, or boundary between the dissepimentarium and tabularium (cf. text-fig. 3*b*). The diameter of the fully developed tabularium may range from 28 to 46 mm. However, in an adult corallum, this diameter remains fairly constant (variations of 1 or 2 mm.) despite marked constrictions of the dissepimentarium. The constrictions were produced when the polyp contracted inward from the inclined lip of the calice, interrupting the formation of dissepimental tissue, but not of intrathecal skeletal elements.

The number of major septa is commonly 56 to 78, but up to 82 may be present. The number of septa remains nearly constant in the adult stage of a corallum. The septa form continuous, blade-like, vertical partitions intrathecally, but vary in their continuity extrathecally. Where the septa are continuous extrathecally, the dissepiments are of simple or herringbone type; where the septa are discontinuous, the dissepiments are larger and lonsdaleoid. Minor septa may be semi-continuous extrathecally, or poorly developed (represented only by isolated septal crests on the dissepiments), or absent. Only in a few individuals do the minor septa project intrathecally.

During ontogeny, the polyp secreted and rested on a succession of medially flattened (or very slightly depressed) tabulae, which are sharply curved down at the margins. A rhythmic arrangement of closely spaced incomplete tabulae and more widely spaced complete tabulae is discernible in many specimens. The tabulae are deeply depressed in the cardinal fossula, into which projects a short cardinal septum.

The skeletal elements within the tabularium (most commonly the septa in the cardinal quadrants) show varied stereoplasmic thickening. In some individuals, this affects the septa and tabulae in all quadrants, but the development is not consistent during ontogeny. Juvenile portions tend to show more thickening than adults (compare Salée 1910, pl. 3, fig. 1*b–f*), and in adults, the skeletal structures are usually thinner in areas of constrictions and geniculations.

Variation. It becomes evident from detailed examination of the coral morphology that certain biocharacters were markedly affected by environmental conditions. The curves and geniculations which the coralla show have been attributed to instability of the bottom sediments in which the corals rested (Hubbard, *in litt.*). Periodic constrictions of the epitheca in some instances are associated with geniculations and may have a related cause. The groups of widely spaced tabulae correspond in age to constrictions of the dissepimental zone, and Ma (1937, p. 9) related such changes in growth form to seasonal temperature variations. Clearly, the dependence on environment of features such as total diameter, geniculations, spacing of tabulae, and intrathecal stereoplasmic thickening, renders them of little use in classification. Other biocharacters apparently remained unchanged during what evidently were crises in the ontogeny of individuals. The most significant of these are the intrathecal diameter, the number of septa, and certain septal characteristics, such as extrathecal continuity. Closely related to continuity of the septa

was the nature of the dissepiments, and these apparently were fairly consistent in form throughout ontogeny.

The Streedagh assemblage comprises a wide group of variants, some recognized before (Lewis 1927, p. 380) and others (not distinguished by Lewis) which significantly expand his concept of the species. The main variations are summarized below. About 10 % of the studied assemblage were not classified because of poor or incomplete preservation. All figured specimens bear catalogue numbers of the Hunterian Museum, University of Glasgow.

Form A (Specimen C. 7471a–e). Individuals included in this group are few in number (less than 5% of the Streedagh assemblage). They characteristically possess a predominantly lonsdaleoid dissepimentarium and consequently markedly discontinuous septa extrathecally (text-fig. 3*a* and *b*). However, the minor septa are commonly as poorly developed as in more typical examples of *C. benburbensis*. The average intrathecal diameter and number of septa are both less than for the remainder of the assemblage (text-figs. 12 and 13) but the number of specimens measured may not be representative.

Form B (Specimens C. 7474a–f and C. 7475a–c). About 10 % of the assemblage are closely similar to the holotype of *C. benburbensis* (Lewis 1927, p. 380, pl. 17, figs. 1*a–b*) and show clearly all the diagnostic features (text-fig. 7). The major septa are mostly continuous extrathecally. Minor septa are well developed near the theca but are reduced to septal crests on the outer dissepiments, and usually few of these septa project intrathecally. The dissepiments are of concentric or herringbone type, and show an irregular spacing, generally quite closely crowded near the theca.

