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THE USE OF DISSOCIATED CRINOID OSSICLES AS BIOSTRATIGRAPHICAL AND PALAEOECOLOGICAL TOOLS IN THE CARBONIFEROUS OF NORTHWEST IRELAND

VOLUME 1 of 2

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Kay Mannifield

A thesis submitted for the degree of Doctor in Philosophy to

the University of Dublin, Trinity College

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DECLARATION

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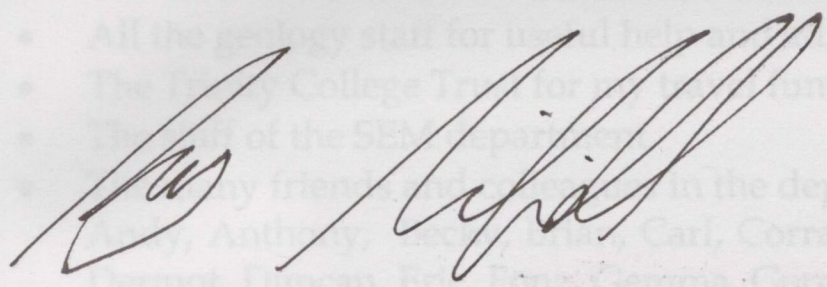

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For my Dad.....

SUMMARY

Fossil crinoids were investigated from the Lower Carboniferous (Viséan) rocks of northwest Ireland. In this area the deltaic Mullaghmore Sandstone Formation stratigraphically separates the Bundoran Shale Formation (Arundian) and the Benbulben Shale Formation (Holkerian-Asbian). These two formations are similar lithologically consisting of clay-rich, calcareous shale interbedded with discontinuous beds, and lenses of bioclastic, often argillaceous limestone. The sedimentary sequence represents the incursion of a fluviodeltaic complex into the Carboniferous sea of northwest Ireland and its subsequent retreat. The Bundoran Shale Formation records the progradation of the delta over prodelta muds, and the Benbulben Shale Formation represents a major flooding surface on the subsequent receding delta. Although several horizons throughout the succession have been sampled, the study concentrated particularly on these two formations since they yielded countless fossil crinoid specimens.

Disarticulated crinoid material was collected in both bulk samples and by hand picking from shale outcrops. Cleaning by soaking in Quaternary-O or hydrogen peroxide and fluoridising using hydrofluoric acid followed laboratory extraction of the ossicles. A binocular microscope was used to examine larger specimens, and their photographs were taken. A Scanning Electron Microscope was used for examining smaller specimens and their SEM images were digitally captured and manipulated on the computer to produce the final plates. Morphometric data was obtained using both microscopes.

The taxonomic study of mostly incomplete crinoid calyces and crowns which were found was carried out. Species of *Litocrinus*, *Phanocrinus*, *Amphicrinus*, *Onychocrinus* and *Platycrinites* had previously been described in the literature, and new genus and species of cladid crinoid is proposed, *Bundoranocrinus vermiculatus* gen. et sp. nov. In contrast to the want of articulated crinoid material, disarticulated material is particularly abundant and consists mainly of columnal ossicles and pluricolumnals, with lesser amounts of thecal plates and brachials. The columnals have been studied in detail with the latera and articular facets showing a great range in morphology. Using morphological and morphometric data, sixty different morphospecies have been proposed and have been left in open nomenclature. The majority of the taxonomic study is devoted to the full descriptions of columnals where in the past has this has been lacking. Particular attention

has been paid been as to their classification and nomenclature. Palaeoecological analysis of the entire fauna of the two shale formations has been undertaken, and autecology of long stemmed crinoids has also been carried out. Results from articulated and disarticulated material has been used to estimate crinoid diversity. The difference in taxonomic content of the columnal assemblages from the Bundoran and Benbulben Shale formations shows that crinoid ossicles will be a useful tool in Carboniferous biostratigraphy.

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CHAPTER 1

INTRODUCTION

1.1. INTRODUCTION

W.I. Ausich and C.G. Messing stated on their World Wide Web site (see 'References'), "*[Crinoid]..skeletal remains are among the most abundant and important of fossils*", echoing the earlier comment of Jeffords (1978, p. T929):

"*The abundance and variety of crinoid parts, especially columnals, make them immediately useful for purposes of biostratigraphy and studies of palaeoecology after they have been adequately described, illustrated, classified and named*".

While crinoids are not taxonomically very diverse in Recent seas, from which around only approximately 600 species have been described, during the Palaeozoic they dominated the echinoderm fossil record. Moore and Jeffords (1968, Fig. 2) indicated that there were 7335 Palaeozoic described species, and since the publication of their study, the number of new species described far outstrips the number sunk in synonymy. The major clades probably first appeared during the Lower Ordovician and during the Palaeozoic experienced many radiations reaching their acme during the Carboniferous. However, the Permo-Trias extinction almost saw the disappearance of the class, as was the case with many other organisms, but the infraclass Articulata persisted through to the Mesozoic and this group of crinoids are still living today. The articulates are represented mainly by unstalked forms (less than 15% of extant crinoids are stalked) in contrast to those of the Palaeozoic when unstalked forms, such as *Agassizocrinus*, formed a minute proportion of described taxa.

The echinoderm endoskeleton, which makes up over 80% of the crinoid body (C. G. Messing, pers. comm. 2000), is complex, comprising a vast number of individual calcite ossicles, united by ligaments and in some cases by muscles, which disarticulate readily *post mortem*. The volume of fossilised crinoid stem material (columnals) far exceeds that of material derived from any other part of the crinoid skeleton and this has been exploited by several workers. However, in general previous studies have not incorporated microscopic material (less than 1 mm) of the kind that forms part of the basis of the

present study. Although the potential use of columnals as biostratigraphical tools has been appreciated by several workers, there are few examples of practical applications of biostratigraphy based on crinoid columnals. This is partly because of disparities in nomenclature and taxonomy between crinoid workers across the globe.

1.2. AIMS OF THIS STUDY

The overall aim of this study was to assess whether disarticulated ossicles of Carboniferous crinoids could be useful in biostratigraphy and palaeoecology.

There were four specific objectives. These were:

- To describe and classify crinoid ossicles (mainly columnals) for the Dinantian of northwest Ireland. The decision was made to describe columnal taxa as numbered morphospecies, and not to use Linnaean binomial nomenclature, for reasons that are discussed in Chapter 5.

- To assess the use of these columnal morphospecies, individually and as assemblages, in biostratigraphy and, if possible, to propose a zonal biostratigraphy for the part of the Lower Carboniferous studied (Chadian to Asbian Stages).

- To assess the palaeoecology of the crinoid animals in this area by using their disarticulated remains in association with other fossil fauna and by sedimentological analysis of the strata in which they occur.

- To describe and illustrate calyces and crowns of previously known and newly discovered crinoids from the area and to assess their taxonomic positions.

1.3. HISTORY OF PREVIOUS WORK ON DISARTICULATED CRINOID OSSICLES

Many workers have named and described disarticulated Palaeozoic crinoid ossicles (mainly columnals) without contributing very greatly to the methodology or general application of such studies; the reader is referred to Webster's (1973, 1977, 1991, 1993) *Bibliography and Index of Palaeozoic Crinoids* for bibliographic details of such work. The

following account of the history of study deals mainly with those publications which either made significant contributions to methodology or deal with material of Carboniferous age or Palaeozoic material from Britain and Ireland. A concise overview of the work carried out on all aspects of crinoids up until 1978 is available in the *Treatise on Invertebrate Paleontology* (Moore and Teichert 1978*a*). A full list of the main authors who have made contributions to the literature on technical descriptions and classification of disarticulated columnals can be found in Section 5.1.

Biostratigraphy using dissociated crinoid ossicles was first specifically discussed by Moore (1939). He was, however, unsure how important the study of dissociated ossicles would be to palaeontology in general and to stratigraphy.

Moore and Laudon (Moore and Laudon 1943) suggested that dissociated crinoid fragments could be useful.

Moore and Jeffords (1968) and **Moore, Jeffords and Miller** (1968) described a large number of taxa and discussed the importance of pluricolumnals in terms of stem development with particular reference to ontogeny (Jeffords and Miller 1968). **Webster** (1974) described a notation for the description of pluricolumnals. There has been surprisingly little work published on the stratigraphical use of disarticulated columnals in the United States since Moore and Jefford's work; an exception is **Webster and Houck** (1998) who described material from the Middle Pennsylvanian of Colorado. The columnals belonged to columnal genera and species of Moore and Jeffords (1968), including *Floricyclus* and *Cyclocaudex*.

Much of the Russian work on crinoid columnals has been carried out by three researchers, **Dubatolova**, **Stukalina** and **Yeltyschewa** (see Webster (1973, 1977, 1991, 1993) for references). Of these three Stukalina, who began publishing on disarticulated crinoid columnals in the mid 1960's, has contributed most on discussions of methodology and taxonomy. She (Stukalina 1967, 1968) investigated the phylogenetic relationships of stems from analysis of their functional morphological changes throughout crinoid evolution. In several papers Stukalina attempted to elucidate a biological evolution of columnals using morphological data only. The results of this work was included in Stukalina (1982) in which she attempted a zonal subdivision and correlation of Lower and Middle Devonian

strata in the USSR, and in Stukalina (1994) where she proposed a biostratigraphical scheme for the Silurian of Mongolia based on crinoids. In Stukalina (1979*a*, 1979*b*) new Ordovician crinoid families were erected based on columnal morphotypes only. Other new 'genera' were proposed from the Carboniferous of Mongolia in Stukalina (1997) and from the Late Permian of Transcaucasia and North Caucasus (Stukalina 1999). Stukalina (1988) attempted to establish genetic links between two columnal morphogenera which she had described (*Decacrinus* and *Pennatocrinus*) because of the similarity of their morphologies (biological traits). She stated that the material used was disarticulated columnals (she did not mention pluricolumnals) and she apparently assumed that the columnals represented different columnal morphospecies. Unless sufficiently long stem portions were used the results of the study are questionable.

Gluchowski, amongst other studies, described 83 taxa of crinoid, some of which are from 'real-species', some from isolated columnals, from the Polish Silurian, Devonian, Carboniferous and Permian (Gluchowski 1981). He also suggested how palaeoecology and diversity changes in different environments could be inferred from different crinoid assemblages in the Givetian and Frasnian of Poland (Gluchowski 1993).

Donovan (Donovan 1984*b*) described Ordovician columnal material from Scotland and compared it with material from Kazakhstan. The material belonged to the morphogenus *Malovicrinus,* previously erected by Stukalina (1968). An unusual (tetrameric) columnal (Donovan 1983) and pelmatozoan columnals (Donovan 1986*a*, 1989*a*) were described from the Ordovician of the British Isles. Other columnals with four-fold symmetry were described in Donovan (1986*b*) and in Donovan and Veltkamp (1993). Other work by this author with reference to crinoid columnals and stem functions can be found in Donovan (1985, 1988*b*, 1989*b*, 1990, 1993, 1994*a*,*b*) and Donovan *et al.* (1986), Donovan *et al.* (1995), Donovan *et al.* (1996), Donovan *et al.* (1997), Donovan and Veltkamp (1990), Donovan and Westhead (1987), Donovan and Wright (1995) and Donovan and Lewis (1997).

Le Menn (Le Menn 1985) produced a memoir discussing the systematics, palaeobiology, evolution, palaeoecology and biostratigraphy using mainly disarticulated crinoid columnals (using the sign Ø for columnal morphospecies) and crinoid stem sections from the Devonian of France. Le Menn (1999) discussed a method by which isolated columnals and columnal assemblages could be used in biogeography. **Ures, Le Menn and Hladil**

(Ures *et al.* 1999) described crinoid columnals, some dissociated and some found with their calyces, from the Middle Devonian of the Czech Republic.

Prokop and Pek (Prokop and Pek 1998) assigned a new morphospecies to the morphogenus *Cyclocaudiculus* Moore and Jeffords, 1968, from the Lower Carboniferous of the Czech Republic. **Prokop and Petr** (Prokop and Petr 1998*b*) described columnals that they classified as *Decacrinus bohemicus* sp. n. (col.), which belonged to the previously erected, distinctive morphogenus *Decacrinus* Yeltyschewa, 1957 (col.).

The study of the stems of Mesozoic crinoids has been much more extensive in relation to the number of crinoid taxa than that of Palaeozoic crinoid stems. As an example, the reader is referred to Simms (1989*b*) in which are described the morphology and functional analysis of some Lower Jurassic crinoid columnals and stems.

Several authors have produced work on Cenozoic and Recent crinoid columnals and stems, mainly the isocrinids and bourgueticrinines. For example, **Donovan** (Donovan 1984*a*) discussed the stem morphology of the Recent crinoid *Chladocrinus* (*Neocrinus*) *decorus* (Wyville Thomson) looking at changes in columnal articular facet morphology throughout the stem and also the stereom microstructure of the columnals. **Donovan and Pawson** (1994) described the skeletal morphology of the bourgueticrinine crinoid *Phrynocrinus nudus* A. H. Clark paying attention to the flexibility of the stem. Donovan (1994*b*) described an early Pleistocene isocrinine fauna from Jamaica. Donovan (1996) compared the morphology and function of the stems of the extant bourgueticrinine crinoid *Democrinus* Perrier and the extant Upper Palaeozoic platycrinitids.

CHAPTER 2

STRATIGRAPHY AND GEOLOGICAL HISTORY OF THE STUDY AREA

In this chapter the stratigraphy of the Dinantian rocks of northwest Ireland is briefly described with more detailed comments on the sections from which samples were collected. The geological evolution of northwest Ireland during the Dinantian is placed in its regional setting.

2.1. STRATIGRAPHICAL DIVISION OF THE DINANTIAN IN IRELAND

In western Europe recent practice has been to divide the Carboniferous into Dinantian and Silesian subsystems, which correspond to the Lower and Upper Carboniferous respectively. However, agreement has now been reached on an international scheme in which the Lower-Upper Carboniferous boundary has been defined at a level equivalent to the Mississippian-Pennsylvanian boundary in North America, which falls within the Upper Carboniferous as previously defined in northwest Europe (Sevastopulo and Wyse Jackson 2000). No agreement has been reached, however, on internationally recognised Series and Stages. In this account, recent western European practice of recognising Tournaisian and Viséan Series as subdivisions of the Dinantian Subsystem is followed. The most widely used Dinantian Stages in Britain and Ireland have been those proposed by George *et al.* (1976) which were outlined by Sevastopulo (1981, Table 12) and are shown here in Figure 2.3.

The Stages proposed by George *et al.* (1976) have, in general, provided a useful framework for analysis of Dinantian stratigraphy, although some re-definition of boundaries may be required (Riley 1993). However, the Courceyan-Chadian boundary cannot be identified by biostratigraphical means and is older than the Tournaisian boundary with which it was intended to be equated. Riley (1993) divided the Chadian Stage into early and late phases with the 'early Chadian' belonging to the Tournaisian and the 'late Chadian' to the Viséan. Sevastopulo and Wyse Jackson (2000) used the term 'Lower Viséan' for the period that equates to the 'late Chadian'. The Tournaisian-Viséan boundary interval in the type Dinant area of Belgium has also provided some stratigraphical problems: the base of the Viséan and the base of the Molinacian, proposed to be the lowest Stage of the Viséan, have been found to be at different biostratigraphical horizons (Conil *et al.* 1989). Lees

(1997) proposed the 'Freyrian' Stage to represent the stratigraphical interval between the base of the Viséan and the base of the Molinacian. The base of the 'Freyrian' in Belgium is older than the base of the Chadian at its stratotype in the Craven Basin of northern England. Lees (1997) proposed that the Chadian stratotype in fact lay in the late 'Freyrian' if foraminiferan assemblages were to be trusted for correlation and this would approximately correspond to the later part of the 'early Chadian'.

The rocks from which crinoid material has been collected in northwest Ireland range in age from Lower Viséan to Asbian. The dating of some formations, particularly the Mullaghmore Sandstone and the Benbulben Shale, is problematic.

2.2. REGIONAL SETTING

Carboniferous limestones outcrop, or subcrop, over most of the country, especially the Midlands. They generally lie below the 120 m contour and form a gently rolling plain (Davies and Stephens 1978). In many places there is a cover of Quaternary deposits (Sevastopulo and Wyse Jackson 2000). Lower Palaeozoic and Devonian rocks crop out in the southwest, southeast and north, and as inliers in the Midlands, and generally form high ground (Davies and Stephens 1978).

At the onset of the Dinantian Ireland lay in tropical latitudes. Around the Devonian-Carboniferous boundary the sea began advancing northwards gradually covering coastal areas of the Old Red Sandstone (ORS) continent (Long *et al.* 1992). This saw the transformation of the southern half of Ireland during the Tournaisian into a tropical sea with shallow water shelves in the Midlands and a deep basin in the south (Sevastopulo and Wyse Jackson 2000). The northwest remained emergent at this time and the margins of the diminishing ORS continent produced terrigenous sediment that was mixed with marine carbonates. At the beginning of the Viséan there was a major change in tectono-sedimentary style which continued to the end of the Dinantian with the development of deeper water basins surrounded by shallow water platforms (Figure 2.5). Shallow water carbonates developed on the platforms and some of this material was transported to the basins where it was interbedded with terrigenous clay and silt. Active faulting on some basin margins produced steep slopes (Sevastopulo and Wyse Jackson 2000). During the Viséan the sea spread further north (Figure 2.6) and finally most of the remainder of the

country was submerged (Long *et al.* 1992).

During the Dinantian, large-scale tectonic processes caused regional subsidence in the northwest of Ireland (Graham 1996) and this probably reactivated underlying Caledonoid trending faults (MacDermot *et al.* 1996). Leeder (1988) (*fide* Graham 1996) suggested an overall extensional regime at this time. The transgression, therefore, advanced over a land surface with varying topography, so the basal beds that were deposited vary greatly in their thicknesses. Amongst other typically fluvial sediments they are represented by a basal conglomerate (MacDermot *et al.* 1996).

2.3. INTRODUCTION TO THE REGIONAL STRATIGRAPHY OF NORTHWEST IRELAND

The localities from which crinoid material has been collected lie to the west of the Ox Mountains in the Sligo Syncline, south County Donegal and north County Mayo (Figures 2.1, 2.2). The stratigraphical terminology, particularly of the lower stratigraphical units, is complicated because of variations in facies. The standard succession is that of the Sligo syncline described by Oswald (1955) (Figure 2.3).

The basal beds of the Carboniferous in northwest Ireland are represented by the Roelough Conglomerate Formation and the 'Bruckless Grits' (south Donegal), Moy (Ballymote Syncline) and Minnaun (north Mayo) Sandstone formations. They were deposited by southeast flowing rivers on a coastal plain (Long *et al.* 1992). The Downpatrick Formation was the successor of these basal beds to the northwest of the Ox Mountains and the succession graduates from near-shore through alluvial, deltaic to fully marine conditions (Long *et al.* 1992). In the Sligo-Leitrim area the basal beds are followed by the Ballyshannon Limestone Formation, which is succeeded abruptly by siliciclastic-dominated rocks, represented by the Bundoran Shale Formation and the Mullaghmore Sandstone Formation (Figure 2.5). The influx of siliciclastic sediment was caused by uplift in the north (Long *et al.* 1992; MacDermot *et al.* 1996), which was the source area (Sevastopulo and Wyse Jackson 2000). The uplift led to a southward progradation of a fluviodeltaic complex (MacDermot *et al.* 1996), the facies produced being coarse-grained, thick and carbonate-poor (Sevastopulo and Wyse Jackson 2000). To the south fine-

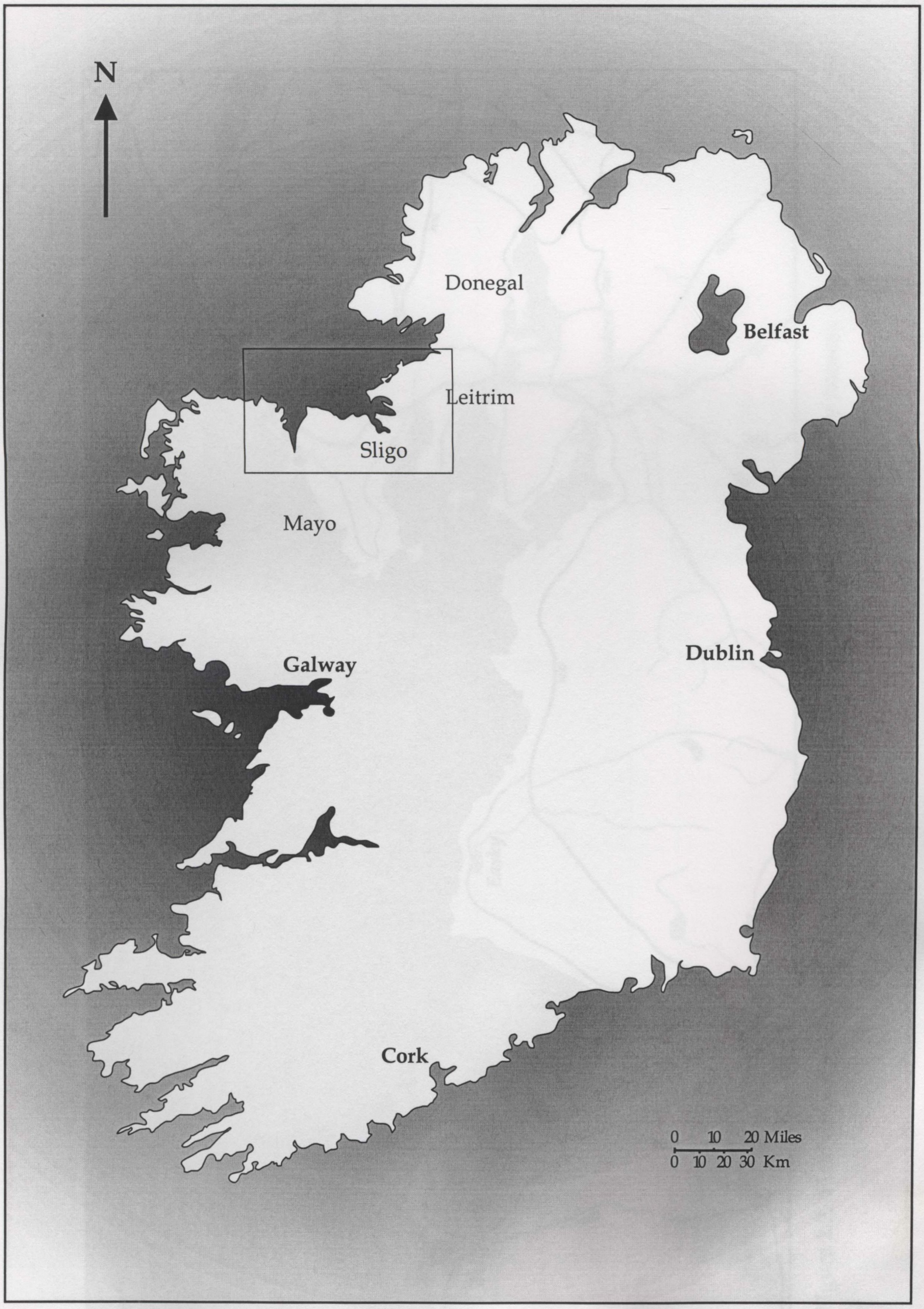


Figure 2.1. Outline map of Ireland showing main cities and towns. Box outlines field area for present study (Figure 2.2.).

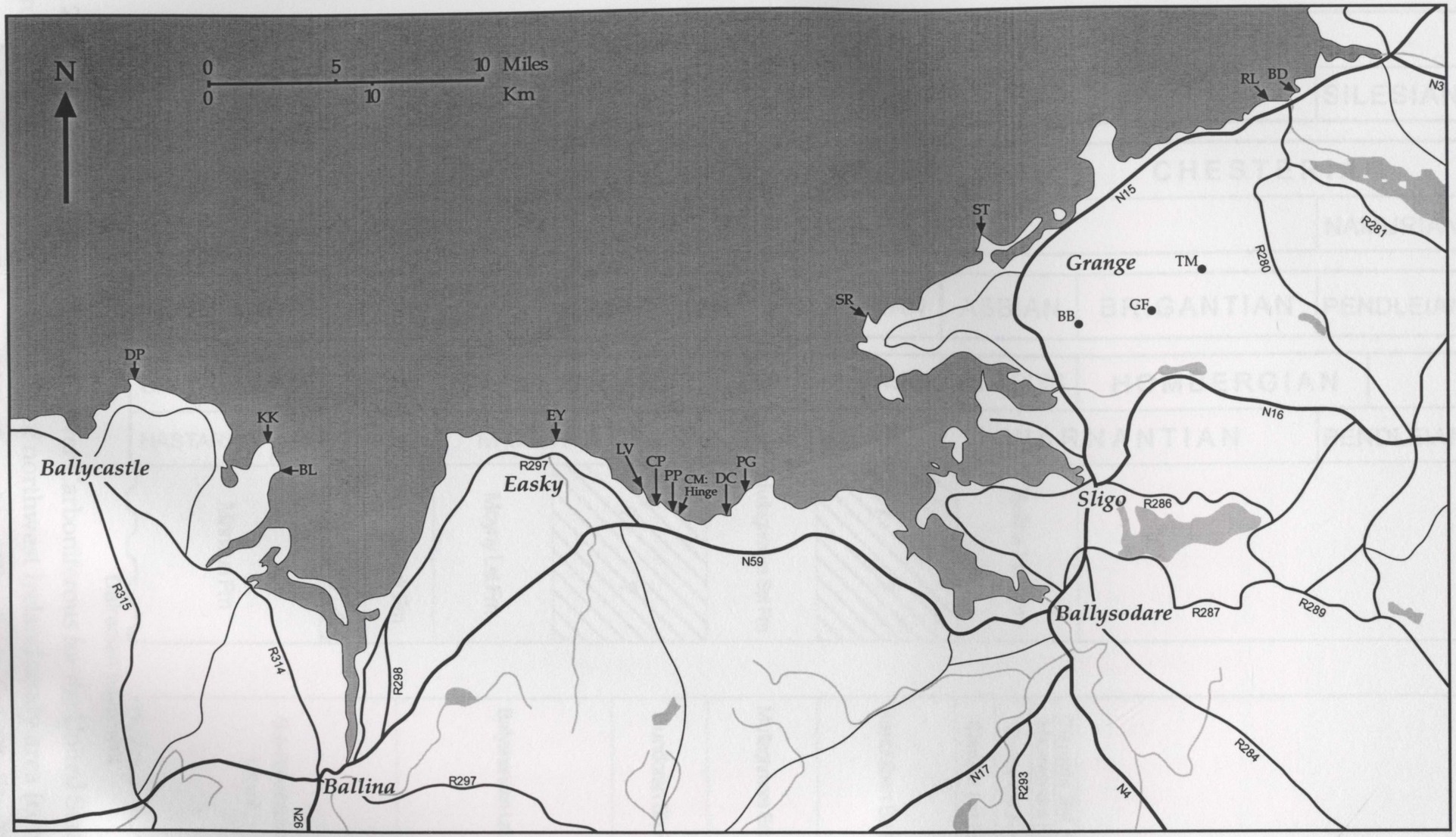


Figure 2.2. Field area of present study showing localities (see Appendix B for full locality names).