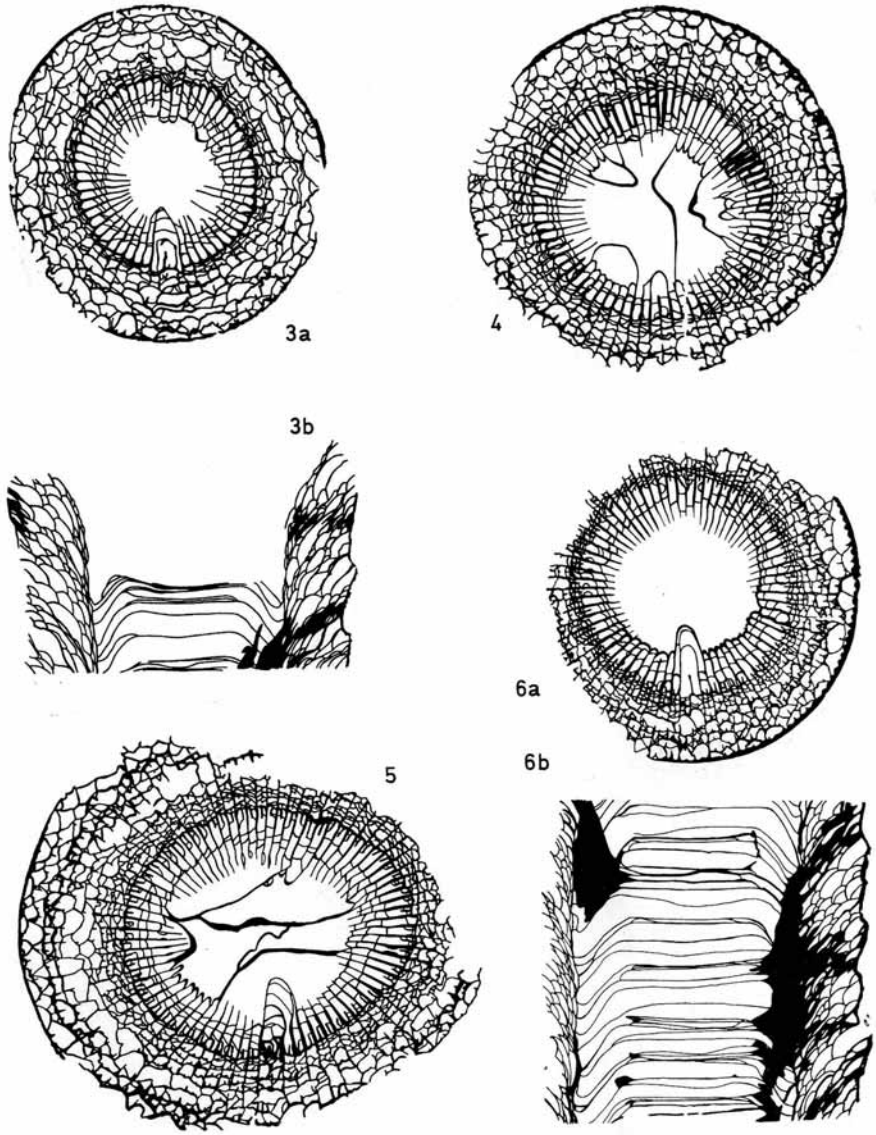
In a few individuals otherwise identical, many of the minor septa project 1–2 mm. into the tabularium. Another morphological variation is shown by several consistently smaller individuals (text-fig. 6*a* and *b*) with finer skeletal elements (although they have the same range in numbers of septa as larger forms).

Form C (Specimen C. 7477a–e). About 10 % of the assemblage lack minor septa, but are otherwise similar to Form B in having more or less continuous major septa and concentric or herringboned dissepiments (text-fig. 9*a* and *b*).