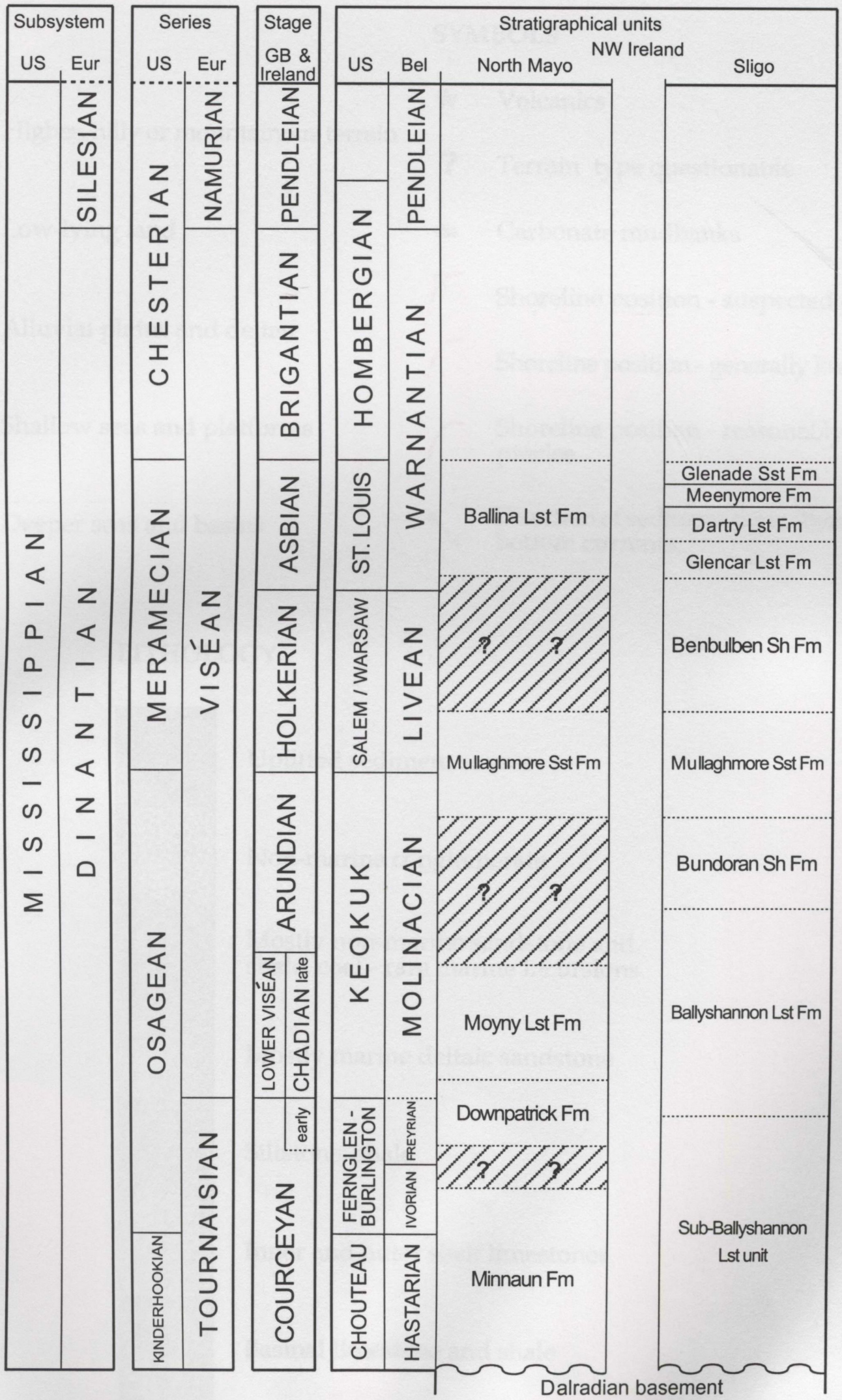
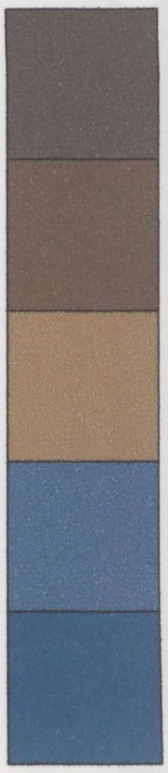


Figure 2.3. Stratigraphical correlation of Lower Carboniferous for the United States, Belgium and Great Britain and Ireland with detail of northwest Ireland study area (compiled after Varker and Sevastopulo 1985; Stone 1991; Geraghty 1996; Graham 1996; MacDermot *et al.* 1996; Lees 1997; Sevastopulo and Wyse Jackson 2000 (after several authors)). [..... = boundary uncertain, -·-·-·- = unit continues further.]

TERRAIN



Higher, hilly or mountainous terrain

Low-lying land

Alluvial plains and deltas

Shallow seas and platforms

Deeper seas and basins

SYMBOLS

Volcanics

Terrain type questionable

Carbonate mudbanks

Shoreline position - suspected only

Shoreline position - generally known

Shoreline position - reasonably precise

Direction of sediment derivation and bottom currents

LITHOLOGY



Uplifted sediment source

Non-marine conglomerate

Mostly non-marine sandstone and shale, coal - rare marine incursions

Mostly marine deltaic sandstone

Siltstone, shale

Inner and outer shelf limestones

Basinal limestone and shale

Starved basin

Figure 2.4. Key for palaeogeographical maps in Figures 2.5. and 2.6. (modified after Cope *et al.* 1992 and Sevastopulo and Wyse Jackson 2000).

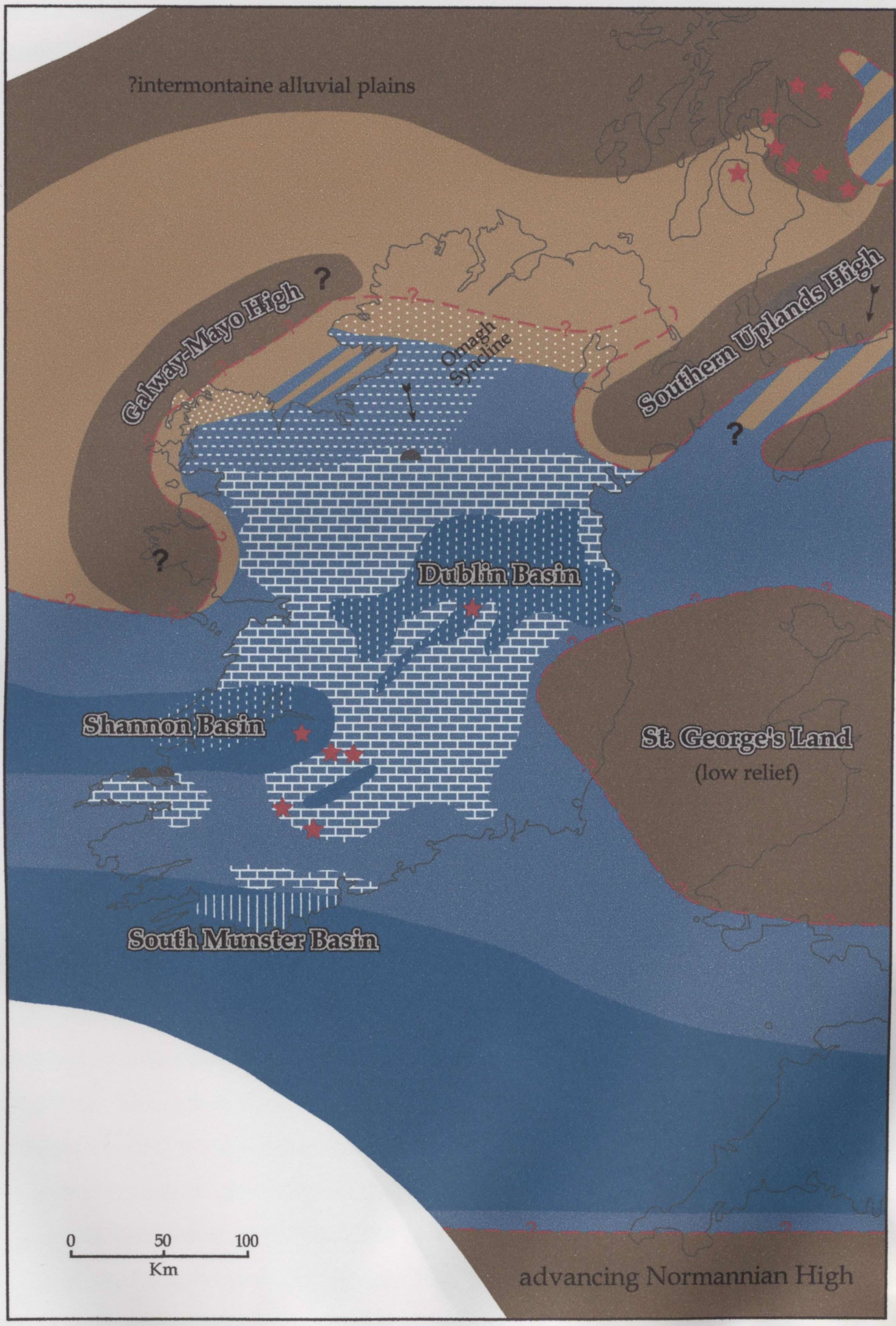


Figure 2.5. Generalised palaeogeographical map for the mid-Arundian (part of the Pu miospore Biozone) at the time of the deposition of the Bundoran Shale Formation (redrawn from Cope *et al.* 1992 and Sevastopulo and Wyse Jackson 2000) (see Figure 2.4. for key to map).



Figure 2.6. Generalised palaeogeographical map for the Asbian at the time of the deposition of the Glencar Limestone Formation and Dartry Limestone Formation (redrawn from Cope *et al.* 1992 and Sevastopulo and Wyse Jackson 2000) (see Figure 2.4. for key to map).

grained, thinner carbonate facies were deposited during this time (Sevastopulo and Wyse Jackson 2000). The rise in sea level then flooded the northwestern delta complex and the muddy marine Benbulben Shale and Glencar Limestone formations were deposited as the land mass was reduced in size and subsided. The Dartry Limestone Formation, with the development of carbonate mudmounds, marked the return of deeper, open marine conditions (Figure 2.6). A regression, and uplift (MacDermot *et al.* 1996), at the end of Dartry Limestone times resulted in the deposition of the Meenymore Formation, which contains peritidal limestones and evaporites, and the deltaic Glenade Sandstone Formation (Sevastopulo and Wyse Jackson 2000). Younger, shallow water, mixed siliciclastic carbonate units occur to the east of the Ox Mountains (Sevastopulo and Wyse Jackson 2000).

2.4. THE SLIGO SUCCESSION

The localities referred to in Sections 2.4 and 2.5 are outlined in Figures 2.1 and 2.2. A key for logs and maps in Appendix A is available in Figure A.1 (p. vi).

2.4.1. BALLYSHANNON LIMESTONE FORMATION

The oldest carbonate unit in the Sligo syncline is the Ballyshannon Limestone Formation (the Lower Limestone of the original Geological Survey), which consists mostly of limestones (Oswald 1955; Philcox *et al.* 1992) (Figure A.26.*a*). At the type locality around Ballyshannon, the limestones occur mostly as bluish-grey, massive, monotonous thickly-bedded or massive, stylolitic, crinoidal packstones with rare shelly horizons (Wright *et al.* 1913; MacDermot *et al.* 1996). Darker, argillaceous, finer-grained limestones are interbedded with thin calcareous shales at the top and base of the formation (MacDermot *et al.* 1996). The lack of shale indicates that the sequence was deposited in shallow water (Sevastopulo and Wyse Jackson 2000). Deeper water developments of the Ballyshannon Limestone Formation are found in the Lough Allen Basin on the eastern side of the Ox Mountains (Philcox *et al.* 1992). The formation lies unconformably on metamorphic basement at Ballyshannon and Rosses Point (MacDermot *et al.* 1996). Further south, around Ballysodare, it overlies conformably a sedimentary sequence initiated by a basal pebbly, coarse-grained calcarenite (MacDermot *et al.* 1996; Sevastopulo and Wyse Jackson 2000 (*fide* Hitzman 1986)). The Ballyshannon Limestone Formation extends from the Chadian into the early Arundian (George *et al.* 1976; Philcox *et al.* 1992).

2.4.2. BUNDORAN SHALE FORMATION

The Bundoran Shale Formation (the Lower Calp Shale of the original Geological Survey) succeeds the Ballyshannon Limestone Formation conformably. The lower part of the formation at the type section at Bundoran (Figures A.26-A.30, A.36) comprises interbedded, commonly discontinuous, thin, argillaceous limestones and dark grey, calcareous, fissile, clay-rich shales (shales rather than 'mudstones' as described by Oswald 1955) that contain an abundant and diverse fauna. They are particularly rich in crinoids, but also contain many brachiopods, corals, bryozoans, sponges, echinoids and other echinoderms. Shales with fewer fossils dominate the middle part of the formation (Figures A.31, A.32, A.35) and silty shales with some interbedded siltstones appear towards the top (Figures A.33, A.34). The sequence is similar to that in the O'Donnell's Rock area in the Ballymote Syncline on the east side of the Ox Mountains described by Dixon (1972).

At Bundoran (Plate 1) the contact of the base of the Bundoran Shale Formation with the underlying Ballyshannon Limestone Formation is seen near Aughrus Point (Locality BD:A (GR 8191 5965)) (Figures A.25, A.26.*a*, A.37). The base of the Bundoran Shale Formation here consists of very fossiliferous, dark grey, calcareous clay shales with interbedded lenticular wackestones and packstones, which commonly have erosive bases (Plate 2, fig. a; Figures A.26-A.30). The shales contain a varied indigenous fauna. It includes abundant and diverse crinoids with fairly long sections of pluricolumnals being very common. Other echinoderms are common, including the echinoids *Maccoya*, which can rarely be seen articulated but more often as a collapsed heap of plates, and *Palaechinus*, asteroid and ophiuroid ossicles, and blastoids. The remaining fauna includes foraminiferans (including *Archaeodiscus* sp., *Endothyra* sp. and *Tetrataxis* sp.), siliceous sponge root tufts (Plate 4, fig. b), corals (*Zaphrentites* sp.), diverse brachiopods (orthids, spiriferids and strophomenids), bryozoans (*Fenestella* sp., *Fistulipora incrustans*, *Rhombopora* sp., *Sulcoretepora parallela* and trepostomes), spirorbid worm tubes, and the gastropod *Euomphalus pentangulatus*. The limestone beds contain a similar fauna, but the fossils are fragmented (Plate 3, figs a, b) due to pre-depositional transport. In the limestones brachiopods are found overturned from their life positions (Plate 4, fig. a), and crinoid stems are generally completely disarticulated, as are crinoid calyces with the exception of the robust *Platycrinites expansus* (M'Coy); some packstone lenses are almost encrinitic (Plate 2, fig. b). On some limestone bedding surfaces thin shale partings have

revealed long articulated stems of almost 2 m (near Locality BD:C (GR 8193 5957)) (Plate 58, figs a, b; Plate 59, figs a, b; Figure A.28; see Section 6.3, Columnal Taxon Number 28) (Mannifield and Sevastopulo 1998) and 0.91 m (Locality BD:H (GR 8180 5895)) (Figure A.32) in length.

At Locality BD:D (GR 8199 5958) (Figure A.29) a bed of about 3 m thickness (bed BD:D1), which comprises very fossiliferous, calcareous, fissile clay shale with three beds of limestone of a few cm thickness, remains undisturbed. [This bed is the 'flexible shale' (FX herein) of Professors G. D. Sevastopulo and N. G. Lane from which they collected many samples in 1972.] Crinoid calyces and crowns identified from this bed include the microcrinoid *Litocrinus*, *Bundoranocrinus vermiculatus*, *Amphicrinus scoticus*, cf. *Onychocrinus polydactylus* and *Platycrinites expansus*. Above this follows a fossiliferous, calcareous, fissile, clay shale bed of about 1 m thickness (bed BD:D2). Fissility in the shale shows that it is slightly inclined and there is small scale thrusting, normal faulting and folding. Bed BD:D3 above this, a limestone of about 0.25 m thickness, is laterally traceable along the top of the disturbed shale below, but remains undisturbed itself, as do the beds above it. The evidence of deformation in bed BD:D2 leads to the inference that this bed acted as a décollement structure.

Further south in Bundoran, at a stratigraphically younger level in the Bundoran Shale Formation (Locality BD:L (GR 8197 5919)) (Figure A.36), the shales remain calcareous and clay-rich with some limestones interbedded with them. Both are still very fossiliferous (Plate 3, fig. b). Small-scale extensional faulting occurs around this locality.

Higher in the section at Bundoran limestones become subordinate (Locality BD:F (GR 8180 5913)) (Plate 6, fig. a; Figure A.31). They are represented by only thin, discontinuous, limy ribs and they become slightly sandy and less fossiliferous. Fossils are much less abundant in the shales, those present being crinoids, which are marked by a much less diverse columnal assemblage, brachiopods, *Zaphrentites* and bivalves. Rare occurrences of *Skolithos* were noted. At Locality BD:G (GR 8176 5901) the shales are unfossiliferous, although more crinoid ossicles and debris appear towards Locality BD:K (G8179 5898) (Plate 5, fig. a; Figure A.35). Other fauna include bivalves, a few solitary horn corals (Plate 5, fig. b), and *Skolithos* burrows are fairly common (Plate 7, fig. b) and are filled with a brown, iron-rich material. A few layers with a concentration of fauna, mainly corals,

occur within this section. The shales here are micaceous and fairly silty; interbedded with them are a few 20 to 60 mm thick, nodular to continuous limy partings or argillaceous limestones. Calcareous nodules appear in bed BD:H4 (GR 8180 5895) that comprises non-recessive, calcareous, silty shale interbedded with recessive, calcareous, clay-rich shale. Transitions between the shales are gradual. Moving further west and up section the shale becomes siltier and less calcareous and clay-rich, and small siltstone beds of less than 0.10 m in thickness appear (Locality BD:J (GR 8141 5875) (Plate 7, figs a, b; Figure A.34) and Locality BD:I (GR 8124 5880) (Figure A.33)) with a few massive sandstone beds of 10s of cms thickness, which in some places show ball-and-pillow structure. In the last thick argillaceous limestone beds (localities BD:I and BD:J) large productoids, *Delpinea* sp. with hinges of 250 mm across and small caninioids are common on the limestone platforms (Plate 6, fig. b).

Below Rochfort Lodge (Locality RL (GR 7987 5895) (Figures 2.2, A.25) the contact with the overlying Mullaghmore Sandstone Formation is exposed. The shales become more silty and micaceous, although still calcareous, and crinoids are still fairly common, at least in some beds which are represented by concentrations of dissociated columnals. A stem section of 17 mm diameter and at least 0.62 m in length, but of unknown columnal type, was found just below the contact in a calcareous, silty shale bed (N. Connolly, pers. comm. 2000). *Fenestella* and brachiopods are also present. Thin, barren, calcareous sandstone beds are interbedded with the shales.

Along the northwest coast of Co. Sligo, from Easky to Aughris Head, an open anticline exposes the Bundoran Shale Formation in its core (Hubbard 1966*a*). The axis of the anticline is located at Portmore (Locality CM:Hinge (GR 4547 3439)) (Figure A.14) between Pollnadivva Pier and Pollbrean near Carrowmoran. The Bundoran Shale Formation crops out from the axis to GR 4530 3453 on the northern limb. Although only a few m of the upper part of the formation crop out the nature of the formation here is very different to the type section at Bundoran. The shales are calcareous and clay-rich and they do not get noticeably siltier high up in the formation even though siltstones, as well as limestones, are interbedded with them. About 2 m below the contact with the overlying Mullaghmore Sandstone Formation the formation contains many shell beds of 10 to 30 mm thickness. The shelly fauna includes high-spired gastropods and orthocones. This fauna is very different to that seen elsewhere within the formation.

The taphonomy of the relatively undisturbed fossils in the clay shales of the lowermost units of the Bundoran Shale Formation at the type locality suggests background deposition in quiet marine water conditions. The colour and faunal content of the shales suggest that they were deposited below wave base on an open marine shelf (Tucker 1991). This was intermittently interrupted by higher energy conditions, represented by the sharp-based limestones, when storm currents disturbed and fragmented the fauna. The silty shales with fewer body fossils followed by the introduction of sporadic laminated siltstones with burrows towards the top of the formation show a typical coarsening-upward sequence of a delta-front (Tucker 1991) and signals a regression. The ball-and-pillow structure indicates syndepostional or early postdepositional deformation as a result of a small seismic event. The entire formation has been interpreted as pro-deltaic, representing the first indication of the distal influx of terrigenous sediment (Sevastopulo 1981; Mannifield and Sevastopulo 1998); it is overlain by the fully deltaic Mullaghmore Sandstone Formation (Sevastopulo 1981). The fauna and a Pu Biozone miospore assemblage indicate an Arundian age for the Bundoran Shale Formation at the type locality (George *et al.* 1976; Philcox *et al.* 1992).

2.4.3. MULLAGHMORE SANDSTONE FORMATION

The Mullaghmore Sandstone Formation (Calp Sandstone) is a clastic dominated facies in a generally carbonate-dominated Dinantian succession and comprises grey feldspathic sandstones, locally with pebbles, grey shales and uncommon limestones (Graham 1996; Sevastopulo and Wyse Jackson 2000). The use of the local name Carrowmoran Sandstone (Hubbard 1966*a*, 1966*b*) for the same unit in northwest County Sligo is not followed here.

The basal contact of the Mullaghmore Sandstone Formation with the underlying Bundoran Shale Formation at Rochfort Lodge (Locality RL (GR 7987 5895)) is marked by the gradual appearance of thick, laterally continuous, locally massive calcareous sandstones, sometimes with pebbles. Similar thickly bedded sandstones are seen at the contact at Portmore, east of Pollnadivva at Carrowmoran (GR 4547 3439 (Locality CM:Hinge)) (Figure A.14), but the contact there is more gradual with shales interbedded with thinner calcareous sandstones.

On the eastern limb of the Carrowmoran anticline near Doonycoy (Locality DC1 (GR 4670 3441)) (Figure A.15) the uppermost bed of the formation is a sandstone containing large

angular pebbles of quartz and other lithoclasts.

At Carrickphatrick (Locality CP1 (GR 4395 3513)) (Plate 10, fig. b; Figure A.12) the uppermost beds of the formation comprise sandy limestones of 0.20 to 0.50 m thickness, which contain a limited fauna including *Siphonodendron sociale* (Phillips), and equal thicknesses of black, very fissile calcareous shales containing few crinoid ossicles (Figure A.13). The boundary with the overlying Benbulben Shale Formation is sharp.

The lowermost beds of the Mullaghmore Sandstone Formation have been interpreted as having been deposited in shallow marine waters (Graham 1996) indicated by the continuing presence of crinoid and other marine fauna. A substantial part of the remainder of the formation is also clearly of marine origin as evidenced by limestones and sedimentary features such as wave ripples. There is a rich ichnofauna in the shales that occur such as *Cruziana*, *Diplocraterion* and *Skolithos* (Buckman 1992). Fluvial deposits have been identified in coarse-grained channel sandstones with cross-strata, which have a palaeocurrent direction indicating sediment influx from the north-northwest (Graham 1996). Owing to the facies sequence and the presence and types of marine body fossils within the facies Sevastopulo and Wyse Jackson (2000) suggested a marine to marginal marine environment of deposition in an overall deltaic sedimentary setting (Hubbard 1966*a*; Sevastopulo 1981). Around Doonycoy the pebbly sandstone is the pebbly lag of Graham (1996), which he interpreted to represent a rapid rise in sea level that occurred towards the top of the formation. George *et al.* (1976) considered the Mullaghmore Sandstone Formation to be Holkerian in age. However, spore samples from outcrop at Mullaghmore and Carrowmoran (Higgs 1984) and from boreholes in County Leitrim (Philcox *et al.* 1992) have yielded TS Biozone miospore assemblages, which are thought to indicate a late Arundian to Holkerian age (Riley 1993).