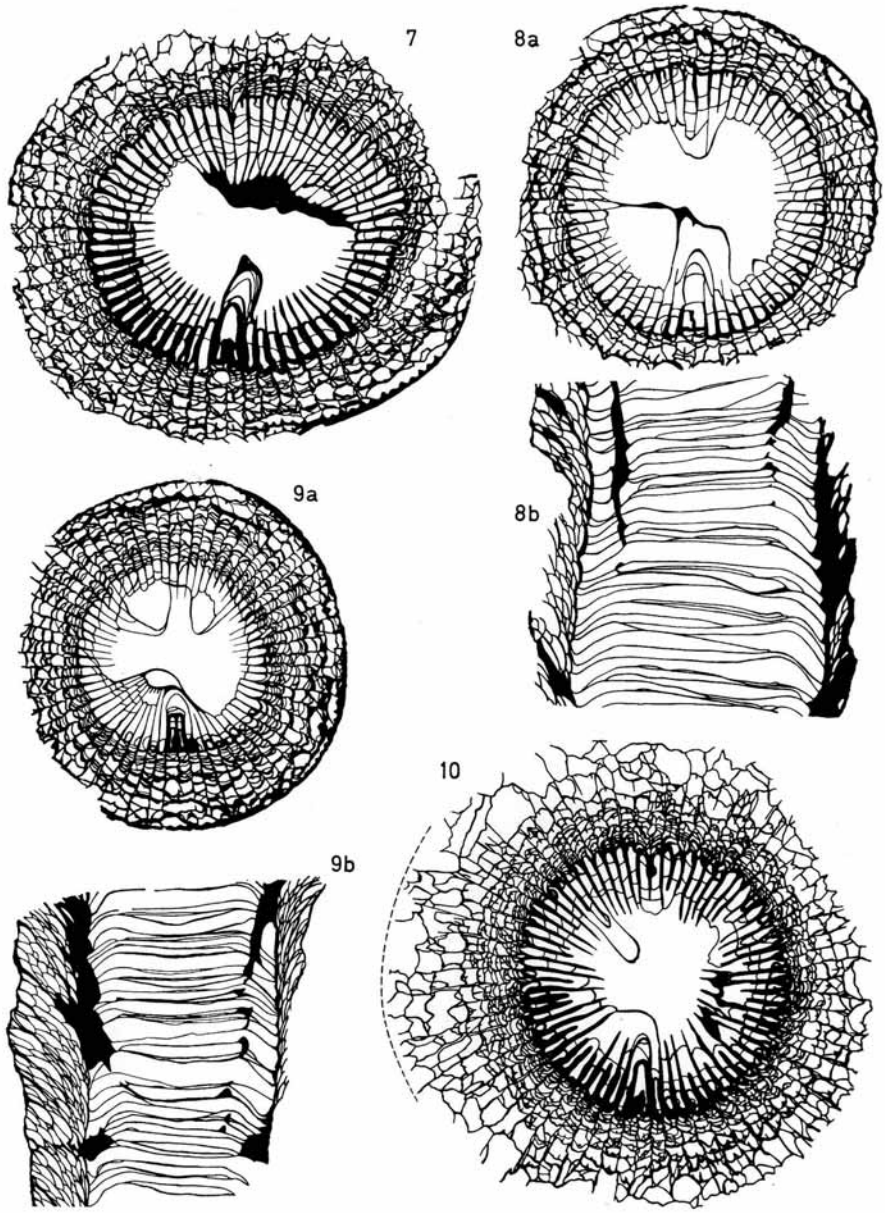
Form D (Specimens C. 7478a–l and C. 7479a–e). About 10 % of the assemblage can be referred to this distinctive form. Specimens are generally of large size, and usually the major septa are split along their axial planes and contorted in the dissepimentarium (text-fig. 10). The dissepiments commonly have lost their concentric or herringbone aspect and appear as sinuous or angulated plates between the septa. In a few otherwise similar forms (text-fig. 11*a* and *b*), the major septa are split less commonly. The skeletal distortions are not a result of geronticism as they are evident in more juvenile stages of the few complete coralla studied.

Measurements of number of septa and adult intrathecal diameter fall within the range of variation of the assemblage, but both measurements average consistently greater than the assemblage average (text-figs. 12 and 13).

Transitional forms (Specimens C. 7472a–c, C. 7473 and C. 7476a–e). The complete artificiality of separating the assemblage into distinct morphological types is obvious from examination of the remaining specimens. Approximately 25 % of the total may be described as morphologically transitional between Forms A and B, i.e. showing a skeletal development intermediate between those with lonsdaleoid dissepiments and