2.4.4. BENBULBEN SHALE FORMATION

The Benbulben Shale Formation (the Upper Calp Shale of the original Geological Survey) is dominated by dark grey, clay-rich, calcareous shales with subordinate argillaceous limestones, and thicker bioclastic limestones that become more common towards the top of the formation when shales become subordinate. It is similar to the stratigraphically older Bundoran Shale Formation, but the shales are more calcareous and less fissile and generally lack silty horizons. The shales contain especially abundant and diverse crinoid

columnals, as well as calyces of *Onychocrinus polydactylus*. In addition, they contain a rich, fully marine fauna including bryozoans (*Fenestella* sp. and trepostomes), brachiopods (*Spirifer*, productoids and others), corals (*Zaphrentites* sp., *Palaeosmilia* sp., *Siphonophyllia* sp. and small caninioids) and ossicles of the echinoid *Maccoya*. The shales lower down in the formation have a tendency to be more fossiliferous. The limestones contain a similar fauna to the shales, but the fossil material is not easy to isolate from the matrix.

East of Barnarobin (Locality BB (GR 6865 4570)) (Figure A.22), below the southwestern corner of Benbulben Mountain (Plate 8), there is a steep outcrop face of about 10 m high (Plate 9, fig. a) on the slope. The limestone ribs average about 0.10 m in thickness with fissile grey calcareous shales predominating. Here columnals fall out of the soft shales and come to rest on the sheep tracks (Plate 9, fig. b), making bulk sampling simple. Columnals of Columnal Plesions A and B are common here. Other fauna include echinoids (indicated by disarticulated ossicles), brachiopods (*Spirifer* sp. and productoids), corals (*Zaphrentites* sp. and *Siphonophyllia* sp.), bryozoans (*Fenestella* sp. and trepostomes), gastropods and spirorbid worm tubes.

At Tievebaun two stream sections (Localities TM1 and TM2 (GR 7694 5105) and Localities TM3 and TM4 (GR 7745 5092), on the Leitrim-Sligo county boundary) (Figure A.24), where there is a complete section of 99 m of the Benbulben Shale Formation exposed (MacDermot *et al.* 1996), limestones are especially subordinate. Again the soft shales are very fissile and contain abundant fossil material. Crinoid columnals are the dominant bioclasts.

The lowest beds of the formation are represented at Carrickphatrick at localities CP1 and CP2 (GR 4395 3513 and GR 4393 3512) (Figures A.12, A.13) in a stream section of which the lowermost beds are occasionally covered by the water when the stream level, or tide, is high (Plate 10, fig. b). They comprise grey, calcareous, clay-rich shales that contain crinoid columnals, bryozoans (*Fenestella* sp. and trepostomes) and brachiopods, which are interbedded on a small scale (beds are a few cms thick) with bioturbated bioclastic limestone ribs whose high content of bioclasts comprise mostly crinoid columnals, with some small corals and brachiopods. In the west of the bay at Locality CP3 (GR 4366 3522) a cliff section of about 9 m high (Plate 10, fig. a) consists entirely of the Benbulben Shale Formation. Again, clay-rich shales are interbedded with limy ribs and the fauna are

similar as at the other Carrickphatrick localities, but a gastropod *Euomphalus* sp., ?sponge spicules and productoids have been identified.

The formation at Doonycoy (Locality DC1 (GR 4670 3441)), on the east of the anticline (at CM:Hinge) (Figure A.15), is thinner than on the western limb although the boundary with the overlying Glencar Limestone Formation is unclear, just as it is on the western limb. The lower part of the formation comprises interbedded shales with subordinate limestones with the proportion of limestones increasing upwards.

At Streedagh (localities STa and ST1 to ST5) (Plate 11; Figures A.18, A.19, A.20.*a-f*) the formation is represented by about 45 m of interbedded shale and limestone, but the lower contact is not seen. The shales are generally very clay-rich, calcareous and not particularly fissile. At some horizons, however, the shales are silty and barren mudrocks occur. The limestones are commonly argillaceous, usually bioturbated and may be wavy-bedded. Silty limestones occur, generally with parallel or cross laminations and commonly with burrows. The interbedded limestones and shales vary from 0.10 m to only a few cms in thickness, and in the latter case the limestones are more argillaceous and the shales less calcareous and recessive. Fossils are present throughout the formation and are especially abundant in much of the shales. The fauna include corals (*Zaphrentites* sp. and small caninioids), brachiopods (*Spirifer* sp. and productoids), bryozoans (*Fenestella* sp. and trepostomes) and the trilobite ?*Brachymetopus* sp.. Crinoid columnals are very common as disarticulated specimens, but are not fragmentary, and columnals from Columnal Plesion A are especially common. The fossils in some cases are siliceous, or pyritised. Towards the top of the section (Locality ST5 (GR 6331 5126)) (Figures A.20.*d-f*), just to the east of the boathouse, fossils in general become less common. Columnals are rarely found and when they are present they are very small (less than 50 mm diameter). *Zaphrentites* sp. and small caninioids seem to be the only other body fossils; bioturbation and burrows also occur. The limestones become thicker, cleaner and more flaggy or wavy-bedded from hereon with the transition up into the Glencar Limestone Formation.

A platform at the base of a small cliff marks the contact between the Benbulben Shale Formation and the overlying Glencar Limestone Formation at Serpent Rock (localities SR1 to SR4) (Figure A.17). Trepostome bryozoans seem to disappear at the upper contact with the younger formation.

A sharp contact occurs between the Mullaghmore Sandstone Formation and the overlying Benbulben Shale Formation, and this is probably representative of a major flooding surface (Sevastopulo and Wyse Jackson 2000). The lithological sequence is the representation of the onset of a marine transgression with open marine shelf mudrocks interbedded with carbonate ramp limestones (see Tucker 1991). The boundary between the Benbulben Shale Formation and the overlying Glencar Limestone Formation is harder to determine than the basal contact of the formations. The boundary is very gradual (as mentioned by Hubbard *et al.* 1965) as limestones occur interbedded with the shales near the top of the unit, at the base of the unit and also at some points within the unit. The upper part of the formation in the Slisgarrow-Big Dog area (MacDermot *et al.* 1996, figure 17), to the east of the Ox Mountains, is thought to interfinger with the younger Glencar Limestone Formation on a large scale (Philcox *et al.* 1992), which may explain the difficulty faced when trying to identify the boundary between the two formations in the Sligo Syncline. In Sligo, at Benbulben Mountain and Tievebaun Mountain, the TS Biozone miospore assemblage occurs in the lower part of the formation indicating a Holkerian age and the TC Biozone miospore assemblage occurs in the upper part of the formation indicating an Asbian age (Higgs 1984). The TC Biozone assemblage also occurs in the Slisgarrow borehole (Philcox *et al.* 1992). George *et al.* (1976) mentioned that the upper part of the formation also yields corals of Asbian age.

2.4.5. GLENCAR LIMESTONE FORMATION

The Glencar Limestone Formation (Upper Limestone) is comprised of argillaceous, often bioturbated limestone interbedded with subordinate calcareous mudrock or shale (Oswald 1955; Hubbard *et al.* 1965; Philcox *et al.* 1992), which becomes very uncommon in the higher part of the formation. It is thought to be cyclic where it was measured around Benbulben Mountain, Glencar and the Swiss Valley in north Sligo (Schwarzacher 1964). Fossils are abundant locally and consist mainly of the corals *Siphonophyllia* sp., *Syringopora* sp., *Siphonodendron* sp., *Lithostrotion* sp. and *Caninia* sp., along with large productoids. Crinoid debris is relatively uncommon. The fossils are generally silicified.

The Glencar Limestone Formation is exposed around the headland at Lackavarna (Locality LV:1 (GR 4279 3581)) (Figure A.10). The section here consists of a sequence of calcareous, ferrous, clay-rich shales and limestones interbedded generally on a 0.10 m scale, although at some levels the beds are only a few cms thick (Figure A.11.). The

limestones are commonly bioturbated and contain crinoid ossicles, large *Spirifer* sp., large productoids and some large caninioids. The shales contain an abundant and diverse fauna of crinoid ossicles that are easily picked out of the soft, clay-rich rocks. They also contain bryozoans (*Fenestella* sp. and trepostomes), brachiopods (*Spirifer* sp. and productoids), caninioid corals, and a few bivalves and gastropods. *Zaphrentites* sp. and *Zoophycos* also occur in both lithologies. The body fossils are often pyritised, especially around the vicinity of the intruded Tertiary dykes. Moving higher up section the amount of limestone increases with the thickness of beds also generally increasing. The shale, although still very clay-rich, also becomes silty up section. Neither the lower or upper contact was observed. In the bed LV:1 at Lackavarna marine ostracods are present in the limestones and some of the limestones are tabular and laterally traceable.

At Serpent Rock (localities SR1 to SR4) (Figure A.17) thick (more than 0.10 m thick), wavy-bedded, at some levels argillaceous, limestones are interbedded with thin mudrocks. Both lithologies contain *Siphonophyllia* sp. and thickets of *Siphonodendron* sp., the latter commonly comprising entire shale thicknesses; individual colonies may be laterally extensive measuring over 2 m in diameter in some occurrences. Large inverted productoids are present, as well as crinoid columnals, which generally measure over 10 mm in diameter, *Fenestella* sp. and *Caninia* sp.. Small, thin thickets of crinoid debris (smaller columnals) with horn corals occur locally.

At Streedagh Point the transition of the Glencar Limestone Formation with the underlying Benbulben Shale Formation is exposed (Figure A.18). The transition occurs at localities ST5 (GR 6331 5126) (Figure A.20.*d-f.*), directly outside the boathouse, ST9 (GR 6281 5023) and ST10 (GR 6290 5030) (Figure A.21). Lithologically shales become subordinate, measuring about 0.10 m thickness in the lowest beds and then becoming only a few cms thick further upwards in the section. Limestones become thicker (10s of cm thick) and they are clean, flaggy, and hard and splintery when hammered. They become thicker and wavy-bedded further up in the section. Bioturbation occurs in the base and uppermost portions of the wavy-bedded limestones. The central portion of each of these beds appears not to be bioturbated and contains bioclasts, especially in the lowest part. The three portions are delineated by planar contacts whereas the unit itself has hummocky upper and lower surfaces. This implies three stages of deposition occurred within the unit, the central one being deposited in higher energy conditions, although all were

deposited in turbulent waters. Along with the introduction of the clean, thickly bedded flaggy and wavy-bedded limestones come a distinct fauna that consists mainly of large caninioids and colonial corals. At localities ST6, ST7 and ST8 *Siphonophyllia* sp. is very common covering many of the exposed bedding surfaces. They may measure up to 90 mm in diameter and 0.66 m in length. *Lithostrotion* sp. and smaller *Siphonodendron* sp. occur as very large colonies together with *Siphonodendron sociale* (Phillips) and *Siphonophyllia* sp.. However, some bedding planes have concentrations of inverted large productoids on their upper surfaces. Where crinoid columnals appear in the limestones they measure over 10 mm in diameter. All these elements of the fauna are also seen as debris within the limestone units, but are not particularly common and are hard to identify. In the subordinate shale beds, which are recessive, tiny (less than 5 mm diameter) crinoid columnals occur together with brachiopods. Both faunal elements are few in number.

Phanocrinus cf. *calyx* has been found at two localities (approximately GR 7668 5082 and GR 7520 4224), in what is probably the Glencar Limestone Formation.

The sequence is marine and was deposited in a similar environment to that of the Benbulben Shale Formation, which it succeeds. The coral fauna of the Glencar Limestone Formation indicates an Asbian age.

2.4.6. DARTRY LIMESTONE FORMATION

The Dartry Limestone Formation comprises two main facies. First are the carbonate mudmounds (mudbanks/'reefs') whose slopes can be seen to dip at approximately 45° at their edges (Gleniff (Figure A.23)). These Waulsortian-like mudmounds contain a diverse fauna including productoids, bryozoans, goniatites and blastoids, but corals are rare (Sevastopulo and Wyse Jackson 2000). The second facies is the well-bedded, fine-grained, argillaceous, dark, cherty limestones (Oswald 1955; Schwarzacher 1964; Hubbard *et al.* 1965; Philcox *et al.* 1992; Sevastopulo and Wyse Jackson 2000), the chert bands and nodules delineating the bedding (MacDermot *et al.* 1996). Corals are common in the limestones and are commonly silicified. They include *Lithostrotion* sp., *Clisiophyllum* sp., *Dibunophyllum* sp., and some solitary forms (Sevastopulo and Wyse Jackson 2000) such as caninioids that are uncommon (Hubbard *et al.* 1965). The two facies indicate a fully marine environment with deeper waters than during the deposition of the Glencar

Limestone Formation. The coral fauna with *Dibunophyllum* sp. and an NM Biozone miospore assemblage from the Slisgarrow borehole indicates an Asbian age (Philcox *et al.* 1992; Sevastopulo and Wyse Jackson 2000).

2.4.7. MEENYMORE FORMATION, GLENADE SANDSTONE FORMATION AND YOUNGER DINANTIAN UNITS

Although float material of the Meenymore Formation occurs on the top of the Dartry Mountains, there are no good outcrops (G. D. Sevastopulo, pers. comm. 2000). The Glenade Sandstone Formation is a deltaic sandstone unit that does not contain marine fossils, but which does include plant material (Sevastopulo and Wyse Jackson 2000). There are no complete sections of the formation in the Sligo or Leitrim areas (MacDermot *et al.* 1996). Younger formations have been removed by erosion in County Sligo.

2.5. THE NORTH MAYO SUCCESSION

2.5.1. MINNAUN FORMATION

In north Mayo the Minnaun Formation overlies unconformably the Dalradian basement (Figure 2.3) and is exposed in cliff sections at Downpatrick Head (Graham 1996, Fig. 13) and Bunatrahir Bay (Long *et al.* 1992; Graham 1996, Fig. 4; Sevastopulo and Wyse Jackson 2000). It is comprised of mainly medium to coarse-grained sandstones that were deposited by southeast-flowing rivers (Sevastopulo and Wyse Jackson 2000). Subordinate mudrocks are present in the lower part of the formation that become increasingly significant upwards (Graham 1996).

2.5.2. DOWNPATRICK FORMATION

At Downpatrick Head about 90 m of the Downpatrick Formation is exposed in the cliff section and it appears to thin westwards (Graham 1996). Outcrops west of Ballina contain a mixture of pale grey sandstones and calcareous siltstones, with lesser amounts of dark grey fine-grained limestone (Long *et al.* 1992).

At Downpatrick Head (Locality DP1 (GR 1231 4273)) the contact between the Downpatrick Formation and the overlying Moyny Limestone Formation occurs (Figures A.2, A.4). A micaceous sandstone forms the lowest accessible bed at the cliff top. This is followed by a slightly silty, calcareous shale and a lime mudstone which is bioturbated

and similar to a lime mudstone seen at Locality DP2 (GR 1265 4291), except there the bed contains gastropods, apparently the most abundant fauna, brachiopods, crinoid columnals and burrows. The sequence at Locality DP1 (Figure A.3) continues up through fully marine limestones and then into marginal marine sandstones, shown by the cross-bedding in the uppermost unit and crinoid columnals and gastropods.

The formation comprises near-shore marine mudrocks and siltstones, deltaic and alluvial sandstones and siltstones, and fully marine interbedded bioclastic limestones and calcareous shales. Micritic palaeosols contain no fauna and are thus evidence for exposure (Graham 1996). However, most of the other micrites are tabular and contain fauna such as ostracods and gastropods, and are bioturbated. These are thought to have formed in lagoonal waters of abnormal salinity (Graham 1996) and overall the facies are interpreted as marginal marine with a tidal influence (Sevastopulo and Wyse Jackson 2000). The formation is evidence for a marine transgression representative of the gradual transition into the overlying fully marine Moyny Limestone Formation. The formation is older than early Viséan, probably late Courceyan to lower Viséan in age.

2.5.3. MOYNY LIMESTONE FORMATION

At Downpatrick Head the Moyny Limestone Formation (Moyny Point Member of Long *et al.* 1992) is represented by interbedded tabular bedded, fossiliferous limestones and subordinate calcareous shales, and the base is taken to be where these facies begin to dominate (Locality DP1 (GR 1231 4273)) (Long *et al.* 1992; Graham 1996). About 50 to 75 m of the formation is present around the Downpatrick headland with thinning to the west, probably due to erosion and non-deposition (Graham 1996).

At localities DP3a (GR 1277 4282) and DP3b (GR 1284 4280) (Figures A.2, A.4), in a natural 'amphitheatre', the formation is represented initially by a micrite pavement that forms the base of the 'amphitheatre'. This measures about 1.3 m in thickness and the surface reveals *Syringopora* sp. with fragments of crinoid columnals and brachiopods. Above this a very fissile, calcareous, silty shale occurs which dips at a greater angle that the beds above and below. Columnals are present, but are by no means abundant occurring only sporadically, and appear to be monotypic. A few limy partings occur at the base of the shale, while nearer the top 0.10 m thick laminated siltstones from the bed above interfinger. This unit contains more than one type of crinoid columnal morphospecies. A

calcareous shale with septarian concretions occurs above followed by a calcareous sandstone that is fully marine as shown by the fauna present. No fossils occur in the non-calcareous silty shale interbedded with siltstone that lies at the top of the section.

The sequence of sediments is interpreted as representing fully marine conditions (Long *et al.* 1992; Sevastopulo and Wyse Jackson 2000). Although the facies are dated as post-Courceyan in age (early Viséan (Sevastopulo and Wyse Jackson 2000)), all appearing to belong to the Pu miospore Biozone (Higgs *et al.* 1988), this biostratigraphical knowledge does not yet allow a precise correlation of the carbonates (Graham 1996). There is no evidence of Arundian foraminiferal faunas (G. D. Sevastopulo, pers. comm. 2000).

2.5.4. MULLAGHMORE SANDSTONE FORMATION

To the west of Killala Bay the Mullaghmore Sandstone Formation succeeds the Downpatrick Formation where it comprises sandstones, flagstones and siltstones (Long *et al.* 1992). In the west, around northwest Mayo, fluvial channel sands are most common and in the east marine facies are more common (Graham 1996).

The upper contact of the Mullaghmore Sandstone Formation with the overlying Ballina Limestone Formation is seen at Kilcummin Head on the east (Locality KK3 (GR 2112 3800)) and the northwest (Locality KK4 (GR 2068 3826)) of the headland (Figures A.5, A.6). Fully marine sandstones are overlain by very different rocks in the uppermost 2.4 m of the formation which, are seen especially well at the eastern locality. Here, the last fully marine, massive calcareous sandstone is laterally traceable around the cliff with a constant thickness of about 1.5 m. Above this is a sequence of intensely bioturbated, light green, calcareous mudrocks and thinner sandy limestones. The highest mudrocks sometimes contain ostracods and the foraminiferan *Endothyra*, and often have wide burrows. Some of the limestones contain crinoid ossicles and brachiopods. A coarse, sandy, bioclastic limestone that overlies this facies marks the abrupt contact with the Ballina Limestone Formation.

The Mullaghmore Sandstone Formation is representative of a major advance of river deltas from the north (Long *et al.* 1992), except for the uppermost few m. Graham (1996, Fig. 25) has pointed out that the micritic rocks in the uppermost few m of the formation are palaeosols and that the burrows are representative of marine conditions. At

Kilcummin Head and Bunatrahir Bay the age of the oldest foraminiferan is late Arundian (Graham 1996).

2.5.5. BALLINA LIMESTONE FORMATION

The Ballina Limestone Formation is comparable to the Glencar Limestone Formation of the Sligo succession (Sevastopulo and Wyse Jackson 2000) (see Section 2.3.5). It comprises mainly well-bedded, sometimes wavy-bedded, dark-grey, fine-grained limestones and dark grey calcareous marine shales. In the lower part of the succession (Ballina Limestone Formation (Lower) of MacDermot *et al.* 1996) calcareous shales are as thick as the dark grey fine-grained muddy limestones with which they are interbedded, but the shales become subordinate and are interbedded with cleaner limestones higher up in the succession (Ballina Limestone Formation (Upper) of MacDermot *et al.* 1996) (Long *et al.* 1992). Chert bands or nodules may occur (Long *et al.* 1992). In the lower part of the formation caninioids and *Siphonodendron* sp. occur with *Lithostrotion* sp. appearing in the upper part (MacDermot *et al.* 1996). *Zoophycos* is a common trace fossil (Graham 1996; MacDermot *et al.* 1996).

At Kilcummin Head (GR 2094 3835 (Locality KK1) and GR 2086 3834 (Locality KK2)) (Figure A.5) the platform on the cliff top is formed by a coarse, sandy, bioclastic limestone that contains small, angular quartz pebbles. The upper surface is hummocky, which is thought to be a diagenetic feature rather than being the form of the seabed at the time of deposition (J. R. Graham, pers. comm. 1999). The limestone contains a varied fauna including *Zaphrentites* sp., a few *Siphonophyllia*, cerioid ?*Michelinia* sp., *Fenestella* sp. and crinoids, which are seen as dissociated and fragmentary ossicles. At localities KK3 (GR 2110 3800) (Figure A.6) and KK4 (GR 2068 3826) in cliff sections this same limestone bed has a sharp contact with the shales below. Large bioclasts and small, angular quartz pebbles suggest that the bed represents a lag deposit formed on a major flooding surface (J. R. Graham, pers. comm. 1999). This bed is taken as the basal contact of the Ballina Limestone Formation with the underlying Mullaghmore Sandstone Formation by MacDermot *et al.* (1996) and is therefore representative of the Ballina Limestone Formation (Lower).

To the south of Kilcummin Head there is a small cliff section at Ballinlena Pier (Locality BL (GR 2130 3680)) (Figures A.5, A.7) which exposes interbedded sandy and non-sandy

bioclastic limestones and silty calcareous shales, all of which vary in thickness. Fauna within these beds include some large productoids and other brachiopods, large *Siphonophyllia* sp., *Zaphrentites* horn corals, dasyclad algae, *Fenestella* sp., *Endothyra* sp. and dissociated crinoid ossicles, which are especially abundant in the shales, but seen only as fragmentary remains in the limestones. *Lithostrotion* corals are present on the limestone platform surfaces on the foreshore. Owing to their lithology and faunal content, the rocks at this locality are representative of the Ballina Limestone Formation (Upper).

At Kilrusheighter (Locality PG (GR 4835 3503)) (Figure A.16) there are interbedded sandy limestones of 0.20 to 0.30 m in thickness and calcareous shales of less than 0.10 m thickness. Some of the limestone beds are hummocky on both their upper and lower surfaces, and some have only hummocky lower surfaces with more planar upper surfaces. Some limestones are bioturbated throughout, and some only near the top of the bed. The limestones contain horizontal to slightly oblique *Siphonophyllia* sp., *Lithostrotion* sp., smaller fasciculate *Siphonodendron* sp. together with the larger *Siphonodendron sociale* (Phillips) and large inverted productoids. Several gastropods were observed in one bed. Crinoid ossicles were seen mainly as fragmentary remains. The shales in-between contain large (80 mm diameter) horizontal *Siphonophyllia* sp. and some of the shales appear to contain fairly abundant crinoid ossicles. The fossils are silicified. This is part of the Ballina Limestone Formation (Upper).

On the foreshore at Easky (Locality EY1 (GR 3876 3857)) (Figure A.8), County Sligo, the Ballina Limestone Formation (Upper) is represented by bioturbated, thick (0.20 to 0.75 m thick), wavy-bedded limestones with hummocky upper and lower surfaces, which are interbedded with subordinate muddy shale partings of less than 0.15 m thickness (Figure A.9). At this locality limestones are cleaner and more thickly bedded and shales are much less common and thinner than in the Ballina Limestone Formation at Kilcummin Head and Ballinlena Pier. However, they still show bioturbation. Large *Siphonophyllia* sp. occur in both shales and limestones and appear to have a horizontal attitude in both cases. However, this apparent horizontal attitude of all these corals may be due to diagenesis. Upper surfaces of limestones also reveal *Siphonodendron sociale* (Phillips), *Lithostrotion* sp. and *Siphonophyllia* sp.. Few large (more than 10 mm diameter) crinoid columnals occur within the limestones along with large productoids and trepostome bryozoans. Crinoids are also seen as fragmentary remains, but are not a major component of the limestones.

Other fauna include the microfossil *Sphaerinvia* (*incertae sedis*).

The Ballina Limestone Formation represents a change to fully marine conditions (Long *et al.* 1992) from the underlying fluviodeltaic Mullaghmore Sandstone Formation. Deposition occurred on a carbonate shelf (Long *et al.* 1992) as represented by the limestones and muddy shales, the limestones representing times of higher energy conditions. Fauna occurring at the base (Graham 1996) and just above the base (MacDermot *et al.* 1996) of the Ballina Limestone Formation indicate Asbian age.

CHAPTER 3
MATERIALS AND PROCESSING METHODS

3.1. SAMPLING

3.1.1. INTRODUCTION

This study is based on material collected from several formations (Downpatrick Formation, Moyny Limestone Formation, Ballina Limestone Formation, Bundoran Shale Formation, Mullaghmore Sandstone Formation, Benbulben Shale Formation and Glencar Limestone Formation), mainly calcareous shales and limestones, from the Lower Carboniferous of Counties Donegal, Leitrim, Sligo and Mayo in northwest Ireland (see Chapter 2 and Figures 2.1, 2.2, 2.3). Many of the beds sampled, especially the shales, had previously been shown to contain abundant fossil crinoid material, and in particular units (the Glencar Limestone Formation) corals had been previously well documented (Hubbard 1966*b*, 1970).

In the present study it has been found that corals, crinoids, brachiopods and bryozoans are particularly common, along with echinoids, ophiuroids, blastoids, foraminiferans, gastropods and sponges (see stratigraphical logs in Appendix A). During, and following, sampling it was apparent that the shales of the Bundoran Shale and Benbulben Shale Formations yielded the most crinoid material of all the sampled formations. Thus, samples collected from these formations are the ones that have been studied in depth in this study.

3.1.2. METHOD

The localities chosen to be sampled were studied in the literature (see M'Coy 1844; W. B. Wright 1913; Hubbard *et al.* 1965, 1966*a*, 1966*b*, 1970; Sevastopulo 1969; MacDermot *et al.* 1983; Long *et al.* 1992; MacDermot *et al.* 1996; Graham 1996). The sites were visited and their localities as names and grid references were recorded (see Appendix B). Beds were measured and their lithology determined as far as was possible in the field. Lithological logs were drafted at localities where it was practicable (Appendix A); for other exposures a description of the outcrop was recorded. Samples of shales, and to a lesser extent limestones and siltstones, were collected, sealed in sample bags and immediately labelled. Large bulk samples of shale (approximately 3 to 4 kg) were collected wherever possible.

However, where this was not practicable smaller samples were collected by picking visible fossil material out of the rock. To avoid contamination sample bags were used only once.

Samples were labelled according to their geographical position and, where appropriate, with some reference to their position within a lithological log. These samples have been inserted into stratigraphical logs in Appendix A.

3.2. PROCESSING

3.2.1. INTRODUCTION

Several methods of processing material were employed to achieve optimum cleaning of crinoid fossil fragments before specimens were suitable for examination by microscopy and subsequent plate production. Limestones, siliciclastics and, where possible, shales were thin sectioned for petrographical analysis of the rocks. For a brief outline of extraction and cleaning processes used on particular samples see Appendix F.

3.2.2. QUATERNARY-O SHALE DISAGGREGATION

3.2.2.1. Introduction

Quaternary-O is a "high molecular weight quaternary ammonium surface-active agent" (Zingula 1968), *i.e.*, a cationic surfactant (a surfactant reduces the surface tension of a liquid). Unfortunately, commercial production of Quaternary-O has ceased, but there were sufficient stocks in the Department of Geology, Trinity College to allow completion of this project. It works as a material for disaggregating shales by physically adsorbing carbon chain molecules into pore spaces of the rock (Peterson *et al.* 1983) that essentially breaks the rock up. The process involves the boiling of shales in a weak solution of Quaternary-O and water as described by Zingula (1968) and Peterson *et al.* (1983). The technique was modified from that previously described by those authors by altering the duration that the shales were boiled. In addition the material was subsequently soaked for prolonged periods of time in the Quaternary-O solution.

3.2.2.2. Method

A quarter to half a teaspoon (approximately 2 to 3 ml) of Quaternary-O was dissolved in a small amount of hot, but not boiling, water in a glass beaker before being added to about

one litre of water in a heavy-bottomed enamel pan. The solution was fairly weak as Peterson *et al.* (1983) suggested that too high a concentration reduces the effectiveness of the surfactant. Pieces of shale measuring up to 60 mm across and 20 mm thick, and only enough to cover the bottom of the pan, were immersed in the solution, and the pan was then placed on a gas-ring within a fume cupboard for further heating. After reaching boiling point the mixture was simmered for about one-and-a-half hours. Zingula (1968) suggested that samples should not be boiled for more than one hour because longer periods of immersion in Quaternary-O would result in the etching of the carbonate fossils. Etching of the crinoid ossicles did not occur in samples processed in this study. As water evaporated it was regularly replaced by adding fresh water in an attempt to maintain a constant volume of about one litre. To encourage disaggregation of the shale, and to prevent it sticking to the base of the pan, the mixture was agitated by stirring approximately every ten minutes with a metal rod. Scum that collected on the surface of the solution was removed as it formed. After ninety minutes the heat was removed and the mixture was left to cool down. Where the shale had not broken down substantially, the samples were left for up to a week in the solution to 'soften' them further. These samples were stirred every day to encourage the breakdown of the shale and, by the end of the week, the shale was soft enough to be broken up completely by hand, and this was carried out while the shales were still wet[1].

Once disaggregation was complete the samples were washed and sieved. The sieves used were 20 mesh (largest aperture dimension of 750 μm), 60 mesh (largest aperture dimension of 250 μm), and 120 mesh (largest aperture dimension of 125 μm). The 20 mesh sieve was placed over the 60 mesh sieve, which, in turn, was placed over the 120 mesh sieve. The rock and Quaternary-O mixture was poured into the uppermost sieve, ensuring that all the sediment from the bottom of the pan was flushed out into the sieve using water. Continual flushing of water and agitation allowed separation of the samples into fractions. The residue of each fraction was washed into a filter paper and left to dry slowly in an oven.

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[1] Although etching occurs with prolonged boiling in Quartenary-O (Zingula 1968), this does not happen when the shales are simply soaked in the solution.

3.2.2.3. Problems

This method was particularly time consuming as the pan had to be supervised continuously. Although this process left ossicles free of the shale matrix, the articular facets of many of the specimens were still unclear, being obscured by a calcareous clay matrix. This was further removed by scrubbing the specimens with a soft toothbrush in a weak solution of water and household detergent, or by using one or more of the following methods.

3.2.3. HYDROGEN PEROXIDE CLEANING

3.2.3.1. Introduction

This process involved the immersion of relatively clean crinoid ossicles, which had been hand picked from shale or had been treated with Quaternary-O, in a hydrogen peroxide bath. The immersion time of the specimens was dependent on a) the clay or mud content of the shale from which the sample had been taken, b) the strength of the hydrogen peroxide (20% or 30% by volume), and c) the amount of matrix obscuring the morphological details. For some samples from the Benbulben Shale Formation (locality BB), where the fossils were in a particularly delicate state, this process was the only option for cleaning the ossicles. Had they been put into hydrofluoric acid they would have been destroyed.

3.2.3.2. Method

Samples were placed in a glass beaker and hydrogen peroxide was added until the material to be cleaned was completely covered. The amount of specimens in the beaker at any one time generally covered no more than half the bottom of the beaker, as many more would have hindered the cleaning of the specimens. The concentration of the hydrogen peroxide was either 20% or 30% by volume. Specimens were left until effervescence ceased. Effervescence in 20% solution was not particularly vigorous and it usually took a few hours for it to stop. At a concentration of 30% the effervescence was more vigorous so specimens were left in the solution for a shorter period of time. In both cases, following washing in tap water specimens were brushed with a soft toothbrush in water, which commonly cleaned their surfaces sufficiently for study.

3.2.3.3. Problems

Where specimens were left in the solution for a long period of time, especially at the

higher concentration, their surfaces became etched. This occurred even when using the lower concentration when all reaction (effervescence) appeared to have ceased.

The hydrogen peroxide treatment removed only the most loose matrix. It was found that some specimens were not sufficiently cleaned during this process so they were subsequently treated with acid by one of the following techniques.

3.2.4. HYDROFLUORIC ACID CLEANING AND ALTERATION OF CALCITE TO CALCIUM FLUORIDE

3.2.4.1. Introduction

This technique was first described by Cookson and Singleton (1954) for rendering calcareous translucent microfossils. It was subsequently used by Grayson (1956) for the same purpose, by Sohn (1956) in ostracod studies, and by Upshaw *et al.* (1957) on microfossils who termed the process "Fluoridization". The successful use of hydrofluoric acid in the preparation of echinoderm material has been demonstrated by Sprinkle and Gutschick (1967) for blastoids, and by Sevastopulo and Keegan (1980) for revealing the stereom microstructure of fossil crinoids.

The process involves the immersion of calcitic, fossil crinoid material with adhering clay minerals in hydrofluoric acid. The hydrofluoric acid dissolves the clay minerals and converts the calcite to fluorite by the following reaction:

$CaCO_3$	+	2HF	=	CaF_2	+	CO_2	+	H_20
Calcite (Limestone)	+	Hydrofluoric Acid	=	Calcium Fluoride	+	Carbon Dioxide	+	Water

3.2.4.2. Method

Crinoid ossicles (and other calcitic fossils) were placed in small polythene beakers. The beakers were placed in a fume cupboard in a palynology laboratory and hydrofluoric acid was poured into them until the material was completely covered. When all the clay matrix had been dissolved the hydrofluoric acid was safely disposed of and the samples were washed by decanting them in water at least eight times. Towards the end of the washing phase powdered calcium carbonate was added to the water in the beakers to neutralise fully any acid that may have still been present within the pores of the stereom microstructure. This was necessary because of the dangerous nature of hydrofluoric acid.

When the samples were washed the material was dried in an oven and was then safe to handle.

The amount of time that immersion was carried out for was dependent on a) the amount of obscuring matrix within and on the specimen, b) the strength of the hydrofluoric acid, and c) the type and stability of the material of which the specimen was preserved. It was suggested by Upshaw *et al.* (1957) that the smaller the sample, the higher the acid concentration used and the less the immersion time. They suggested that larger specimens might be destroyed due to the violent expulsion of carbon dioxide. However, it has been found that using full strength (40-45%) hydrofluoric acid for *all* ossicles was suitable provided that they were free from large amounts of matrix. Large columnals and pluricolumnals that measured more than a few mm up to over 25 mm diameter, were immersed for up to eleven minutes in 40-45% hydrofluoric acid. If the samples were initially relatively free of obscuring matrix then immersion time could be as short as two minutes. Longer immersion times were needed for specimens that had their morphological features obscured by a substantial amount of adhering matrix. Specimens that were initially fairly soft and delicate (mainly due to being weathered, especially material obtained from very muddy, clay shales of the Benbulben Shale Formation at localities BB and TB) were immersed for very short periods of time, if it was thought that they would tolerate immersion at all without being destroyed. Pieces of shale, which had not been fully disaggregated using other methods, were immersed in hydrofluoric acid with a lower concentration of 3.6%. This strength of acid was achieved by diluting 25ml 40-45% hydrofluoric acid in 250ml water.

The material was immersed for one week in the 3.6% solution. After this time, the shale had commonly not broken down fully, but many of the ossicles had fallen out. They had been fully replaced by calcium fluoride. Especially good results were obtained with the 3.6% hydrofluoric acid solution for ossicles that were in the 1 mm diameter size range.

3.2.4.3. Results

The results of this process were variable. Sometimes columnal ossicles were completely eliminated of obscuring matrix so that all details of the facet were disclosed. Even the lumina and claustra, which are often the hardest morphological details to decipher when only partially cleaned (especially in pluricolumnals the lumen is plugged with cement,

calcite and other smaller ossicles), could be seen on many specimens.

On closer inspection it was apparent that the stereom microstructure was often revealed. Particularly good results were obtained for further study of this in the specimens that had been immersed in the lower concentration of acid for a long period of time. However, this varied from sample to sample. Those samples that had been previously exposed to inland weathering more frequently clearly displayed their microstructure following treatment.

Morphological features of other fauna, including brachiopods, corals, bryozoans and calcareous microfossils, were also more clearly visible following treatment with hydrofluoric acid.

3.2.4.4. Problems

Unfortunately, when specimens were fully altered to calcium fluoride they underwent a volume reduction. This was emphasised by concentric cracks seen on the articular surfaces and cracks seen on the latera. Cracked sections occasionally fell off the specimens. However, this was only a problem for smaller specimens that had been completely altered to calcium fluoride having been immersed for long periods of time.

Etching occurred on specimens that were exposed to strongly concentrated acid for a long duration, thus obscuring the detail of the stereom microstructure.

If there was a lot of matrix obscuring morphological details of the specimens, the results obtained were not as good as those from specimens that had little original matrix. In some cases the articular facets could not be cleaned at all.

3.3. EXAMINATION OF CLEANED MATERIAL

3.3.1. PICKING SAMPLES

Residues from sieving following treatment with Quaternary-O, and samples obtained from the other processes, were placed in a gridded petri dish and examined under a binocular microscope. Microscopic crinoid ossicles and other microscopic fossil fauna were picked out of the residues using a very fine paintbrush, which was moistened to make the material stick to it. These specimens were mounted in cavity slides using a

semi-permanent glue (gum tragacanth and a bactericide of clove oil (Geraghty 1996)). Larger specimens were mounted on Blu-Tack® in small, shallow, cylindrical, clear plastic dishes with tight fitting lids.

3.3.2. EXAMINATION USING BINOCULAR MICROSCOPE WITH CAMERA LUCIDA ATTACHMENT

3.3.2.1. Method

Residues were sorted through, as described in the previous section, under a Wild Heerbrugg M5-49234 binocular microscope with camera lucida attachment at powers x6 to x50. A sheet of white A4 sized paper was affixed to the table below the microscope lens and another one beside it. Individual columnals, of which most of the morphological details could be seen, were mounted on the paper under the lens using Blu-Tack® to keep them in place. The microscope was adjusted so that the highest power, which kept the entire columnal articular facet in the field of view, was used. Using the camera lucida attachment of the microscope the morphological details were drawn onto the second sheet of paper. A fibre optic light source with two arms was used. This allowed one beam to be directed at the specimen itself and a second to be directed onto the paper where the drawing was made. The second light could be moved around the paper to optimise the balance of light between the specimen and the drawing. Using a ruler, the dimensions of morphological details were recorded.

3.3.3. EXAMINATION USING SCANNING ELECTRON MICROSCOPE (SEM)

3.3.3.1. Method

Following the cleaning of micro-, and most macroscopic ossicles, individual specimens were mounted on SEM stubs. Larger specimens were fixed to stubs using a colloidal carbon cement. Only one specimen was attached to each stub. Small and delicate specimens were attached using glue tabs and as many as six specimens could be mounted on each stub. They were then placed in a bell jar evaporator, which created a vacuum, where they were coated in a thin film (about 250 Å) of gold. After coating, the specimens were placed on the stage of a Scanning Electron Microscope. In the early part of the project, the instrument used was a Leica 360 SEM (Stereoscan range, Cambridge Instruments), the lowest magnification being x6. In the later stages of the project, the instrument was a Hitachi S-3500N SEM, the lowest magnification being x25.

Morphometric measurements of some specimens and their morphological features were taken on the VDU using the built-in point measurers and recorded. The SEM images themselves (at 72 dpi) were captured digitally on a P.C. computer and saved as TIFF (the Leica) or bitmap (the Hitachi) files.

3.3.3.2. Problems

The gold coating of specimens had to be even and sufficiently thick to prevent surface electrical charging as this impeded the quality of the image produced under the SEM.

Because the lowest magnification that could be achieved on the Hitachi SEM was x25, an entire facet of any specimen over 2 mm diameter would not fit as a single image on the VDU. In order to attain the required entire image of the facet it was necessary to capture several slightly overlapping images, which could then be fitted together using Adobe Photoshop™ (see Section 3.4.2). As many as seventeen images were required for larger specimens, e.g. specimen 43.T-BB (Plate 77, fig. a). The Leica SEM, with its magnification of x6, was faster at imaging larger specimens since the entire lateral surface of a fairly large pluricolumnal could be fitted onto a single image (e.g. specimen 10.T-G, Plate 44, fig. b). However, as can be seen from this plate the image was distorted.

The Hitachi SEM has a maximum tilt of 60° so images of latera or facets occasionally had to be taken at an oblique angle. However, this sometimes helped with accentuating sculpture on the latera or features of the articular facets of the columnals.

Removal of some small, delicate specimens from SEM stubs following examination resulted in them breaking. Specimens were glued back together using non-viscous acetone-diluted Paraloid 72 glue crystals.

3.3.4. ADDITIONAL EXAMINATION TECHNIQUES

Lateral surface sculpture and cirrus scars could be seen more clearly on some specimens if they were rolled in Plasticine® and then the impression examined. Moore *et al.* (1968, Plate 2) illustrated the use of modelling clay for this purpose.

3.4. PRODUCTION OF PLATES FOR ILLUSTRATION OF MATERIAL

3.4.1. INTRODUCTION

Plates were produced either digitally from scanning electron microscopy (as opposed to scanning electron micrographs captured on photographic film with a camera attached to the SEM, which is not cost effective), or from standard photographs taken on a camera attached to a monocular microscope.

3.4.2. COMPUTER DIGITAL IMAGES

3.4.2.1. Introduction

This process proved to be a most versatile tool for the production of plates. Illustrations of columnals and their morphological features were found to be as good as those produced from photographic film and could be reproduced cheaply and quickly.

3.4.2.2. Method

TIFF or bitmap files containing digital images were saved from the computer (attached to the SEM) onto high density ZIP® diskettes. The files were opened in Adobe® Photoshop® 2.0, 4.0 or 5.0.2 on an Apple Macintosh® computer. Here, it was possible to prepare the images for producing plates of optimum quality.

Bitmap files were captured in RGB mode so the colour had to be removed to change the image to greyscale mode. This produced an image with 256 shades of grey and thus increased the output quality. TIFF images were already in greyscale mode. Although both sets of images had a resolution of 72 dpi, the images produced by the bitmap files were of better quality.

The selected portion of each image was cropped and pasted into a new document with a black background. Where multiple images were required to make a single output image the cropped portions were imported into a document as separate layers and moved around into the correct position, much like a photomontage, and then the layers were merged down. The contrast and brightness was altered until the desired levels were achieved. The area surrounding the selected image was filled in black, using various items selected from the toolbar, in order to make the images stand out. The scale bar was

selected and modified. In several cases cracks had appeared in specimens following hydrofluoric acid immersion. In others hairs or dust had been trapped within the SEM and thus appeared with the specimen on the image. Such defects could be removed from the images using various Adobe® Photoshop® tools. Where this was carried out it has been mentioned in the plate description.

Some specimens were consistently found to be crushed and thus possessed an elliptical facet outline (e.g. members of Columnal Plesion A). Manipulation to correct the outline of such deformed columnals was done on the computer using the skew and other tools on the already produced image in Adobe® Photoshop®. This was preferable to using the technique of tilt correction described by Veltkamp and Donovan (1984) whereby the stage is tilted within the SEM to produce a circular outline before the image is digitally captured. [This computer technique was not available to Veltkamp and Donovan in 1984.] This latter method was used on specimen 1b.T-J8 (Plate 23, fig. a) on its second visit to the SEM.

Once all the corrections had been made to the images in Adobe® Photoshop® they were copied and pasted into Aldus® FreeHand® 4.0 or Adobe® Illustrator® 8.0, the latter application being preferable. The size of each image could then be altered if desired and several images could be arranged on the page of a single document. The images could be moved around freely on the page and labelled accordingly with plate numbers and the scale bars amended. Once ready the final images were printed out on high quality ink-jet paper.

3.4.2.3. Problems

Each TIFF and bitmap file was of a large size (over 454k and over 1.1Mb respectively) so could not be stored on a standard floppy diskette. Saving these files onto high density ZIP® diskettes meant that many images could be stored onto a single diskette and subsequently worked on from there.

3.4.3. PHOTOGRAPHIC IMAGES

3.4.3.1. Introduction

Some specimens were too large to be placed in the SEM, or deemed too delicate, so had to be photographed with a standard photographic camera.

3.4.3.2. Method

Specimens were prepared for photography firstly by cleaning to remove any dust or loose matrix. They were then thinly coated in a film of ammonium chloride to increase the visibility of morphological features. This was carried out by the heating of ammonium chloride crystals in a purposely designed piece of apparatus. This consists of a fine glass bulb with an elongate tube extending from one end to which a rubber 'squeezy ball' is attached to act as a pump. The other end of the bulb has a small nozzle opening and, apart from this, the device is airtight. A small amount of ammonium chloride powder was placed in the bulb and heated over a Bunsen burner in a fume cupboard. On heating the ammonium chloride underwent sublimation and the vapour was carefully pumped onto the specimen. Handling of the specimens was carried out by the use of tongs. Following the photography this coating was removed with water to avoid etching of the specimens by hydrochloric acid, which, forms by the combination of moisture in the air and ammonium chloride (Benson 1965).

The coated specimens were placed on a matt black card. Illumination was provided by frosted bulbs and specimens were lit from top left. When needed a sand box was used to secure and correctly orientate the specimens. The camera was mounted on a stand above the specimens. High speed ISO 100 black and white film was used. The camera was adjusted to obtain the largest depth of field possible. Once focused, photographs were taken of the specimens at 0.125-, 0.25- and 0.5-of-a-second exposure. Standard photographic prints were made from the negatives.

3.4.3.3. Problems

Owing to the large size of some specimens, it was difficult to produce an even coat of the sublimate, so more than one attempt was required.

3.5. CURATION OF SAMPLES

All specimens and samples that were processed, including thin sections, were given TCD specimen numbers. The curation method can be found fully explained in Appendix C.

3.6. SUMMARY

Studies of crinoid ossicles requires that specimens are thoroughly cleaned. Cleaning techniques that were used successfully in this study included immersion in the surfactant 'Quaternary-O' and in hydrogen peroxide and fluoridisation. The importance of using these techniques is highlighted by specimen 5.V2-L1. Before fluoridisation it was not possible to see the articular facet and the specimen was wrongly classified as a Taxon Number 3 columnal when it is, in fact, a Taxon Number 5 columnal.

Morphometric study has been carried out using SEM images and drawings made with a camera lucida attachment to a binocular microscope. It has been found that measurement of specimens in some cases has been unsatisfactory when using the SEM. This is because the distance from the top of a specimen to the stage is not accounted for in the point measurers on the VDU. Therefore, using the camera lucida may be a more satisfactory method, especially with larger specimens when a relatively larger amount of error is acceptable. However, this method could also have its drawbacks. Compare the differences in measurements on specimen 33.T-D1. The point measurer is the more satisfactory method for very small specimens, *i.e.* those columnals that are smaller than about 2 mm diameter.

Illustration of specimens, which constitutes a major part of the study of crinoid ossicles, has been carried out largely using digitally captured SEM images rather than by traditional photographic techniques. This has reduced substantially the cost of illustration whilst maintaining high quality.

CHAPTER 4

CRINOID SKELETAL MORPHOLOGY

4.1. INTRODUCTION

The class Crinoidea belongs to the phylum Echinodermata, all members of which characteristically have a water-vascular system and a calcitic mesodermal skeleton, which is made up of many individual plates (ossicles). The class Crinoidea belongs to the subphylum Pelmatozoa because crinoids generally have a stem. It is distinguished from other pelmatozoan classes by possession of arms, which contain extensions of the coelomic systems. Like most other pelmatozoans, crinoids exhibit pentaradiate symmetry.

The number of ossicles making up the skeleton of a single crinoid may range from less than 50 in some microcrinoids (G. D. Sevastopulo, pers. comm. 2000) to more than two million in some large taxa (Ubaghs 1978*a*). The range of size of crinoids also varies greatly. The largest crinoid theca may be up to 100 mm or more in its maximum height and diameter. The smallest crinoids are microcrinoids whose thecae may be a mere 1 mm in height and diameter (Ubaghs 1978*a*).

During life the skeleton is covered with a thin epidermis. Crinoids generally consist of a crown, which contains the main body cavity and is supported by the main part of the pelma, *i.e.*, the stem. The morphological features discussed below are usually, but not always, present in fossil and Recent crinoids. [Figure 4.1 shows the basic morphology of a crinoid. A glossary of terms is provided in Section 4.4.]

4.2. THE CROWN

The crown (or corona) comprises the theca, which consists of the calyx and the tegmen, and the arms that may have pinnules attached to them.