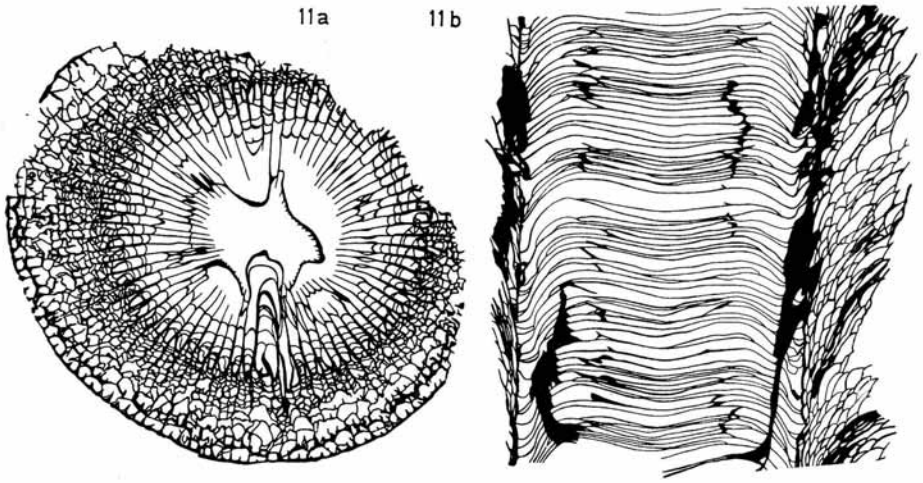


TEXT-FIGS. 3–6. *Caninia benburbensis*. Figured specimens bear catalogue numbers of the Hunterian Museum, University of Glasgow. All are at natural size. 3*a*, *b*. Form A. C. 7471b, C. 7471d. Transverse and longitudinal sections. Epitheca complete but partly obscured by silicification. 4, 5. Intermediate forms A–B. C. 7472b, C. 7473. Transverse sections. 6*a*, *b*. Form B. C. 7474b, C. 7474d. Transverse and longitudinal sections. Specimens represented by text-figs. 4–6 all show the effects of penecontemporaneous abrasion.



TEXT-FIGS. 7–10. *Caninia benburbensis*. 7. Form B. C. 7475b. Transverse section. Epitheca mostly obscured by silicification. 8*a*, *b*. Intermediate form B–C. C. 7476b, C. 7476d. Transverse and longitudinal sections. 9*a*, *b*. Form C. C. 7477d, C. 7477b. Transverse and longitudinal sections. Specimens represented by text-figs. 8 and 9 both show the effects of penecontemporaneous abrasion. 10. Form D. C. 7478i. Transverse section. Dissepimentarium partly abraded. Silicified epitheca approximately at dashed line.

septal crests, and those with concentric dissepiments and fairly continuous major septa. In this group, the minor septa show varied development—virtually absent in some (text-fig. 4) and well developed in others (text-fig. 5).



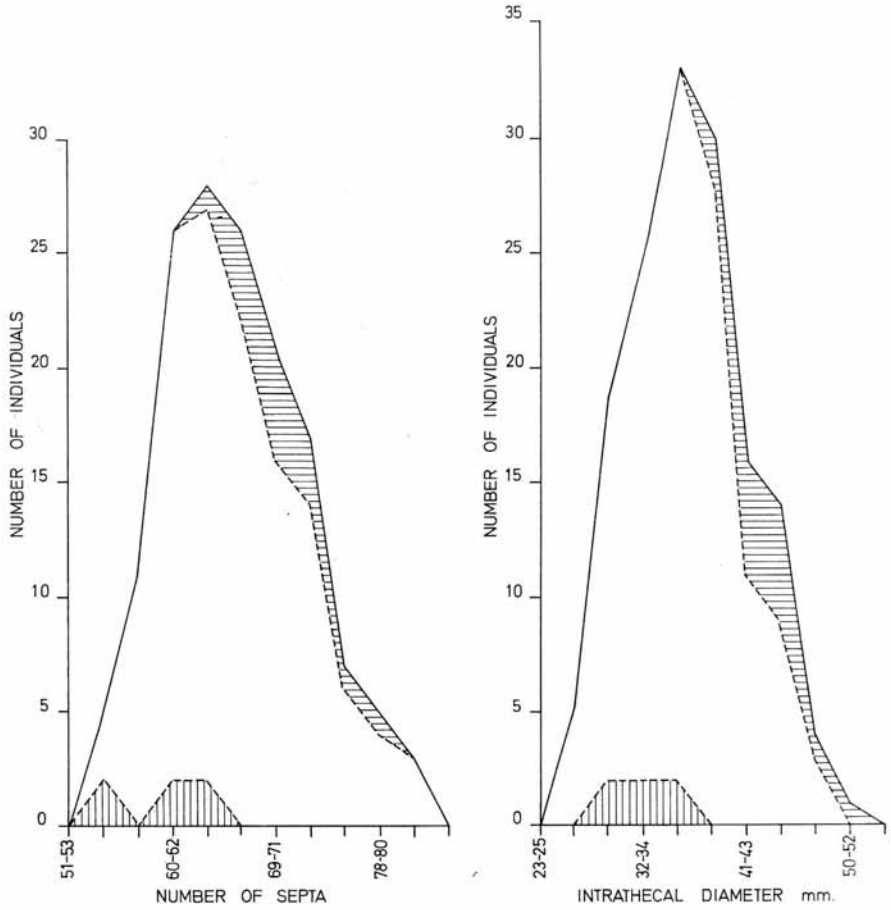
TEXT-FIG. 11*a*, *b*. *Caninia benburbensis*. Form D. C. 7479d. C. 7479b. Transverse and longitudinal sections. Deep penecontemporaneous abrasion on counter-cardinal surface.