4.2.1. ORIENTATION OF THE CROWN

The crown, with its pentaradiate symmetry, may be divided into five rays, each with an interray between them (Ubaghs 1978*a*). The rays are positioned where radials occur and,

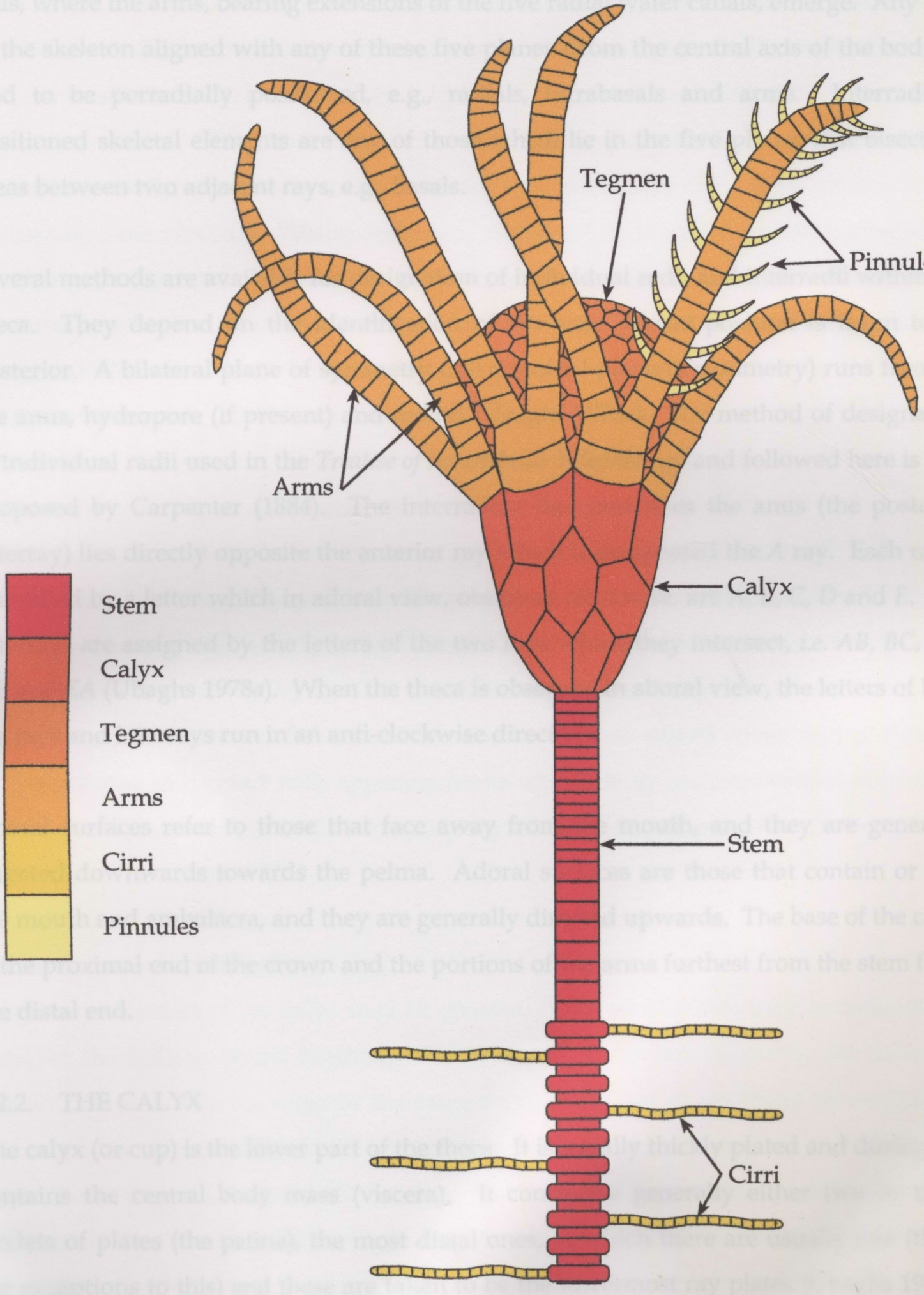


Figure 4.1. Schematic diagram showing basic morphology of a crinoid. The different colour shades illustrate susceptibility to postmortem disarticulation, the lighter colours disarticulating primarily. The order of complete disarticulation may be expected to be the pinnules followed by the cirri, arms, tegmen, calyx and finally the stem into individual columnals.

thus, where the arms, bearing extensions of the five radial water canals, emerge. Any part of the skeleton aligned with any of these five planes (from the central axis of the body) is said to be perradially positioned, e.g., radials, infrabasals and arms. Interradially positioned skeletal elements are any of those which lie in the five planes that bisect the areas between two adjacent rays, e.g., basals.

Several methods are available for designation of individual radii and interradii within the theca. They depend on the identification of the anus whose position is taken to be posterior. A bilateral plane of symmetry (the crinoidal plane of symmetry) runs through the anus, hydropore (if present) and mouth (Ubaghs 1978*a*). The method of designation of individual radii used in the *Treatise of Invertebrate Paleontology* and followed here is that proposed by Carpenter (1884). The interradius that possesses the anus (the posterior interray) lies directly opposite the anterior ray which is designated the *A* ray. Each ray is identified by a letter which in adoral view, observed clockwise, are *A*, *B*, *C*, *D* and *E*. The interrays are assigned by the letters of the two rays which they intersect, *i.e. AB*, *BC*, *CD*, *DE* and *EA* (Ubaghs 1978*a*). When the theca is observed in aboral view, the letters of both the rays and interrays run in an anti-clockwise direction.

Aboral surfaces refer to those that face away from the mouth, and they are generally directed downwards towards the pelma. Adoral surfaces are those that contain or face the mouth and ambulacra, and they are generally directed upwards. The base of the calyx is the proximal end of the crown and the portions of the arms furthest from the stem form the distal end.

4.2.2. THE CALYX

The calyx (or cup) is the lower part of the theca. It is usually thickly plated and during life contains the central body mass (viscera). It comprises generally either two or three circlets of plates (the patina), the most distal ones, of which there are usually five (there are exceptions to this) and these are taken to be the lowermost ray plates (Ubaghs 1978*a*) and have generally been termed radials (however, see below p.48). In dicyclic calyces two circlets of plates lie below the radial plates. The most proximal circlet is the infrabasals, of which there may be one to five (ankylosis of plates means their number is reduced), and the central circlet being the basals, of which there are generally five. Monocyclic calyces have only one circlet of plates below the radials, the basals, whose number also may vary

from one to five. Within the class Crinoidea the number of plate circlets has been used in classification. The infrabasal and radial plates are positioned perradially, while the basals are positioned interradially. However, it has been suggested by Simms (1994), Mannifield (1995) and Ausich (1997) that any of the circlets may be missing, not necessarily the infrabasals. Amongst the disparids there are taxa with more than three circlets in the aboral calyx, the most distal being compound radials. Jobson and Paul (1980) interpreted that in the cladid *Aethocrinus* the lowest circlet of plates, which are aligned with meres of the stem, represent additional meres of the stem rather than infrabasals as suggested by Ubaghs (1972). Simms (1994) agreed there were four circlets of plates in the calyx of *Aethocrinus*. Ausich (1996) named the four circlets; the most proximal circlet previously identified as 'basals', are lintels; 'inferradials' and 'radials' of previous literature are infrabasals; and 'superradials' are radials. Where compound radials are absent so are basal plates and radials, so that 'basals' of previous literature are lintels and 'radials' are infrabasals. Following this proposal of aboral cup plate homologies Ausich (1997) put forward a new phylogenetically based crinoid classification scheme. Articulation between calycal plates is generally by smooth surfaces (zygosynostosial). However, facets with deep depressions (fossae) for connective tissue, various raised areas and a rimmed peripheral area to connect with apposing facets articulate by manosynostosis also occur. Some calycal plates may articulate by symplexy where the surfaces of the adjoining facets are crenulate (see Section 5.2.2.1).

4.2.2.1. Accessory plates of the calyx

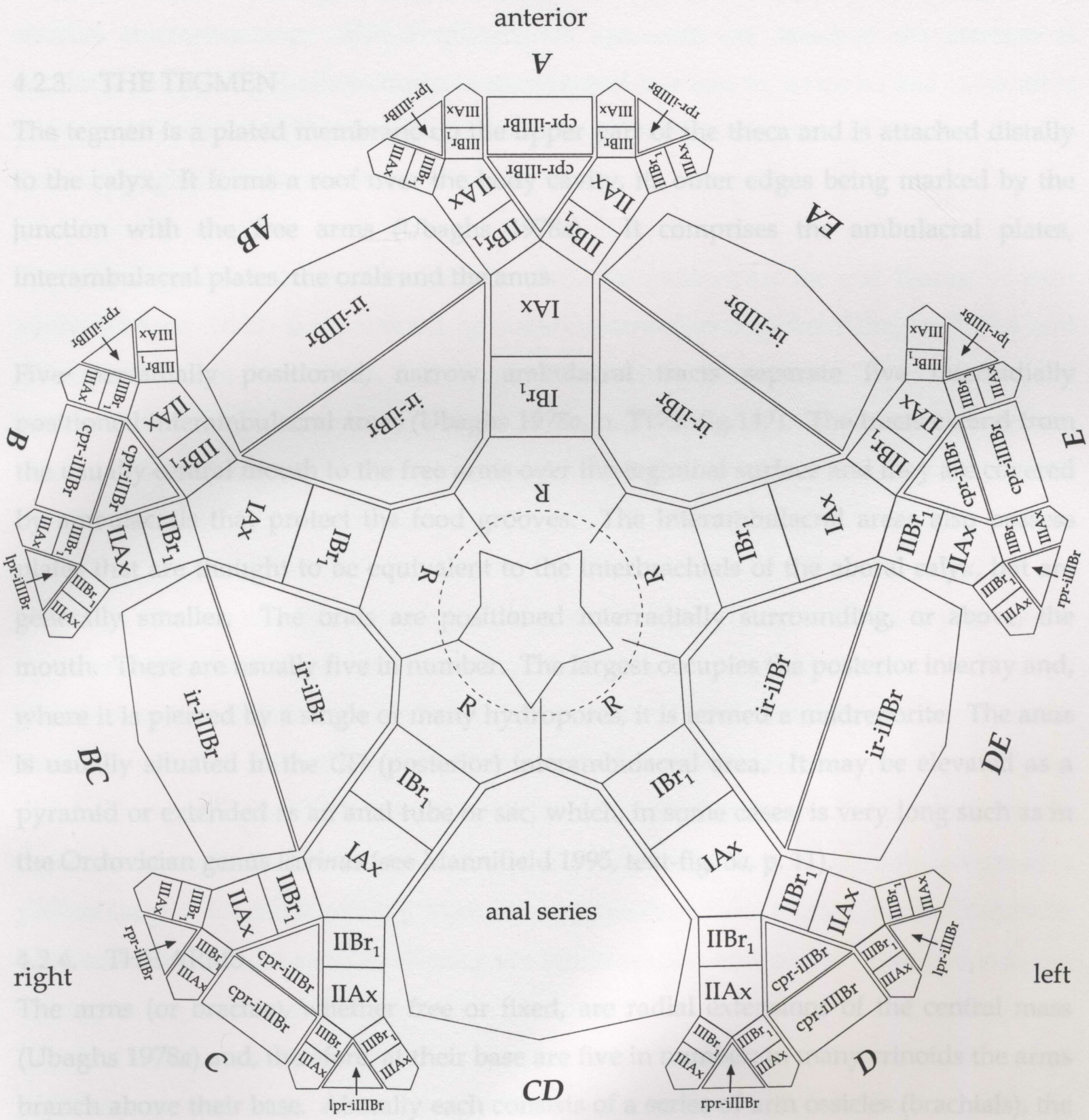
Secondary elements of the calyx may be present. Interradial plates may be intercalated between the radials. Fixed brachials, which are primarily arm elements, are united to adjacent plates within the calyx by the same types of sutures as are found between other calycal plates. Interradially positioned interbrachials occur between these fixed brachials from above the radials up to the level of free brachials and, thus, to where the arms become free (see Glossary, Section 4.4). This may be just at or above the upper limit of the calyx. Interbrachials may be positioned perradially between higher fixed brachials of a ray. The widening of the calyx by these plates accommodates the internal organs.

4.2.2.2. Anal plates of the calyx

The radial circlet, fixed brachials (if present) and/or basal circlet may be interrupted by plates of the anal series in the *CD* interray. Above the height of the basals the anal series

Figure 4.2. Explanation of interbrachial terminology used herein, mainly for flexible crinoids. When describing or labelling plates the ray or interray must be the first thing mentioned. Diagram is in aboral view. 'right' and 'left' at the beginning of the next part of the description are used to distinguish the two halves of a ray, seen in normal lateral view. 'central' is used to describe the plates in the central portion of the ray. 'interradial' or 'perradial' indicate whether the interbrachial is positioned between rays or within rays respectively. Following is a full list of interbrachial terms used and their abbreviations:

R	radial
IBr_1	primibrachial *1*
IAx	primaxillary
$IIBr_1$	secundibrachial *1*
IIAx	secundaxillary
$IIIBr_1$	tertibrachial *1*
IIIAx	tertaxillary
cpr-iIIBr	central perradially positioned intersecundibrachial
cpr-iIIIBr	central perradially positioned intertertibrachial
rpr-iIIIBr	right perradially positioned intertertibrachial
lpr-iIIIBr	left perradially positioned intertertibrachial
ir-iIBr	interradially positioned interprimibrachial
ir-iIIBrr	interradially positioned intersecundibrachial


anterior
A
AB
EA
B
E
BC
DE
C
CD
D
anal series
right
left
posterior
ir-iIBr
IAx
IBr1
R
IIBr1
IIAx
cpr-iIIBr
IIIBr1
IIIAx
lpr-iIIIBr
rpr-iIIIBr

plates replace, and are often similar to, the interbrachials. These plates have some connection with the anus, probably helping to widen the calyx for accommodation of the rectum. The calycal plates directly adjacent to the anal plates are often altered in shape relative to those elsewhere in the calyx. Different arrangements of anal plates, useful in classification, occur within the class.

4.2.3. THE TEGMEN

The tegmen is a plated membrane on the upper part of the theca and is attached distally to the calyx. It forms a roof over the body cavity, its outer edges being marked by the junction with the free arms (Ubaghs 1978*a*). It comprises the ambulacral plates, interambulacral plates, the orals and the anus.

Five perradially positioned, narrow ambulacral tracts separate five interradially positioned interambulacral areas (Ubaghs 1978*a*, p. T175, fig.147). The tracts extend from the usually central mouth to the free arms over the tegminal surface and they are covered by ambulacrals that protect the food grooves. The interambulacral areas also possess plates that are thought to be equivalent to the interbrachials of the aboral calyx, but are generally smaller. The orals are positioned interradially surrounding, or above, the mouth. There are usually five in number. The largest occupies the posterior interray and, where it is pierced by a single or many hydropores, it is termed a madreporite. The anus is usually situated in the *CD* (posterior) interambulacral area. It may be elevated as a pyramid or extended as an anal tube or sac, which, in some cases, is very long such as in the Ordovician genus *Iocrinus* (see Mannifield 1995, text-fig. 6*a*, p. 11).

4.2.4. THE ARMS

The arms (or brachia), whether free or fixed, are radial extensions of the central mass (Ubaghs 1978*a*) and, therefore, at their base are five in number; in many crinoids the arms branch above their base. Aborally each consists of a series of arm ossicles (brachials), the most proximal of which originates from, and is articulated closely with, the distal face of a radial. Each arm is therefore positioned perradially. The arm facet, whether it be on the radial or a higher brachial from where the arm firstly articulates freely, may be much narrower than (angustary), almost as wide as (peneplenary) or as wide as (plenary) the distal margin of the plate which it occupies (Ubaghs 1978*a*).

Brachials may be fixed in the calyx or free. Free brachials are generally aborally rounded to different degrees. Adorally they are longitudinally grooved (adoral groove) and, when united as an arm, carry extensions of the coelomic canals, nervous system and other organs. During life brachials are united by both ligaments and muscles as can be deciphered by morphology of the articular facet and by the type of meshwork of the stereom microstructure. Where collagenous ligaments are attached the stereom is regularly galleried, but where muscles are attached it is coarse, irregular and labyrinthic (Lane and Macurda 1975; Macurda and Meyer 1975; Macurda *et al*. 1978). Articulation between brachials is discussed more fully in Section 5.2.2.4.

The adoral grooves, during life, house ambulacral grooves on the soft tissues of their adoral surface which are protected by covering ambulacral plates (Ubaghs 1978*a*) and ciliated. The tube feet, which line the pinnules, secrete mucus and capture suspended food particles from the water and direct it back to the mouth via the ciliated grooves (Gislén 1924; Nichols 1960; Breimer and Lane 1978). The food reaches the mouth through the arm openings, which are holes at each arm base (Ubaghs 1978*a*).

The arms of some crinoids are as much as 1 m in length (Ubaghs 1978*a*), but generally they are much shorter and often no more than twice the height of the theca. The most proximal ossicle of an arm is the first primibrachial, which is termed fixed if it is within the calyx and free if it articulates with a radial. Some brachials may have two sloping distal shoulders from which two series of brachials are then borne (bifurcation). These brachials are called axillaries, and the most proximal axillary of an arm is termed a primaxillary. Brachials arising from the primaxillary are termed secundibrachials, brachials arising from secundaxillaries are tertibrachials, and so on. Brachitaxis is the term given to a series of brachials, which terminate with an axillary in a branching arm. The first brachitaxis would include primibrachials, those directly following the radial, plus the primaxillary, which is the first axillary brachial distal to the highest primibrachial.

If branching produces two arms of the same size then bifurcation is isotomous. The upper sloping shoulders of an axillary brachial may be notably unequal in size and therefore bear two unequally sized branches and this ossicle is called a subaxil. This type of bifurcation is termed heterotomy. The large branch is a continuation of the main arm

branch (ramus) from which smaller branches (ramules) may be borne, on both or one side only. These ramules may divide further and may be pinnulate themselves.

4.2.5. THE PINNULES

Where the shoulders of a subaxil are very unequal in size the branch borne from the smaller shoulder is a pinnule. This comprises uniserially arranged individual ossicles called pinnulars. Pinnules usually arise from alternating sides of successive brachials (holotomy). Generally, they are slender and do not bifurcate. They have ciliated ambulacral grooves similar to those of the arms with which they are continuous. Pinnules do not occur in all orders of crinoids, being absent from flexibles, most disparids and some cladids (Ubaghs 1978*a*). All post-Palaeozoic crinoids characteristically possess pinnules (Ubaghs 1978*a*), which are generally densely arranged (Breimer 1978).

4.3. THE PELMA

The pelma comprises the stem, which may possess or lack cirral appendages, and the holdfast. The proximal end of the pelma is that which is nearest to the calyx.

4.3.1. THE STEM

The stem (column/stalk) is made up of many individual discoid ossicles called columnals which are stacked in a way which resembles a packet of Polo® mints. If two or more columnals are found articulated they are termed a pluricolumnal (Ubaghs 1978*a*). In some taxa, mostly of early Palaeozoic crinoids, individual columnals comprise up to five portions (meres) that are visible in both lateral and transverse view (Ubaghs 1978*a*). Carboniferous crinoids, with the exception of *Barycrinus*, have holomeric (undivided) columnals.

The columnals are held together by collagenous ligaments (muscles are lacking, although some contractile filaments have been reported by Birenheide and Motokawa (1996)) which give rise to characteristic galleried stereom microstructure (Macurda and Meyer 1975; Roux 1975; Macurda *et al.* 1978; Donovan 1989*b*, and others). Adjoining columnals are held together by intercolumnal ligaments, which penetrate only the outermost layers of stereom. A noditaxis, at least in isocrinid stems, is held together by through-going ligaments (Baumiller and Ausich 1992) which penetrate and pass through all internodals

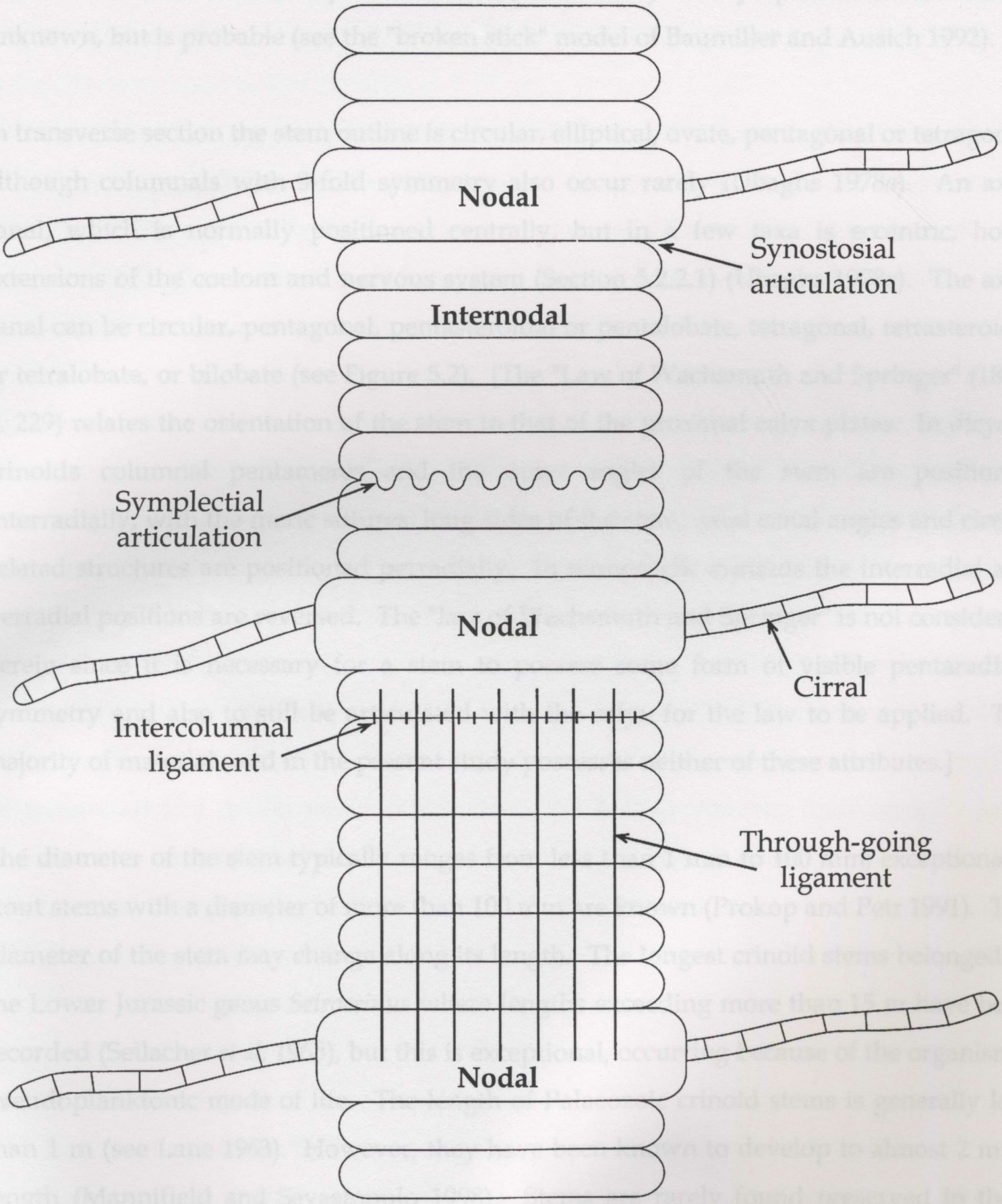


Figure 4.3. Schematic diagram of a portion of an isocrinid stem. Through-going ligaments connect an entire noditaxis together, while the intercolumnal ligaments connect only adjacent columnals to one another (modified after Baumiller and Ausich 1992).

and some way into the nodal of the noditaxis (Figure 4.3). Through-going ligaments do not penetrate synostosial articulations. Whether through-going ligaments terminated at the end of each noditaxis in primitive stems, which only had symplectial articulation, is unknown, but is probable (see the "broken stick" model of Baumiller and Ausich 1992).

In transverse section the stem outline is circular, elliptical, ovate, pentagonal or tetragonal, although columnals with 3-fold symmetry also occur rarely (Ubaghs 1978*a*). An axial canal, which is normally positioned centrally, but in a few taxa is eccentric, holds extensions of the coelom and nervous system (Section 5.2.2.1) (Ubaghs 1978*a*). The axial canal can be circular, pentagonal, pentasteroidal or pentalobate, tetragonal, tetrasteroidal or tetralobate, or bilobate (see Figure 5.2). [The "Law of Wachsmuth and Springer" (1885, p. 229) relates the orientation of the stem to that of the proximal calyx plates. In dicyclic crinoids columnal pentameres and the outer angles of the stem are positioned interradially, with the meric sutures, long sides of the stem, axial canal angles and cirrus-related structures are positioned perradially. In monocyclic crinoids the interradial and perradial positions are reversed. The "law of Wachsmuth and Springer" is not considered herein since it is necessary for a stem to possess some form of visible pentaradiate symmetry and also to still be articulated with the calyx for the law to be applied. The majority of material used in the present study possesses neither of these attributes.]

The diameter of the stem typically ranges from less than 1 mm to 100 mm; exceptionally stout stems with a diameter of more than 100 mm are known (Prokop and Petr 1991). The diameter of the stem may change along its length. The longest crinoid stems belonged to the Lower Jurassic genus *Seirocrinus* where lengths exceeding more than 15 m have been recorded (Seilacher *et al.* 1968), but this is exceptional, occurring because of the organisms' pseudoplanktonic mode of life. The length of Palaeozoic crinoid stems is generally less than 1 m (see Lane 1963). However, they have been known to develop to almost 2 m in length (Mannifield and Sevastopulo 1998). Stems are rarely found preserved in their entirety.

Many post-Palaeozoic crinoid groups, such as those belonging to the order Comatulida, lack a post-larval stem and retain only one cirriferous columnal (the centrodorsal). However, in Palaeozoic forms the situation is quite different and almost all taxa possessed a stem throughout ontogeny.

Stems which are uniform or almost uniform throughout their entire length are termed *homeomorphic* (Ubaghs 1978*a*). The morphology of the articular facets of the component columnals is identical throughout the stem and each columnal maintains a nearly constant height and diameter.

Heteromorphic stems are composed of columnals that differ in such characters as their sculpture, shape and dimensions, columnals of one type being intercalated with those of other types. They generally display a regular pattern of different sized columnals, usually larger nodals, often with cirri attached, and smaller internodals between them. This pattern is referred to as a noditaxis. Noditaxes are discussed further in Section 4.3.1.

Xenomorphic stems are those in which two or more portions (for example, proximal and distal) may be differentiated. Each portion has its own distinct morphology and can, therefore, be recognised by the proportions, outline, sculpture and arrangement of its component columnals (Ubaghs 1978*a*). The changes between different parts of the stem may be gradual or abrupt (Moore 1939). Where only three portions are distinguished they are termed the proxistele, mesistele and dististele, the first being the most proximal to the calyx, and the latter the most distal from it (Ubaghs 1978*a*). Some Recent isocrinids (for example, *Annacrinus wyvillethomsoni*) have stems in which more than five portions can be recognised and similar xenomorphic stems are known from the fossil record. Some portions of a xenomorphic stem can be homeomorphic while others are heteromorphic (Figure 4.1). Each portion has been produced at a different stage of ontogeny (Ubaghs 1978*a*) since the outline of the base of the calyx would have had to alter to produce columnals with differing outlines.

4.3.1.1. Growth of stems and columnals: general

The growth of stems and their component columnals is effected both by addition of new columnals and by growth (accretion) of these and earlier formed columnals (Ubaghs 1978*a*). Accretion causes columnals to grow in both height and diameter. This is demonstrated by concentric growth lines that can be seen in transverse thin section and by relative changes in radii of features of the articular facet that are observed in longitudinal thin section. Obviously, growth can also be inferred simply from changes in overall dimensions of the columnal and features of the articular facet. Combinations and variations of the growth rates of individual columnals determine growth rate of the whole

stem, its flexibility, and whether it is a constant diameter throughout its length. Where the stem tapers, growth rates of the relevant columnals determines whether this occurs in a proximal or distal direction. Autotomy can result in stems which have lost an original tapered portion (Baumiller *et al.* 1995). The growth of columnals and stems during ontogeny was described by Jeffords and Miller (1968), although they did not specifically identify the specimens that they used to illustrate their discussion.

Homeomorphic stems have their oldest columnals located distally, the youngest columnals being proximal to the calyx where new columnals are introduced (Ubaghs 1978*a*). Uniform growth by accretion also occurs, but no further columnals are added by intercalation.

In heteromorphic stems nodals (N, using the terminology of Webster 1974) originate as columnals that are formed at the proximal end of the stem (Ubaghs 1978*a*). They are the largest and earliest formed columnals, whose diameter is dependent on the size of the base of the calyx where propagation is initiated (Seilacher *et al.* 1968) and subsequent growth. In isocrinids nodals are commonly cirriferous (cirrinodals), but not always so (nudinodals). Both cirrinodals and nudinodals may occur in the same stem. Internodals (IN) arise by intercalation between nodals away from the most proximal region of the stem (Ubaghs 1978*a*), although Wulff and Ausich (1989) mentioned that it is not known whether internodals are secreted distal to the aboral calyx or in the same positions as nodals with delayed further growth. The first internodals to be intercalated are designated as priminternodals (IN1). Between a nodal and its adjacent priminternodal a secundinternodal (IN2) may be intercalated. Then, between all adjacent columnals, tertinternodals (IN3) may be intercalated, and so on with quadrinternodals (IN4) and quinqueinternodals (IN5), at least in the model case. However, internodal intercalation may not be as regular as this, as noted by Moore *et al.* (1968) and Webster (1974).

The series of internodals between two nodals is an internode, and an internode in addition to its most distally positioned adjacent nodal is a noditaxis (pl., noditaxes). The highest order in a noditaxis is a nodal, followed by priminternodals, and so on. Intercalations continue until the characteristic noditaxis pattern for a species or genus is attained, although since nodals are being added in the proximal region this general rule does not apply in this portion of the stem. Columnals also continue to grow individually

by accretion until the characteristic specific or generic dimensions are achieved.

There are rare examples of two orders of cirrus-bearing columnals (see, for example, Webster 1974, text-fig. 4c, redrawn from Bather 1900, fig. XVII-1). Webster (1974) commented that one possibility would be to term the larger nodals priminodals and the smaller secundinodals. However, he considered the differences between the two sets of nodals simply reflected a difference in the height of nodals along a length of stem, presumably as a result of different growth rates after they had formed at the base of the calyx. Ubaghs (1978*a*, T70) suggested that where two orders of columnals are cirriferous either two orders of nodals are present, or there are cirriferous internodals. Either explanation is possible. Taking Columnal Taxon Number 38 (see p. 233) as an example, this taxon shows four orders of cirrus-bearing columnals, which are referred to herein as nodals, priminternodals, secundinodals and tertinternodals. Excepting the latter, since there is only one cirriferous tertinternodal, these three orders are notably higher than the lower orders so it could be inferred that they are all nodals growing at different rates. Equally, these (excepting the highest order which is definitely a nodal) could be cirrus-bearing internodals, but it is not known whether these lower order cirrinodals have through-going ligaments (which hold a noditaxis together (Section 4.3.1)) or not. Without knowing the positions of these through-going ligaments for this particular taxon, neither theory can be proved.

Webster (1974) introduced a scheme for describing concisely the distribution of columnals in a stem and identified several different patterns of intercalation of internodals within a noditaxis. The Type I pattern includes nodals (N) and priminternodals (1) only. It may vary from a simple N1N1 arrangement to a N11N11 (written as $N1_{1\text{-}2}$), N111N111 (written as $N1_{1\text{-}3}$) and so on. The Type II pattern includes nodals, priminternodals and secundinternodals (2). The simplest arrangement is N212, but priminternodals and secundinodals may alternate and be many in number, for example,. N212121212 (written as $N(21)_{4}2$).

Since nodals only are added proximally, it follows that there is an increasing number of internodals moving distally along the stem. It is generally the case that priminternodals are larger than secundinternodals, and so on. However, internodals may be undifferentiated, and the distinction between them becomes more difficult distally, as, for

example, in the Triassic articulate crinoid *Encrinus liliiformis* discussed by Seilacher *et al.* (1968).

Xenomorphic stems may change their outline distally to proximally (for example, from circular to pentasteroidal in the Recent *Endoxocrinus parrae* Gervais, 1835, studied by the current author in the collections of the Natural History Museum, London). There are two possibilities for the growth of such a stem. Firstly, the area of generation, that is the base of the calyx, may change its shape during its ontogeny since its shape governs the columnal outline proximal to the calyx. As mentioned by Simms (1989*a*), the diameter of a columnal is determined by the size of the base of the calyx if further accretionary growth is minimal. The second possibility is that the outline may change away from the calyx by accretion. Whichever is the case, flexibility of such a stem would be variable along its length.

Overall, flexibility of a stem is greatest where columnals are at their lowest. This is generally found to be in the most proximal region of the stem because this is where the new, lowest columnals (nodals) are added. However, *Seirocrinus* had its most flexible stem portion distally (but not at the very end of the stem which was rigid because of many nodals with cirri which acted as a holdfast (Seilacher *et al.* 1968)) because many orders of low internodals were situated there. Columnals with pentamerous outlines have increased ability to flex in five directions because the long sides may be used as hinges. This also gives more stability because the column is less likely to rotate (Donovan 1984*a*).

There have been relatively few studies of the growth of the stem in fossil crinoids but relevant information can be found in the descriptions and illustrations of some taxa in the literature many of which clearly show changes in the morphology of columnals during ontogeny.

4.3.1.2. Growth of the stem: cladid crinoids

The term 'cladids' refers to a paraphyletic group of dicyclic Palaeozoic crinoids from which the Flexibles and the Articulates were derived.

There are surprisingly few descriptions of the ontogeny of the stem in this group of

crinoids, which, in terms of specific diversity, dominated Palaeozoic faunas, particularly those of the late Palaeozoic. Bather (1891) described *Dictenocrinus* [*Botryocrinus*] *decadactylus* from the Wenlock Limestone of Dudley and showed how the pentameric columnals of the distal part of the stem change to holomeric columnals higher. Stukalina (1988) described the ontogenetic changes observed in the stem morphospecies *Pennatocrinus* and *Decacrinus* (thought to be cladids) that are pentasteroidal and decasteroidal respectively in the outline of their areolae ('ligamentary fields'). In *Decacrinus* the area of the asteroids increase through ontogeny, the lumen remains about the same size, crenulae become wider and the outline of the stem changes from round or rounded pentagonal to more pentagonal. In *Pennatocrinus* the areola does not appear until the later stages of ontogeny when it is narrow. Stukalina assumed that the oldest (distal) part of the stem, showed the morphological characteristics of the early stages of ontogeny. In two different morphospecies of *Decacrinus, i.e., D. ovalis* Stukalina (Text-fig. 12, *2*, p. 24) and *D. pennatus* Stukalina (Text-fig. 12, *3*, p. 24), the most proximal columnal (youngest) of the former is similar to the most distal (oldest) of the latter. Also, the two figured stages for the onogeny of *P. subpennatus* Yeltyschewa (Text-fig. 12, *1*, p. 24) are like the two earliest figured stages of *D. ovalis* (Text-fig. 12, *2*, p. 24).

4.3.1.3. Growth of the stem: flexible crinoids

The proxistele is differentiated from the mesistele and dististele in most flexibles (Lane 1978). It generally measures less than 20 mm in height (Wulff and Ausich 1989), and its component columnals are very low, wide and firmly united to each other. They narrow in diameter distally, but maintain approximately the same height (Wulff and Ausich 1989). It is often found attached to the calyx in fossil specimens. In *Eutaxocrinus curtus* (Williams) small individuals have few columnals in the proxistele, but large specimens have many (Goldring 1923), indicating intercalation or addition of columnals during ontogeny. However, the number of component columnals in the proxistele may change only very slightly, or not at all throughout ontogeny, e.g. *Taxocrinus colletti* White (Springer 1920). The individual columnals grow slightly in height to increase the overall length of the proxistele (Springer 1920).

In small specimens of certain species, *e.g., Taxocrinus colletti* White, *Eutaxocrinus alpha* (Williams) and *Gnorimocrinus cirrifer* Springer, 1920 (Springer 1920, Pl. LVI, fig. 10, Pl. L, fig. 5, Pl. XLVII, fig. 12; Lane 1978), the mesistele and dististele comprise very high, barrel-

shaped columnals that become higher distally. Larger individuals have much lower columnals with straight latera (Springer 1920, Pl. XLVII, fig. 7). It is inferred that while the height of these columnals remains fairly constant during ontogeny, their diameter increases by further addition of stereom (Lane 1978). This may be related to the palaeoecology of the animals that first attained a necessary minimum height above the substrate by producing elongate columnals before secondarily strengthening the stem (to support the growing crown) by increasing the diameter of the columnals (Springer 1920; Lane 1978). However, *Mespilocrinus* specimens retain the inferred 'juvenile' columnal form throughout ontogeny (Lane 1978).

The generating columnal (Strimple and Frest 1979) is a high and wider columnal which separates the independently growing proxistele and mesistele (Wulff and Ausich 1989). Strimple and Frest (1979) proposed that columnals of the proxistele and mesistele were both inserted at the proximal points on studying the regenerated stem of *Euonychocrinus simplex*. In the xenomorphic stem of the late Mississippian crinoid *Taxocrinus* cf. *T. whitfieldi*, wedge-shaped columnals occur both directly below and directly above the generating columnal (Wulff and Ausich 1989). This proves the original hypothesis of Ausich (1977) that growth does indeed take place from both of these points and in opposite directions.

4.3.1.4. Growth of the stem: articulate crinoids

Simms (1989*a*) investigated the early ontogeny of stemmed articulate crinoids from the Mesozoic. He found that in isocrinids and encrinids new nodals are initiated directly below the calyx where they are low, but they become rapidly higher and cirriferous as they move distally along the stem. Once a columnal attains a certain height, there is no further significant increase in height. Priminternodals are inserted between nodals; then there is very regular intercalation of secundinternodals, tertinternodals and so on (Donovan 1984*a*; Simms 1989*a*). Intercalation usually occurs only in the most proximal stem region and only until a set pattern is reached for that particular crinoid type. The oldest columnals, therefore, are found in the distal stem even though they may have a smaller diameter than those proximally and a more juvenile morphology, e.g. *Chladocrinus psilonoti* (Quenstedt). Exceptions to the growth by intercalation rule are seen in some members of the Pentacrinitidae, such as the Jurassic genus *Seirocrinus*, whose internodal intercalations continued indefinitely (Seilacher *et al.* 1968). This genus also demonstrates

that growth may occur by accretion since it has a constant diameter throughout the length of its stem (Simms 1989*a*). Similarly, some articulate stems may taper proximally (Simms 1989*a*).

4.3.1.5. Growth of the stem: disparid crinoids

Homeomorphic stems appear to be common within the Disparida and it is assumed that they grew by addition of new columnals at the proximal end of the stem and accretion of those columnals already formed. However, more complex patterns are seen in a number of taxa, in which there is a well defined proxistele, such as *Pisocrinus* and members of the Allagecrinidae. In a study of *Pisocrinus*, Ausich (1977) proposed that new columnals were added at the distal point of the proxistele and the proximal point of the mesistele. Warn and Strimple (1977) contended that new columnals were initiated at a similar position in allagecrinids which show a xenomorphic stem with a proxistele distinguished by a rapid expansion in diameter of very low columnals close to the base of the calyx. Conspicuously heteromorphic stems occur in such taxa as *Cincinnatticrinus*, *Ectenocrinus* and *Ohiocrinus* (Warn and Strimple 1977), in some of which the stems are also markedly xenomorphic. Warn and Strimple (1977, p. 43 *et seq.*) described the complex growth history of the pelma of *Cincinnatticrinus brachialis* in which the juvenile pelma consisted of a 'lichenocrinid' multiplated holdfast. Pentameric columnals produced below the calyx developed to holomeric columnals further down the column and between these internodals were inserted. The most distal part of the stem in the adult was homemorphic and, according to Warn and Strimple, terminated at point at which autotomy had occurred.

4.3.1.6. Growth of the stem: camerate crinoids

Brower (1974) commented that symplexy was the common mode of articulation in camerate crinoid stems. Growth of columnals occurs by an increase in their height and width, and as this occurs widths of culmina increase and new ones are intercalated. Brower *et al.* (1978) stated that in more than fifty percent of the stems studied growth was by intercalation.

4.3.2. THE CIRRI

Cirri (sing., cirrus) are generally unbranched appendages that project outwards from, although not necessarily at right angles to, the latera of specific columnals (most nodals and some priminternodals and sometimes lower orders of nodals) in particular taxa of

crinoids. They comprise a series of ossicles named cirrals, which are arranged in much the same way as are columnals in the stem. Their lengths are variable depending on their function. They are termed pluricirrals where two or more are found articulated together. The transverse section of cirri is normally circular, but in a few taxa it may be elliptical. There is no obvious correlation between the shape of a columnal and that of its cirrals; stems with a pentagonal section may bear cirrals, which are circular in section (for example, see Columnal Taxon Number 5, p. 183) or elliptical (for example, *Isocrinus*). The diameter of cirri may be very small in comparison with that of the columnal with which they articulate, or be almost as wide as the columnal. The cirri may be cylindrical or barrel shaped. Their articular surfaces are simpler than those of columnals with generally only a crenularium, with few crenulae, an areola and a lumen, so they probably had minimal flexion. Cirrals are perforated by an axial canal, generally centrally located, that connects to the axial canal of the stem and, thus, also holds extensions of the coelom and nervous systems. The axial canal may be circular or bilobate in outline. In the latter case it is possible that the coelom and nerve cords were separated during life. The zygocirral is the cirrus most proximal to the stem.

Extant crinoids generally have five cirri per columnal, but fossil crinoids may have anywhere from one to six projecting from a single columnal. The cirri are generally positioned evenly around the circumference of a columnal and thus, where there are five, at 72° from each other. This arrangement is consistent with pentaradiate symmetry. Cirri articulate with columnals at a cirrus socket (nodicirral articulum/cirrus scar/cirrus facet) which is usually located at mid-height of the columnal. The scars are generally circular in outline, concave, and may be directed normal to, or upward, or downward from the latus. Each may have a crenularium, an areola (which generally slopes downwards towards the centre of the facet) and a lumen. Two cirri may arise from a single cirrus socket. Rarely, cirrals may be axillary causing the cirri to branch in a way similar to that of bifurcating arms (see Section 4.2.4, p.50). [Donovan (1993, 1996) suggeted that "radicles" articulate by symplexy or synostosy and lack contractile tissues, as in the bathycrinids. "Cirri" articulate by synarthry and may include contractile tissues allowing reattachment (Holland and Grimmer 1981), as in the isocrinids and comatulids. However, in the present study, although the cirrus sockets are symplectially articulating it is not thought that they always act as root-like structures, especially when they occur intermittently and in the proximal region of the stem (see description of Columnal Taxon Number 28, p.

215).]

Cirri articulate with the centrodorsal (most proximal columnal) of extant comatulids and are used in locomotion and are prehensile because, in this order, they are fairly flexible and elongate. Also, in the stalked crinoid *Cenocrinus asterius* four or five cirri from several nodals along the length anchor the reclined stem to the substrate using the terminal claws (Macurda and Meyer 1974). In some isocrinids these cirri may release their grasp and crawl on the sea-floor using their cirri (Birenheide and Motokawa 1998). The general purpose of cirri in fossil crinoids that emerge from cirriferous columnals is not known precisely. However, since in some stems cirral diameters increase distally (Mannifield and Sevastopulo 1998) they probably were radicular and acted as a holdfast (Section 4.3.3).

Pseudocirri differ from cirri in that they comprise only a solitary long ossicle. Cirripores are tiny holes that are seen on the latera of some columnals, usually at mid-height, which lead, via a small canal, to the axial canal of the stem. The purpose of these features is unknown. Abortive cirri ('incipient' of Donovan 1996) have a similar canal and they appear as small nodes or tiny nodicirral articula.

Radicular cirri are root-like cirri that project from the distal end of some stems. These are rarely found intact, unless the crinoid fossil has been exceptionally preserved *in situ*. [See Donovan 1986*a*, p. 13.]

Ubaghs (1978*a*) pointed out that there is a lack of detailed knowledge on Palaeozoic crinoid cirri. This may be for the following reasons. Cirri tend not to be preserved articulated with the stem from which they originated. A distinction between cirri and small columnals cannot necessarily be made when looking at disarticulated material. However, because of their simple articular facet morphologies and the characteristics mentioned above it may be possible to distinguish cirrals from columnals. Pluricirrals may possess characteristic 'spinelets' along one side (Moore *et al.* 1968) which are not found on pluricolumnals.

4.3.3. THE HOLDFAST

The holdfast ("attachment structure" of Brett 1981) is formed by columnals and cirri in the

distal part of the stem and acts as an anchorage structure. The morphology of representative holdfasts was described by Brett (1981) and Ubaghs (1978*a*). Brett (1984) reviewed the form and function of the holdfasts of Silurian pelmatozoans. There is considerable variation in the structure and function of the holdfast in different crinoids. The holdfast may be a disc cemented to a hard substrate or, in the early Palaeozoic, a discoidal structure that is made up of small polygonal platelets a holdfast on which the genus *Lichenocrinus* is based (Prokop and Turek 1997). *Lichenocrinus* is found attached to shells and other organic debris that act as a hard substrate. However, in general discoidal holdfasts are rarely preserved, even within sediments that contain abundant stem material. More unusual adaptations of radicular cirri include cirri from a grapnel-like holdfast in *Ancyrocrinus* and the hollow float of *Scyphocrinites* (Brett 1981).

4.4. GLOSSARY OF TERMS

The following list of terms used in the text has been gathered from various sources, mainly from Moore *et al.* (1968) and Moore, Ubaghs *et al.* (1978). Some new terms are proposed herein (in **bold**), and the meanings of some previously described terms are redefined (*). References to figured examples are given after some of the following descriptions.

A *ray* The anterior ray opposite the posterior *CD* interray. In adoral view, running clockwise, subsequent rays are designated *B*, *C*, *D* and *E* rays (Figure 4.2).

AB *interray* The right anterior interray positioned between the *A* and *B* rays. In adoral view, running clockwise, subsequent interrays are designated *BC*, *CD*, *DE* and *EA* interrays.

abaxial Across the articular facet of a columnal, moving outwards, *i.e.*, in the direction away from the axial canal.

aboral The surface of the body which faces away from the mouth (syn., *dorsal*).

aboral cup The aboral part of the body between the column and free arms (syn., *calyx*).

aboral ligament fossa A semicircular depression on the aboral side of any perradial ossicles, e.g. brachials and radials, for the attachment of ligament fibres between apposing ossicles (Figure 5.6).

aboral skeleton All of the aborally positioned calcareous parts of the body comprising columnals, attachment structures, centrodorsal, cirrals, centrale, infrabasals, basals,

radials, brachials and pinnulars.

adaxial Across the articular facet of a columnal, moving inwards, *i.e.*, in the direction towards the axial canal.

adoral The surface of the body which faces towards, and contains, the mouth (syn., *ventral*).

adoral groove Furrow on the adoral surface of free brachials and pinnulars that, during life, contain the food groove and extensions of essential body systems (Figure 5.6.*a, b*).

adoral ligament fossae Depressions on the adoral side of any perradial ossicles, e.g. brachials and radials, for the attachment of ligament fibres between apposing ossicles (Figure 5.6.*c, e, f*).

adoral skeleton All of the adorally positioned calcareous parts of the body comprising orals, ambulacrals, adambulacrals, interambulacrals, interbrachials and some anals.

ambulacral Small plate which covers part of the food groove on the arm or tegmen.

ambulacral groove A simple or branched furrow, underlain by the epidermis, in the adoral surface of the tegmen, arms and pinnules. Occupies the adoral groove of the calcareous skeleton.

ambulacrum On the adoral surface of body, simple or branched area radially extending from mouth onto tegmen, arms and pinnules. Includes ambulacral groove and its associated structures such as the tube feet (syn., *ambulacral tract*).

anal Any of the plates positioned in the *CD* (posterior) interray excluding interbrachials and fixed pinnulars. In some crinoids, some plates of the *C* ray are included (Figure 6.11.*f*).

anal notch Notch that may be present on *CD* oral of certain crinoids for reception of anal plate.

anal pyramid A low, usually conical elevation surrounding the anus on the tegmen.

anal sac Greatly elevated, usually inflated sac, which is an extension of the tegmen. Found only in cladids and disparids (Figure 6.3).

anal tube Structure that varies in shape, but which is generally high, and that has an anal opening at its summit. Seen in some camerates, cladids and disparids, flexibles and articulates.

anal X (X). Anal plate disposed in *CD* interray distal, and to the left of the radianal, if present (Figure 6.7). Seen in cladids and disparids and flexibles.

angustary Distal articular facet of a radial which is much narrower that the width of the plate itself. The outline is somewhat horseshoe-shaped (Plate 13, figs a, b).

aniradial Radial, or superradial, with left shoulder bearing anal X or anal sac and right shoulder bearing the most proximal brachial of the arm(s). Common in disparids and cladids.

anitaxis (pl., *-taxes*). The series of anal plates of the posterior interray (Figure 6.11.*f*).

ankylosis The fusion of adjacent ossicles by calcareous deposits. The suture lines between the ossicles may disappear.

anterior The frontal direction, or the *A* ray. Opposite to posterior.

apposing facet A facet that juxtaposes another.

areola (pl., *areolae*) *(A)*. On the articular facet of a columnal, cirral or cirrus socket, the generally smooth, planar or gently sloping to slightly concave area lying between the crenularium or articular rim, and the lumen or perilumen (Plate 80, fig. a).

areola index (Ai). Ratio of total mean diameter of areola to that of articular facet multiplied by 100 (this and other indices explained fully in Section 5.2.4).

arm Evagination of body above radial from the theca, Composed of brachials, with or without pinnules, and containing coelomic canals.

arm facet Articulate surface on radial, or brachial, for attachment of the free arm.

arm trunk A ramule-bearing arm of some camerates.

articular facet (F). On any articulating ossicle, especially a columnal, cirral, cirrus socket or brachial, the surface serving for muscular or ligamentary articulation with apposing facet (syn., *articulum*, pl., *-articula*). On columnal, cirral or cirrus socket, composed of lumen and surrounding zygum (Figure 5.3).

articular rim A raised edge of some circular articular facets (Plate 49, fig. b).

articulation Flexible to almost rigid ligamentary, or ligamentary and muscle, union between apposing articular facets of adjoining ossicles.

asteroidal Greek word for star shaped. In present context, used as a suffix for the description of the outline of various morphological features of the columnal articular facet.

atomous An arm ray which does not branch.

attachment disc A disc shaped holdfast at the distal terminus of the stem.

autotomy The casting off of an arm or the stem. Regeneration of the body part may follow.

**axial canal* A longitudinally continuous void occupying generally the centre of a columnal which has no lateral expansions (spatia) or constrictions (claustra). It holds longitudinal extensions of the coelom and nervous systems. The transverse outline is

the same as the widest part of the lumen. Similar void also penetrates cirrals, arms, pinnules and thecal plates (Figure 5.5). The outline of the axial canal is variable.

axillary (Ax). A brachial with two distal shoulders, equal or unequal in size, to support two arm branches (Figure 6.7). Ranked according to position after branching in the arm.

azygous basal Of a tripartite basal circlet, the smallest plate.

B *ray* The right anterolateral ray, in adoral view.