Approximately 30 % of the assemblage are individuals morphologically intermediate between Forms B and C (text-fig. 8*a* and *b*). A series of individuals may be recognized in which the minor septa gradually diminish and ultimately disappear (as in Form C). Among these are specimens showing progressively finer skeletal elements, and generally smaller size (as some of Form B).

Similarly, Form D cannot be separated distinctly from the remainder of the assemblage. Characters such as bifurcating major septa and irregular dissepiments can be seen (although much less prominently) in various specimens which have been included in the preceding Forms (e.g. text-fig. 7).

Remarks. The variations evident in the assemblage are most reasonably regarded as variations within a single species. Any or all of the variants may be found on a single bedding plane within the section, and there are no significant differences in the vertical distribution of the various forms. The identification of complete intermediate series among the recognized forms makes any systematic division of little practical value.

Lewis (1927, p. 380) concluded that the ancestry of *C. benburbensis* may be found among earlier forms of *C. cylindrica* (Scouler). The latter has been reported in several nearby areas in rocks of early Viséan age (Caldwell 1959, p. 174; George and Oswald 1957, p. 173; Simpson 1955, p. 399), and this has been confirmed by personal examination of a complete Viséan sequence in the Ballymote syncline south of Sligo. In this sequence, *C. cylindrica* is quite common in rocks of Seminulan and pre-Seminulan age,



TEXT-FIGS. 12–13. Frequency curves of *Caninia benburbensis*. Vertical and horizontal ruling represents the frequency of Form A and Form D, respectively.

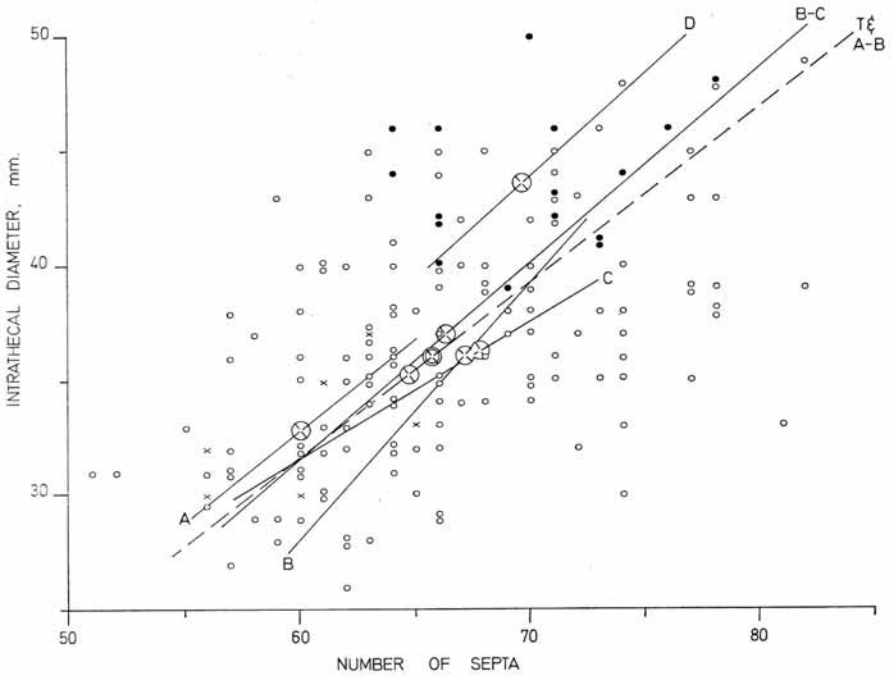
and *C. benburbensis* is found in rocks of late Seminulan age but most commonly in those of the *Dibunophyllum* Zone. The essential characters which have been used to distinguish the two species are as follows:

Caninia cylindrica

1. Tooth-like septal crests on the dissepiments (no continuous septa outside the theca).
2. Minor septa projecting about 2 mm. intrathecally.
3. Large and irregular interdissepimental spaces becoming smaller inwards and formed by lonsdaleoid dissepiments.