BC *interray* The right posterolateral interray positioned between the *B* and *C* rays, in adoral view.

basal (B, pl., *BB).* Circlet of one to five plates below the radials, which are usually positioned interradially.

basaltiform Columnals with pentagonal outlines and straight latera (Plate 36, fig. a).

bifascial field On elliptical columnals, and sometimes cirrals, shallow to moderately depressed smooth areas occupying the spaces on either side of the fulcral ridge (Plate 18). Serve for ligamentary attachment.

biserial arm Brachials arranged in double row, longitudinally offset by 50%, with their pointed lateral sides meeting midway forming a zigzag suture line (not seen in disparids and flexibles).

brachial (Br, pl., *Brr).* Any arm plate above the radial belonging to the main branch excepting pinnulars, interbrachials, ambulacrals and adambulacrals (Plate 104). May be axillary. May be included in the theca (fixed brachials) or not (free brachials). Ranked according to position after branching in the arm.

brachitaxis (pl., *-taxes*). A brachial series of a branching or non-branching arm. In the former it includes a series of adjoining brachials, following the radial (primibrachitaxis) or a higher axillary brachial, plus the next axillary brachial at the distal end of the series.

C *ray* The right posterior ray, in adoral view.

CD *interray* The posterior interray positioned between the *C* and *D* rays. Usually the widest ray owing to the inclusion of the anus or anal plates.

calycal Anything relating to the calyx, usually ossicles of the calyx.

calyx The lower part of the theca excluding any part of the tegmen (syn., *aboral cup*) (Figure 4.1).

canalicula (pl., *-culae*). Radially disposed canals leading from axial canal of stem to cirrus on columnal latera, usually at columnal mid-height.

central perradial(ly positioned) interbrachials In normal lateral view, any ossicles of the calyx intercalated between secundibrachials of a ray and/or between higher ordered fixed brachials; they are positioned in the central section of the ray (from intersecundibrachial and upward) (Figure 4.2).

cirral Single ossicle of a cirrus.

cirrinodal Cirrus or cirri-bearing nodals (Plate 75, fig. a).

cirripore Small opening of canalicula on columnal latus.

cirrus (pl., *cirri*). Generally unbranched appendage of stem (Figure 4.1).

cirrus socket Articular facet on latus of nodal for attachment of cirrus (syn., *nodicirral articulum*) (Plate 34, fig. b).

claustral surface The proximal or distal surface of the claustrum.

**claustrum* (pl., *claustra*). The part of the articular facet of a columnal that lies adaxially adjacent to the areola or perilumen. May have inner, central and outer portions with differing inclinations (Plate 46, fig. a). The adaxial surface may have various morphologies. Not part of the axial canal. Stereom differs in density to remainder of columnal.

column The series of ossicles that comprise the stem, excluding cirri and holdfasts (Figure 4.2).

columnal Single ossicle of the stem.

crenella (pl., *crenellae*). Any groove of the crenula.

crenularium (pl., *crenularia*). Any portion of the columnal articular facet that bears crenulae (Figure 5.3). May comprise of more than one portion of the articular facet where the adaxial portion lies at a different angle to the abaxial portion.

crenula (pl., *crenulae*). The collective term for the corrugation created by a crenella and culmen of the crenularium, or on any other sculptureed surface where such a corrugation occurs. May bifurcate to fill space on large facets.

crenulate suture Zigzag line created on the latus where two adjoining columnals meet in symplectial articulation (Figure 5.1; Plate 74, fig. b).

crown The whole upper part of the crinoid body. Excludes the pelma (syn., *corona*).

culmen (pl., *culmina*). Any ridge of the crenula.

cuneate Wedge-shaped.

D *ray* The left posterior ray, in adoral view.

DE *interray* The left posterolateral interray positioned between the *D* and *E* rays, in adoral view.

denticulate Possessing toothlike projections.

dichotomy The division of the arm into two branches that may be isotomous (see below) or heterotomous (see below).

dicyclic A calyx in which two circlets of plates lie proximal to the radials (Plate 15).

dilobate A morphological feature of the columnal articular facet or cirrus socket, especially the lumen, which has two lobes (Plate 71, fig. b).

distal The direction of position away from the polar or central axis, *i.e.* away from the position where the pelma meets the crown or the axial canal of the stem.

dististele The distal portion of the stem.

E *ray* The left anterolateral ray, in adoral view.

EA *interray* The left anterior interray positioned between the *E* and *A* rays, in adoral view.

encrinite A limestone rock that comprises mainly crinoid skeletal debris (Plate 2, fig. b).

epifacet A strongly convex latus that is extrafacetal (Plate 51, fig. b).

E *ray* The left anterior ray, in adoral view.

EA *interray* The left posterolateral interray positioned between the *E* and *A* rays, in adoral view.

equatorial flange A low, generally wide, outward projection from the latus of a columnal that continues equatorially (Plate 50, fig. b).

equatorial ridge A high, outwardly rounded projection from the latus of a columnal that continues equatorially (Plate 54).

food groove Furrow on adoral surface of tegmen, arms and pinnules.

fossa (pl., *-fossae*). Depression on articular facet of an ossicle for muscular or ligamentary attachment (Figure 5.6).

fossula (pl., *fossulae*). Radially disposed canals leading from axial canal of stem to cirrus on latera, usually at columnal mid-height.

free arm Part of arm that is not incorporated into the calyx, and is generally freely mobile.

fulcral ridge Elevated, linear ridge on articular facet acting as a hinge line. Occurs in synarthrial articulation of brachials and columnals, muscular articulation of brachials (Figure 5.6.*d*) and ligamentary articulation of some cirri.

globose Spherically shaped.

height Dimension of ossicle (or calyx or crown) measured in a proximal-distal direction.

heteromorphic Stem or pluricolumnal, or pluricirral, which comprises ossicles with different sizes, morphologies or sculpture (Plate 28, figs c, d).

heterotomy An arm in which dichotomy is unequal (Figure 6.7).

holdfast Any structure used for fixation to a substrate at the distal end of the stem.

homeomorphic A stem, or a portion of a stem, or pluricirral, in which component ossicles are all essentially identical (Plate 92).

hyperpinnulate A brachial that bears two or more pinnules.

infrabasal (*IB*, pl., *IBB*). Any plate belonging to the most proximal circlet in dicyclic calyces.

interambulacral Any interradially positioned plate of the tegmen.

interbrachial (*iBr*, pl., *iBrr*). Any ossicle of the calyx above the basals lying between rays (interradially positioned) and between branches of a single ray (perradially positioned). Excepting anals and fixed pinnulars. Ranked according to their relative position to ranked brachials (Figure 4.2).

interbrachitaxis (pl., *-taxes*). A series of interbrachials.

internodal (*IN*). Any columnal intercalated between two successive nodals. Ranked according to their order of insertion.

internode Series of (or single) internodal(s) between two successive nodals (does not include a nodal) (Figure 4.3).

interradial (*iR*, pl., *iRR*). Plate intercalated between adjacent radials.

interradial area The area between two adjacent radii.

interradial(ly positioned) interbrachials Accessory plates of the calyx higher than basals between rays (excepting anals) (Figure 4.2).

interradial(ly positioned) interbrachitaxis (pl., *-taxes*). Series of interbrachials between rays.

isotomy An arm in which dichotomy is equal or subequal.

latus (pl., *latera*). Outer surface of columnal, cirral or brachial. Not part of the articular facet.

left perradial(ly positioned) interbrachials In normal lateral view, any ossicles of the calyx intercalated between tertibrachials of a ray and/or between higher ordered fixed brachials; they are positioned in the left section of the ray (intertertibrachials and upward) (Figure 4.2).

ligament pit Deep, steep-sided depression in aboral ligament fossa adjoining centre of transverse ridge (Figure 5.6.*a,b*).

**lumen* (pl., *lumina*). Most central cavity of a columnal articular facet, its highest and lowest planes being level with those of the perilumen, areola or claustrum (whichever is directly adjacent to it) (Figure 5.3). Has various outlines and sizes. Generally centric.

manosynostosis A ligamentary articulation characterised by large and deep fossae and a well developed peripheral rim that provides contact with adjacent plate. Different to synostosis in fossae depth and presence of rimmed edges. Common in flexibles.

mesistele The central portion of the stem between the dististele and proxistele.

moniliform A circular columnal with a strongly convex latus (Plate 41, fig. b).

monocyclic A calyx in which one circlet of plates only lie proximal to the radials (Plate 13, fig. a).

monopinnulate A brachial from which only one pinnule is borne.

morphometrics The quantitative description of various morphological features.

nadir The lowest point of a plate which points downwards (Plate 15, fig. c).

nodal (*N*). Columnal of noditaxis generally with greatest height and sometimes width, and often bearing cirri if the stem is cirriferous (Figure 4.3).

noditaxis (pl., *-taxes*). An internode plus its most distally positioned adjacent nodal.

nodose Referring to a columnal or stem, one that bears nodals.

nudinodal A nodal that lacks cirrus sockets.

opposing facets Where two ossicles are juxtaposed, the facets that are furthest away from each other.

oral On the tegmen, any of five interradially positioned ossicles, which form a circlet surrounding the mouth (Plate 14, fig. b).

ossicle Any individual calcareous plate of the crinoid skeleton.

pelma The whole lower part of the crinoid body, mainly the stem. Excludes the crown.

peneplenary Articular facet of a radial, which is almost as wide as the width of the plate itself.

pentalobate A morphological feature of the columnal articular facet or cirrus socket, especially the lumen, which has five lobes (Plate 68).

pentasteroidal Concerning the outline of an articular facet feature, one which has the outline of a five-pointed star ((*Gr.*) = quinquestellate (*L.*) replaces the term 'pentastellate' of some authors which is incorrect, having a Greek prefix and Latin suffix) (Plate 24, fig. a).

pentastichous Having five equally spaced outward projection points (of cirri, set at 72 from each other) emerging from a single stem. These need not necessarily all emerge from the same columnal and several cirri may emerge along each longitudinal line.

perilumen (pl., *perilumina*). On some columnal articular facets a raised inner boundary of the zygum which surrounds the lumen. Can be variously sculptureed (Figure 5.3).

peripheral rim A raised edge of some elliptical articular facets (Plate 18).

perradial Positioned in line with any of the five rays.

perradial(ly positioned) interbrachials Accessory plates of the calyx higher than radials between branches of a single ray (excepting fixed pinnulars) (Figure 4.2).

perradial(ly positioned) interbrachitaxis (pl., *-taxes*). Series of interbrachials between any branches of a single ray.

petalodium Five-rayed symplectial articulation where the five rays have petal-shaped outlines.

pinnular Generally free above the theca, individual ossicle forming the pinnule.

pinnule Generally slender, small, non-bifurcating branchlet borne from a subaxil brachial (Figure 4.1). Attached to the brachial by way of a pinnule socket.

plenary Articular facet of a radial that is as wide as the width of the plate itself (Plate 15, fig. c).

plesion Monophyletic taxa which can be inserted anywhere within a classification without altering the Linnaean rank of the crown group (Patterson and Rosen 1977).

pluricirral A series of two or more cirrals attached to each other (Plate 91, fig. b).

pluricolumnal A series of two or more columnals attached to each other (Plate 76, fig. a).

posterior In the direction of the rear, or the *CD* interray. Opposite to anterior.

priminternodal (*IN1*). First order internodal.

proximal The direction of position towards the polar or central axis, *i.e.* towards the position where the pelma meets the crown or the axial canal of the stem.

proxistele The proximal portion of the stem.

pseudocirrus Outward projections from the latus of a columnal. Differ from cirri comprising only a single long ossicle.

radial (*R*, pl., *RR*). Most proximal plate of any ray (above basals).

radial facet Distal facet of any radial for articulation with primibrachial *1*.

radianal (*RA*). Most proximal *C* ray plate, often moved upwards and left. Adjoins anal *X* or anal opening.

radicular Of cirri, root-like (Plate 59). Often act as an anchorage structure.

ramule (pl., *ramules*). The smaller branch that arises from heterotomy.

ramus In heterotomous branching, the main, generally larger arm branch.

ray The radial plate plus all succeeding plates borne by it including brachials, intercalated perradially positioned interbrachials and pinnules.

rheophilic Organisms that live in areas with water currents that they rely on for feeding.

rheophobic Organisms that avoid areas with water currents.

right perradial(ly positioned) interbrachials In normal lateral view, any ossicles of the calyx intercalated between tertibrachials of a ray and/or between higher ordered fixed brachials; they are positioned in the right section of the ray (intertertibrachials and upward) (Figure 4.2).

**spatium* (pl., *spatia*). A void created and restricted abaxially in its upper and lower boundaries by the claustral (or areola or inner crenularial) surfaces and adaxially by the axial canal outline. Herein, it is not considered as a component of the axial canal (Figure 5.5).

spicule A calcareous element of many echinoderms (Plate 107, fig. b).

spinose Of sculpture, possessing spines.

stem The stalk-like attachment of many crinoids. Comprised of columnals (syn., *column*) (Figure 4.1).

stereom Meshwork microstructure of the calcitic crinoid endoskeleton (Plate 75, fig. b).

subaxil Axillary brachial with unequally sized shoulders giving rise to ramule or pinnule on the smaller shoulder.

subtegminal Below the tegmen of the theca.

suture A line on the latus where adjacent columnals meet indicating the type of articulation.

symmorphy A ligamentary articulation in which one or two denticles interlock with sockets on opposed facet.

symplexy A ligamentary, almost immobile articulation in which culmina interlock with crenellae on opposed facet (Plate 32).

synarthry A ligamentary, reasonably flexible articulation in which opposing facets bear a transverse ridge separating ligamentary fossae (syn., *bifascial articulation*) (Plate 18).

synostosy A ligamentary, reasonably flexible articulation in which opposing facets are concave for attachment of ligamentary fibres (Plate 49, fig. b).

syzygy A ligamentary, almost immobile articulation of some thecal plates and brachials in which culmina meet culmina on opposing facets.

tegmen The upper part of the theca excluding any part of the calyx (syn., *adoral cup*) (Figure 4.1).

theca The crinoid skeleton excluding the pelma and the arms.

tiering The vertical distribution of organisms in a suspension-feeding, benthic marine community (sometimes includes infaunal organisms) (Figure 7.1).

trifascial articulation Articulation in which facets possess three fossae, one aboral fossa and two laterally adjacent adoral fossae, which are separated in some cases by crenulate elevations. Movement is moderate in two directions (Figure 5.6.*c*).

tripartite basal circlet A basal circlet with three basals due to ankylosis. The basal produced are of different sizes (Plate 13, figs a, b).

tuberculate Of sculpture, possessing small rounded protuberances (Plate 45, figs a, b).

uniserial arm An arm in which brachials are arranged in a single row.

vermiculate Of sculpture, having a worm-like pattern (Plate 21, fig. a).

xenomorphic A stem in which two or more portions may be differentiated, often proxistele, mesistele and dististele, each portion having its own distinct morphology.

zygocirral The most proximal cirrus ossicle that articulates with the cirrus socket on a cirriferous columnal Plate 70, fig. b).

zygosynostosis A ligamentary, generally immobile articulation in which opposing facets are essentially flat for attachment of ligamentary fibres and for calcareous deposits.

zygous basal Of a tripartite basal circlet, either of the two larger plates.

zygum The entire columnal articular facet excluding the lumen (Figure 5.3).

CHAPTER 5

TECHNICAL DESCRIPTIONS, CLASSIFICATION AND NOMENCLATURE

A fundamental rule of taxonomic nomenclature is that a name given to an organism applies to the entire organism. In the practice of naming many fossils the entire organism is seldom available. A reconstruction of an organism is often produced by piecing together separate fossil body parts (Bengtson, S. 1985). In some circumstances naming of these separate parts has been carried out by giving each different piece a different name because their origins were unknown at the time. The result is that different names have been assigned to different parts of a single organism (Section 5.3).

Crinoids are commonly named and classified according to the arrangement of the component ossicles (calcareous hard parts) of the calyx at higher taxonomic levels and other parts of the crown at lower hierarchical levels. This is a natural classification. In the *Treatise on Invertebrate Paleontology* (Moore and Teichert 1978*a*), the most recent comprehensive study on crinoids, only a small percentage of the fossil taxa described have any reference to the morphology of the stem or its constituent columnals. Nevertheless, where stems are found associated with their calyx or crown they carry the same name as the calyx. Dissociated skeletal elements, extremely common in the fossil record of some groups of organisms, have previously been assigned names and classified according to their morphologies (artificial classification). In crinoids, the naming of disarticulated ossicles especially of dissociated columnals, often involved Linnaean binomina. Some method of classification was necessary when it was realised that dissociated ossicles could be potentially important in biostratigraphy (Jeffords 1978) (Section 5.3).

In this chapter the description, naming and classification of crinoid columnals is discussed, focusing on the methods applied by previous authors and those applied in this study. Difficulties in using Linnaean binomina are scrutinised.

5.1. TECHNICAL DESCRIPTIONS AND CLASSIFICATION OF DISARTICULATED CRINOID MATERIAL (COLUMNALS) USED BY PREVIOUS AUTHORS

In this section artificial schemes used to classify crinoid skeletal elements are described.

A hierarchical system for crinoid columnal assemblages with names provided from the Roman army (for example, Genus = Manipulus) was proposed by **Croneis** (1938). The scheme was arranged in hierarchies comparable to that of the standard zoological classification of family, genus and species. The Roman names were not intended to be accepted by the International Commission on Zoological Nomenclature (Moore, Jeffords and Miller 1968).

Moore (1939) produced a workable, but artificial, classification, of dissociated ossicles. He placed all parts of the crinoid skeleton into groups with characteristic morphological features that were given descriptive Latinised binomina, as in any usual taxonomic classification, but the names of the ranks were changed. The highest rank was "Division", followed by "Main Group" and "Group". Columnal outline (prefix) was considered more important than lumen outline (suffix). For example, columnals were represented by:

Division CRINOSTYLI (pelma components)
Main Group CYCLOSTYLI

Diagnosis. Circular columnals.

Group CYCLOCYCLOPAE (analogous to genotype (=genus))

Diagnosis. Cyclostyli with circular lumen.

Cyclocyclopa acuticarinata (Section (=species))

Diagnosis. Lumen relatively large, and so on.....

Similar groupings were carried out for "Crinobases", which equate to the most proximal plate circlet, *i.e.* basals or infrabasals, which were further subdivided by shape, height, number of constituent plates and the shape of the stem impression at the base of the circlet. The groupings were merely descriptive because dissociated ossicles belonging to all three subclasses of crinoids could be included within a single group.

The entire classification could be regarded as "pigeon-holing", with Linnaean binomina provided for almost every disarticulated ossicle he described. However, Moore recognised that the true identification of an isolated ossicle could only be carried out if a similar ossicle had been described from a more complete, articulated skeleton. If a guess was made as to the genus and/or species, or a new name given to the isolated ossicle, this could cause confusion in the future. He noted that if each ossicle was considered as an independent entity, with no generic or specific name known or attached, its morphological characteristics could still be described and its stratigraphical position determined. However, it was still necessary to assign some sort of name (Section 5.3). He

recognised that his classification scheme would not be accepted by the International Commission on Zoological Nomenclature (Jeffords 1978).

Moore and Laudon (Moore and Laudon 1943) altered columnal names from Linnaean binomina to a combination of vernacular-Latinised binomina, e.g. *Columnal excentricus*. These names are all *nomina nuda*[1].

A classification in which stems are all placed in a group Caulinaria was proposed by **Vyalov** (1953, 1969) (*fide* Moore, Jeffords and Miller 1968). This group was divided into ranking hierarchical groups of which some (e.g. Planocaulidae) were comparable to family-rank assemblages. This classification scheme has not subsequently been used by anyone else.

Yeltyschewa (1955, 1956, 1959, 1964) provided an artificial grouping scheme based on the outlines of the lumen and columnal. The outline of the lumen (prefix) was considered more important than the outline of the columnal (suffix). For example, a columnal with a pentagonal lumen and circular columnal outline would be called *Pentagonocyclicus*. Other prefixes and suffixes were given for triangular, square, hexagonal and elliptical outlines. This gave thirty-six possible columnal combinations. Only a few of these combinations have been illustrated amongst described columnals. Twelve other columnal outlines and twelve other lumen outlines were proposed. Type species were designated for some of the groups. These names are all also probably *nomina nuda*.

The scheme of Yeltyschewa has been employed by several other Russian workers in systematic descriptions. They include **Dubatolova**, **Stukalina**, **Sizova**, **Avrov**, and **Shao**.

Stukalina used the classification schemes of Yeltyschewa, and Moore (1939). Stukalina (1967) suggested placing (col.) after a generic name to signify 'morphogenus'.

Moore, Jeffords and Miller (Moore, Jeffords and Miller 1968; Moore and Jeffords 1968; Jeffords and Miller 1968) used a classification and nomenclature based on the outline of columnals. Where it was known which order or other taxonomic group columnals

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[1] *Nomina nuda* (naked names) are those that "*as originally published fail to meet mandatory requirements of the ICZN and having no status in nomenclature, are not correctable to establish original authorship and date*" (Moore and Teichert 1978*b*, p. xix).

originated from, they were placed in their correct group. Within each the groups Pentameri, Elliptici, Cyclici and Varii could appear. For example, pentagonal columnals could be represented by:

Order DISPARIDA Moore and Laudon, 1943

[Group PENTAMERI]

Diagnosis. Columns with fivefold development.

This group contains several established families, genera and species with fivefold symmetry. There were also new genera which, it is assumed, the authors were sure belonged to these families.

For disarticulated skeletal remains a similar hierarchical system was proposed for "Subclass and Order Uncertain". This included the use of genera and species as taxonomic groupings. Columnal genera and species of other authors were used.

Jeffords (1978) listed all disarticulated crinoid skeletal element taxa proposed up to that time, but no descriptions were included.

D. K. Wright (1983) described columnal and lumen outlines of Ordovician crinoid ossicles from Wales. The classification was based on that of Moore (1939), Moore and Jeffords (1968) and Moore *et al.* (1968). Fifty-one morphotypes were recognised. A coding scheme was used to replace genus group names, which is close to open nomenclature. Any morphotype belonging to the morphogenus *Cyclocyclopa* was given a code Cc with a number following to denote different morphotypes within the group.

Pelmatozoan columnals from the British Isles were described by **Donovan** (1986*a*, 1989*b*). His descriptive terminology followed that of Moore (1939), Moore *et al.* (1968), Webster (1974) and Ubaghs (1978*a*). He firstly described columnals and stems, which were attached to calyces and crowns, that had previously been only briefly described. He commented that Reed (1897) had used letters of the Greek alphabet for distinguishing columnals, but considered that this was inadequate since there was no indication of phylogeny or morphology. He suggested a semi-artificial scheme and employed names

of morphogenera erected by Stukalina, as well as erecting new morphogenera himself. The classification system of Yeltyschewa (1955, 1956) was used as he considered the outline of the lumen to be more important than that of the columnal (Donovan 1984*a*).

Another artificial scheme was suggested by **Termier and Termier** (1949, 1958, 1974).

5.2. TECHNICAL DESCRIPTIONS OF DISARTICULATED CRINOID MATERIAL USED HEREIN

The following descriptive methods and terms are adapted mainly from the work of Moore (1939), Moore *et al*. (1968), Webster (1974), Ubaghs (1978*a*) and Donovan (1986*a*).

5.2.1. LATUS MORPHOLOGY

The latera (sing., latus) are the outer surfaces of columnals that are not involved in articulation (Figure 5.1). They are generally visible, except in heteromorphic stems where the columnals are so low that they are obscured by higher ordered columnals (Section 4.3.1). A latus outline can be straight, convex or concave (Ubaghs 1978*a*). If it is strongly convex it is said to be an epifacet. Sculpture may be spines, nodes, ridges, flanges, longitudinally oriented striations, grooves, structures related to cirri (Ubaghs 1978*a*) (see Section 4.3.2), or absent in which case the latera are smooth.

5.2.2. ARTICULAR FACET MORPHOLOGY

The articular facet (articulum/facet) is that area by which apposing columnals articulate (Ubaghs 1978*a*). Three types of columnal articulation are explained, along with notes on the types of articulations between brachials. In all cases zygum (pl., zyga) is the term applied to the area of the articular facet outside, and excluding, the lumen (Moore *et al.* 1968; Ubaghs 1978*a*; Donovan 1986*a*) (Figure 5.3). It bears ligamentary fibres that hold together apposing columnal articular facets (Moore *et al*. 1968) (Figure 5.5).