Caninia benburbensis

1. Major septa predominantly continuous extrathecally and sinuous.
2. Minor septa discontinuous for one-half to two-thirds of the extrathecal distance (do not typically project intrathecally).
3. Interseptal spaces with concentric or herringbone dissepiments.



TEXT-FIG. 14. Scatter diagram of number of septa–intrathecal diameter of *Caninia benburbensis*. Crosses represent individuals of Form A; closed circles, Form D; small open circles, the remainder of the population. The reduced major axis for the transitional group A–B coincides with that for the total population (T). The total population mean is marked by the large double circle; others by large single circles.

Of significance is the presence within the Streedagh assemblage of a few specimens (Form A) with certain morphological features in common with *C. cylindrica* (compare the 'transitional forms' of Lewis 1927, p. 380, pl. 16, fig. 6; pl. 17, fig. 4). Statistical analysis of two readily measured parameters, number of septa and intrathecal diameter, indicate that these forms are slightly smaller and have fewer septa than the bulk of the assemblage (text-figs. 12, 13, and 14). Although the specimens may be too few to be representative, they are similar in dimensions to *C. cylindrica* from Tournai (Salée 1910, p. 31, pl. 2–5).

Perhaps also significant are the specimens which Salée (1910, pp. 37–9) described as

Caninia cylindrica var. *Herculina* (De Koninck). In a collection otherwise typical of the species *cylindrica*, the two specimens referred to this subspecies show an extrathecal development strikingly similar to that in typical forms of *C. benburbensis*, namely, greater continuity of the major septa, and considerable reduction of the zone of large lonsdaleoid dissepiments in favour of smaller concentric or herringbone dissepiments.

The specimens ascribed to Form A appear to possess certain distinctive morphological characters which were retained as the caniniid lineage evolved. These characters persisted through Viséan time as the population mode gradually changed toward larger adult individuals with more major septa, with concentric rather than lonsdaleoid dissepiments, and with diminished minor septa.

Text-figs. 12, 13, and 14 show the distinct and perhaps significant departure of Form D from the assemblage average. This may represent a new variation which became established as the lineage evolved. Further study of caniniid populations higher in the *Dibunophyllum* Zone may reveal whether or not this type was successful and increased in proportion with time. As it forms an integral part of the *C. benburbensis* assemblage in the lower D_1 subzone, there is no justification yet for its establishment as a new species. Lewis (1927, p. 380, pl. 17, figs. 2*a–b*, 3*a–c*) described such forms as 'senescent', or a final senile evolutionary stage of the species before it became extinct. This is questionable, as the supposedly senescent forms appeared early in Dibunophyllidan time in extremely successful populations, such as the ones at Streedagh Point, and the caniniid line continued to flourish well into D_2 time.

There is no general agreement on the relationship between *Caninia* Michelin 1840 (type species: *C. cornucopiae*) and *Siphonophyllia* Scouler *in* McCoy 1844 (type species: *S. cylindrica*). Both Salée (1910, p. 27) and Lewis (1927, p. 374) regarded *Siphonophyllia* as a synonym of *Caninia*. Both genera are recognized by Hill (1956, p. F292), in which *Siphonophyllia* is distinguished only on the basis of a wide lonsdaleoid dissepimentarium. In view of the wide range of septal and dissepimental development in *C. benburbensis*, and the as yet incomplete understanding of caniniid phylogeny, both *benburbensis* and *cylindrica* have been referred herein to the genus *Caninia* (*sensu lato*).

CONCLUSIONS

1. A wide range of morphological variation occurs in the Streedagh Point assemblage of *Caninia benburbensis*, and clearly distinguishes it from all earlier assemblages.
2. Certain characters, such as total diameter, geniculations, spacing of tabulae, and stereoplasmic thickening were distinctly dependent on ecological conditions, and varied during ontogeny.
3. Biocharacters such as intrathecal diameter, number of septa, extrathecal continuity of septa, and nature of the dissepiments show a regularity or constancy throughout ontogeny which favours their use in classification.
4. Certain members of the population possess morphological features which strongly affirm an earlier idea that *C. benburbensis* evolved from *C. cylindrica* (Lewis 1927, p. 380). In agreement with this are their respective stratigraphical ranges in Ireland.
5. Certain members of the population show features which may presage the divergence of a new species from the evolving caniniid lineage.

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O. A. DIXON
Department of Geology
University of Ottawa
Ottawa, 2
Canada

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