There are several terms of descriptive terminology which have been used by various authors in the past when describing features of the articular facet or the outline of the

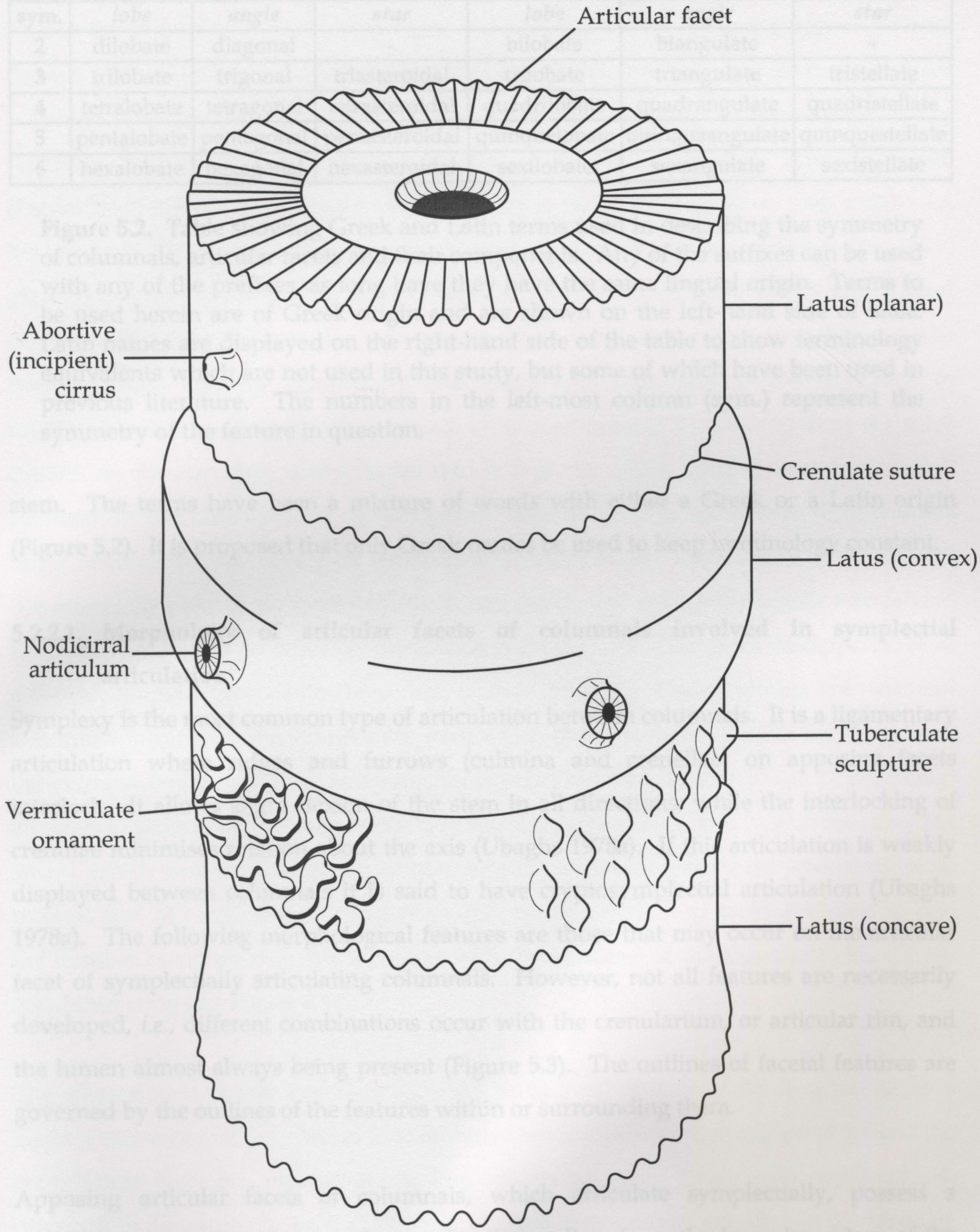

Figure 5.1. Hypothetical pluricolumnal showing lateral criteria used in distinguishing between columnal morphospecies.

	GREEK			LATIN		
sym.	*lobe*	*angle*	*star*	*lobe*	*angle*	*star*
2	dilobate	diagonal	-	bilobate	biangulate	-
3	trilobate	trigonal	triasteroidal	trilobate	triangulate	tristellate
4	tetralobate	tetragonal	tetrasteroidal	quadrilobate	quadrangulate	quadristellate
5	pentalobate	pentagonal	pentasteroidal	quinquelobate	quinqueangulate	quinquestellate
6	hexalobate	hexagonal	hexasteroidal	sexilobate	sexangulate	sexistellate

Figure 5.2. Table showing Greek and Latin terms used in describing the symmetry of columnals, articular facets and their components. Any of the suffixes can be used with any of the prefixes, as long have they have the same lingual origin. Terms to be used herein are of Greek origin and are shown on the left-hand side of table. Latin names are displayed on the right-hand side of the table to show terminology equivalents which are not used in this study, but some of which have been used in previous literature. The numbers in the left-most column (sym.) represent the symmetry of the feature in question.

stem. The terms have been a mixture of words with either a Greek or a Latin origin (Figure 5.2). It is proposed that only Greek names be used to keep terminology constant.

5.2.2.1. Morphology of articular facets of columnals involved in symplectial articulation

Symplexy is the most common type of articulation between columnals. It is a ligamentary articulation where ridges and furrows (culmina and crenellae) on apposing facets interlock. It allows slight flexion of the stem in all directions, while the interlocking of crenulae minimises rotation about the axis (Ubaghs 1978*a*). If this articulation is weakly displayed between columnals it is said to have cryptosymplectial articulation (Ubaghs 1978*a*). The following morphological features are those that may occur on the articular facet of symplectially articulating columnals. However, not all features are necessarily developed, *i.e.*, different combinations occur with the crenularium, or articular rim, and the lumen almost always being present (Figure 5.3). The outlines of facetal features are governed by the outlines of the features within or surrounding them.

Apposing articular facets of columnals, which articulate symplectially, possess a **crenularium** (pl., crenularia) with crenulae that radiate from the inner boundary of the crenularium to the periphery of the facets. Crenulae is the collective term for the crenellae (grooves (sing., crenella)) and culmina (ridges (sing., culmen)) (Ubaghs 1978*a*), and overall they give a corrugated appearance. Crenulae of two apposing facets interlock so that crenellae fit into culmina on one facet and vice versa. Crenulae are not necessarily

straight and may be rounded or have flattened apices and troughs. Neither are they always the same width on a single facet or a constant width along a single crenella or culmen. The crenularium may be narrow and peripheral, in which case the crenulae have a tendency to be simple, *i.e.* unbranched. However, where the crenularium has a relatively large radius[1] the crenulae may bifurcate (Figure 5.4.*a*), or rarely trifurcate (Figure 5.4.*b*) (usually towards the periphery), up to twice, depending on their widths, *i.e.* the narrower (finer) the crenulae the more times bifurcation may occur. Bifurcation takes place in an effort to occupy the space created by growth of the crenularium itself. This is more effective than the crenulae simply growing in width and height as it increases the overall surface area for ligamentary attachment and, thus, reduces the likelihood of rotation between apposing facets. For each bifurcated crenella on one facet there is a short culmen on the apposing facet that fits into it, and vice versa, so that no spaces are left between the two crenularia. A curious growth regime is where, rather than short culmina being intercalated exclusively on the periphery, they are also intercalated adaxially near the inner boundary of the crenularium (Figure 5.4.*c*). For each peripherally intercalated short culmen there is an adaxially positioned short culmen. This gives the appearance of a broken simple culmen with the central portion missing. These culmina are narrower and much lower than the simple ones with which they alternate. On the apposing facet the culmina are adapted for accepting these short culmina in two ways; 1) peripheral bifurcation accommodates the peripherally intercalated culmina, and 2) grooves along the apices, which terminate before the point of bifurcation, accommodate the adaxial culmina. Intercalation of crenulae in the case of peripheral crenularia may be by insertion so that the number of simple crenulae increases with the diameter of the articular facet, but are non-bifurcating (see Figure 6.14).

The intercalation of crenulae on a growing pentagonal articular facet is achieved by a slightly different method. Rather than crenulae being intercalated at any point around the crenularium they are inserted at the five corners as either 1) a single, small culmen disposed in the extremity, or 2) as two shorter, narrower culmina (as compared with those along the long sides) which join, or almost join, at their adaxial ends (Figure 5.4.*d*). On the apposing facet of the adjacent columnal crenellae are counterparts to the culmina.

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[1] The radius does not imply a full radius *per se*. Rather, the width of the morphological feature from its inner to outer boundary following an imaginary diagonal line which may be drawn through the centre of the facet to both peripheries.

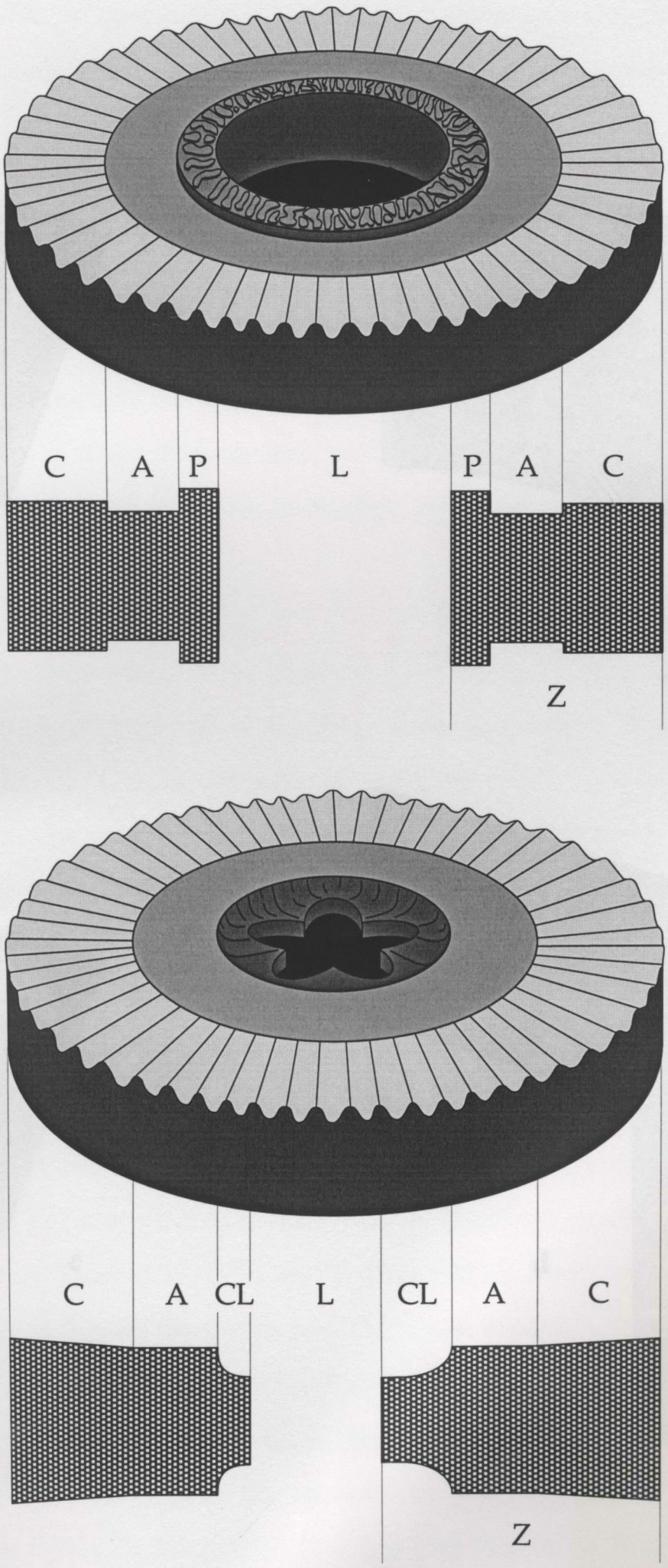


Figure 5.3. Two examples of possible combinations of morphological features involved in symplectial articulation with their appearances in medial longitudinal section illustrated below (C=crenularium, A=areola, CL=claustrum, P=perilumen, L=lumen, Z=zygum).

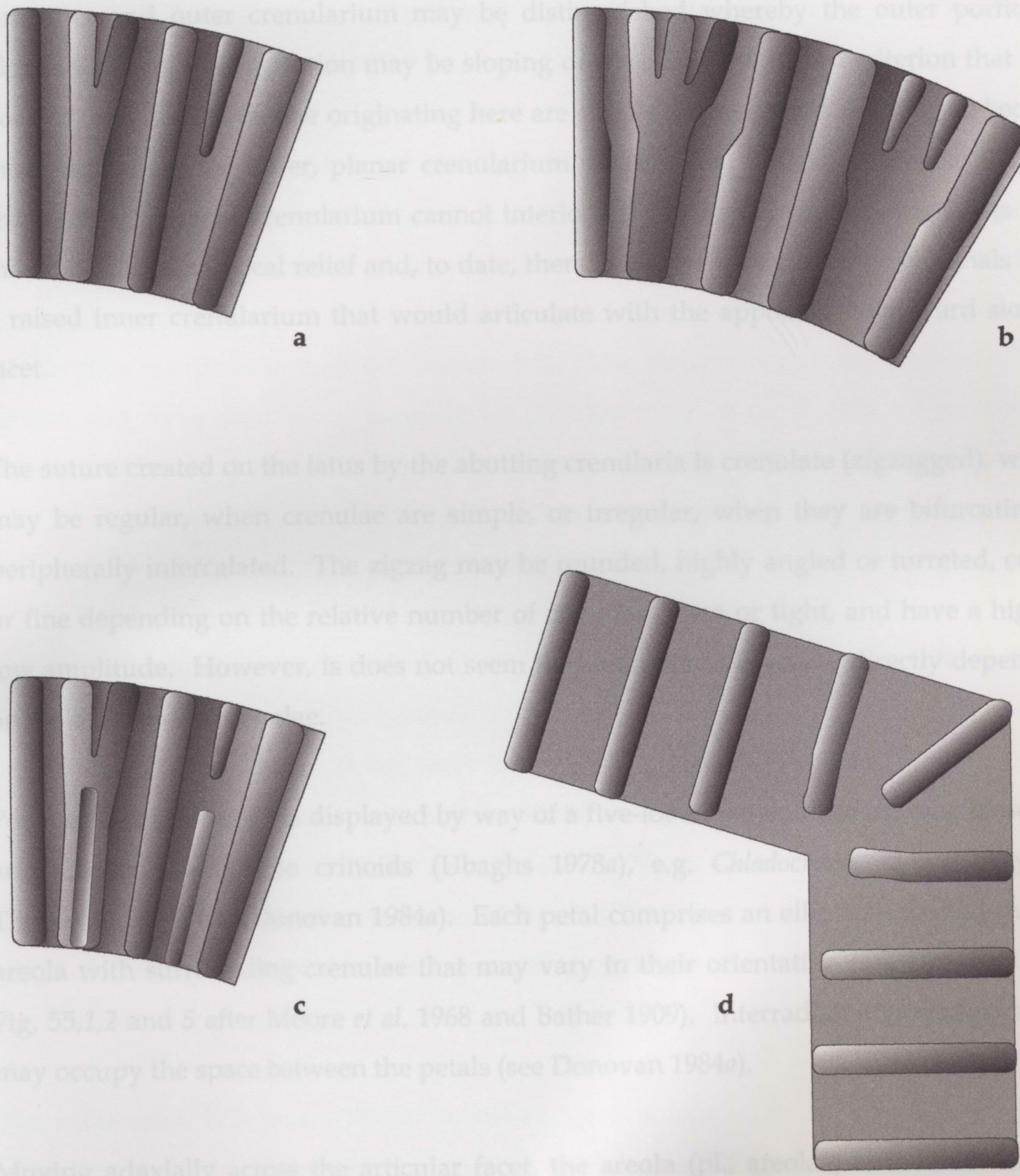


Figure 5.4.*a* to *d*. Diagrammatic examples of crenulae multiplication and growth. *a* shows the most common form of bifurcation of culmen and intercalation of short, peripheral culmen. *b*, rarely seen trifurcation of culmen from same point along its length. *c*, rarely seen intercaltion of broken peripheral and adaxial culmen and culmen with counterpart ridge. *d*, insertion of culmen into corner extremity of pentagonal crenularium.

These crenulae gradually move along towards the centre of the long sides as growth continues and further shorter ones are then formed again in the corners.

An inner and outer crenularium may be distinguished whereby the outer portion is planar while the inner portion may be sloping down adaxially. It is a criterion that both possess crenulae. Crenulae originating here are simple and continue abaxially to become those that cover the outer, planar crenularium. Intuitively, it seems probable that the crenulae of the inner crenularium cannot interlock if there are two apposing facets with this same morphological relief and, to date, there is no evidence that any columnals have a raised inner crenularium that would articulate with the apposing downward sloping facet.

The suture created on the latus by the abutting crenularia is crenulate (zigzagged), which, may be regular, when crenulae are simple, or irregular, when they are bifurcating or peripherally intercalated. The zigzag may be rounded, highly angled or turreted, coarse or fine depending on the relative number of crenulae, open or tight, and have a high or low amplitude. However, is does not seem that the pattern is *always* directly dependent on the relief of the crenulae.

Pentaradiate symmetry is displayed by way of a five-lobed petalodium in some Mesozoic and Cenozoic articulate crinoids (Ubaghs 1978*a*), e.g. *Chladocrinus decorus* (Wyville Thomson, 1864) (see Donovan 1984*a*). Each petal comprises an elliptical- to oval-shaped areola with surrounding crenulae that may vary in their orientation (see Ubaghs 1978*a*, Fig. 55,*1,2* and *5* after Moore *et al.* 1968 and Bather 1909). Interradial interpetaloid zones may occupy the space between the petals (see Donovan 1984*a*).

Moving adaxially across the articular facet, the **areola** (pl., areolae) is the next feature whose periphery reaches the edge of the crenularium. It is generally smooth and planar, or gently sloping downwards adaxially, and lies just below, or level with, the plane of articulation (Ubaghs 1978*a*), *i.e.* up to mid-height of the crenulae (if it lies below the level of articulation a gap would be created between apposing facets of articulated columnals). Both its inner and outer peripheries may slope rapidly upwards to meet with adjacent morphological features. Its outline may be circular, or have a tetraradiate, pentaradiate or hexaradiate symmetry.

Abutting the areola adaxially is the **perilumen**. This is a raised, or apposing sunken, area that surrounds the inner lumen and that commonly shows signs of being worn in its microstructure (Macurda and Meyer 1975). Although it may be smooth on its surface, it often displays a vermiculate, tuberculate or granulate sculpture (Ubaghs 1978*a*) which may interlock with an apposed facet.

Ubaghs (1978*a*) following Moore *et al.* (1968) described the term **claustrum** (pl., claustra) as an axial canal constriction at columnal mid-height. Herein it is to be considered as part of the articular facet. Claustra are any part of a columnal which lies adaxially adjacent to the areola or perilumen and is primarily inclined downwards towards the lumen, but which does not possess crenulae (Figure 5.5). The claustrum may be split into inner, central and outer portions depending on the directions of inclination. However, the outermost portion is always inclined downwards adaxially. The adaxial surface, *i.e.* that which extends longitudinally and which outlines the axial canal, may be planar, convex or concave and may be sculptureed (Ubaghs 1978*a*).

There are discrepancies as to what the axial canal and lumen constitute (see below). In the present study the **lumen** (pl., lumina) is the most central cavity of each columnal, its highest and lowest planes being level with those of the innermost extremities of the abutting facetal feature, *i.e.* perilumen, areola or claustrum. It may be centric or eccentrically positioned within the articular facet. When eccentricity occurs it generally affects the radii of the other features of the facet. Lumina outlines may be circular, elliptical, pentagonal, pentasteroidal, pentalobate, tetragonal, tetrasteroidal, tetralobate or rarely trigonal in shape.

The **axial canal** is a void with no lateral expansions (spatia) or constrictions (claustra) (Figure 5.5). During life it held longitudinal extensions of the coelom and aboral nervous systems. These had straight sides and no lateral projections or expansions, except for canals at mid-columnal height, which continued into cirri or cirrus-related structures (canaliculae (Ubaghs 1978*a*)), or intracolumnal canals (fossulae (Ubaghs 1978*a*)). The transverse outline of the widest part of the lumen is representative of that of the axial canal so the terms used for the lumen outline can be applied here. When columnals are articulated the axial canal is a longitudinal space with straight sides. The exception is when the claustra or lumina have longitudinally convex or concave axial extremities.

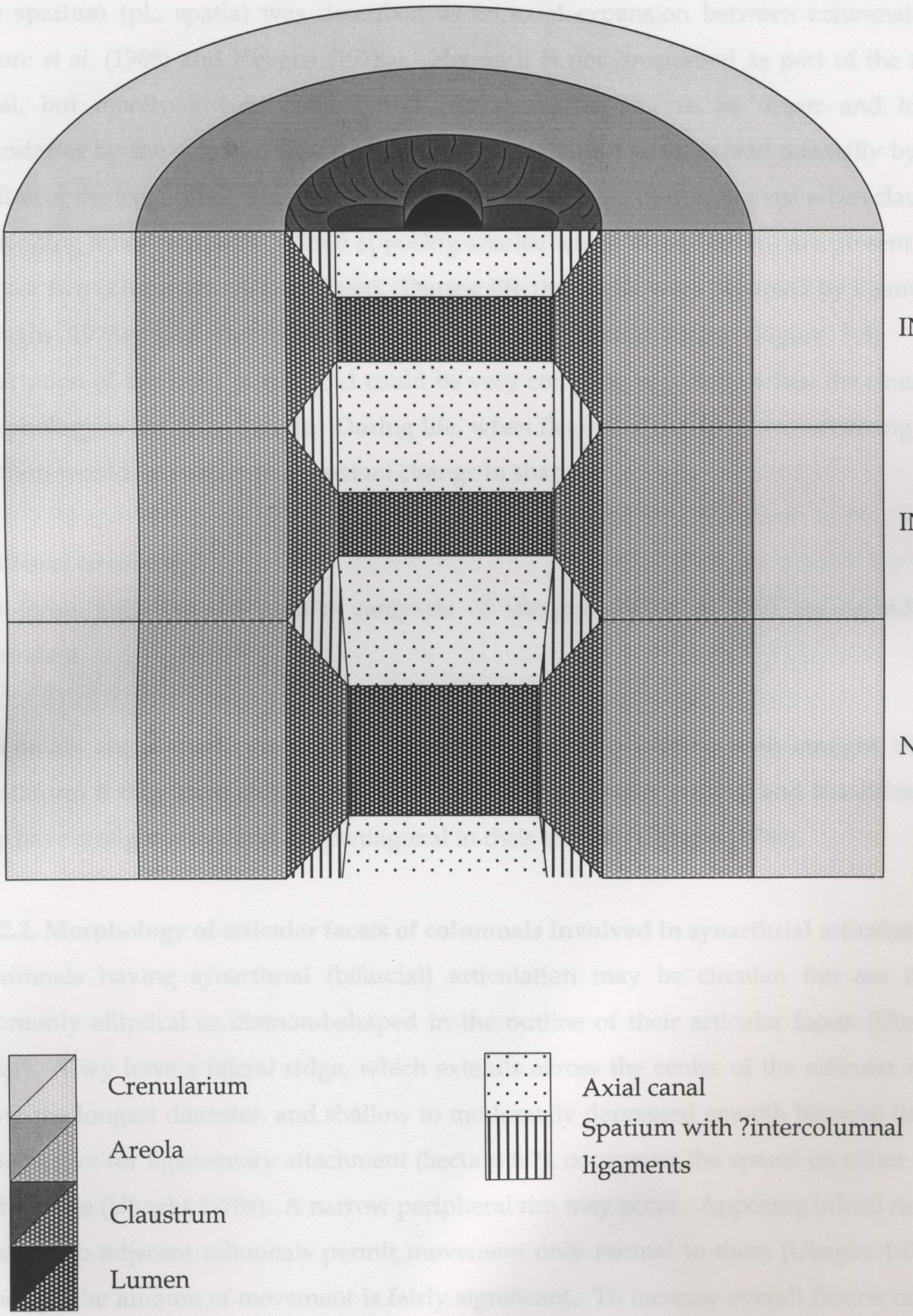


Figure 5.5. Medial longitudinal section of a hypothetical pluricolumnal with two orders of columnal (IN-IN-N). Notice how diameter of lumen (and hence axial canal) may be reduced when penetrating nodals if claustrum extends further adaxially.

The **spatium** (pl., spatia) was described as an axial expansion between columnals by Moore *et al.* (1968) and Ubaghs (1978*a*). Herein it is not considered as part of the axial canal, but merely a void created and restricted abaxially in its upper and lower boundaries by the claustral (or areola or inner crenularial) surfaces and adaxially by the outline of the axial canal. It is obvious, therefore, that spatia may only exist when claustra (or sloping inner crenularia or two apposing areolae which do not touch) are present and at least two columnals are articulated. During life the spatia were occupied by ligaments (Ubaghs 1978*a*) that ran between two apposing claustral facets (Figure 5.5). The description of the form of the void could be very complex, especially when the claustral morphology is less than simple. During life, when flexion of the stem was occurring, the spatium would be subject to a constant change in shape.

Additional terminology

The terms jugulum and jugular ramparts of Ubaghs (1978*a*, p. T79) are considered redundant.

Columnals are termed cylindrical if they are circular in outline with straight latera, moniliform if they have strongly convex latera with a circular outline, and basaltiform if they have straight latera and are pentagonal in their outline (Ubaghs 1978*a*).

5.2.2.2. Morphology of articular facets of columnals involved in synarthrial articulation

Columnals having synarthrial (bifascial) articulation may be circular, but are most commonly elliptical or diamond-shaped in the outline of their articular facets (Ubaghs 1978*a*). They have a fulcral ridge, which extends across the centre of the articular facet along the longest diameter, and shallow to moderately depressed smooth bifascial fields, which serve for ligamentary attachment (Section 6.2), occupying the spaces on either side of the ridge (Ubaghs 1978*a*). A narrow peripheral rim may occur. Apposing fulcral ridges of any two adjacent columnals permit movement only normal to them (Ubaghs 1978*a*), although the amount of movement is fairly significant. To increase overall flexion of the stem, in some columnals (e.g. those belonging to members of the family Platycrinitidae) the fulcral ridges of opposing facets of each single columnal are set at an angle to each other which, when articulated with other similar columnals, gives the appearance of the stem being twisted. When the fulcral ridges are set at right angles to each other the columnal has a tetragonal outline (Ubaghs 1978*a*) (see Moore *et al.* 1968, Fig. 5,*J*). The two

opposing ridges may or may not be seen in lateral view.

5.2.2.3. Morphology of articular facet of columnals involved in synostosial articulation

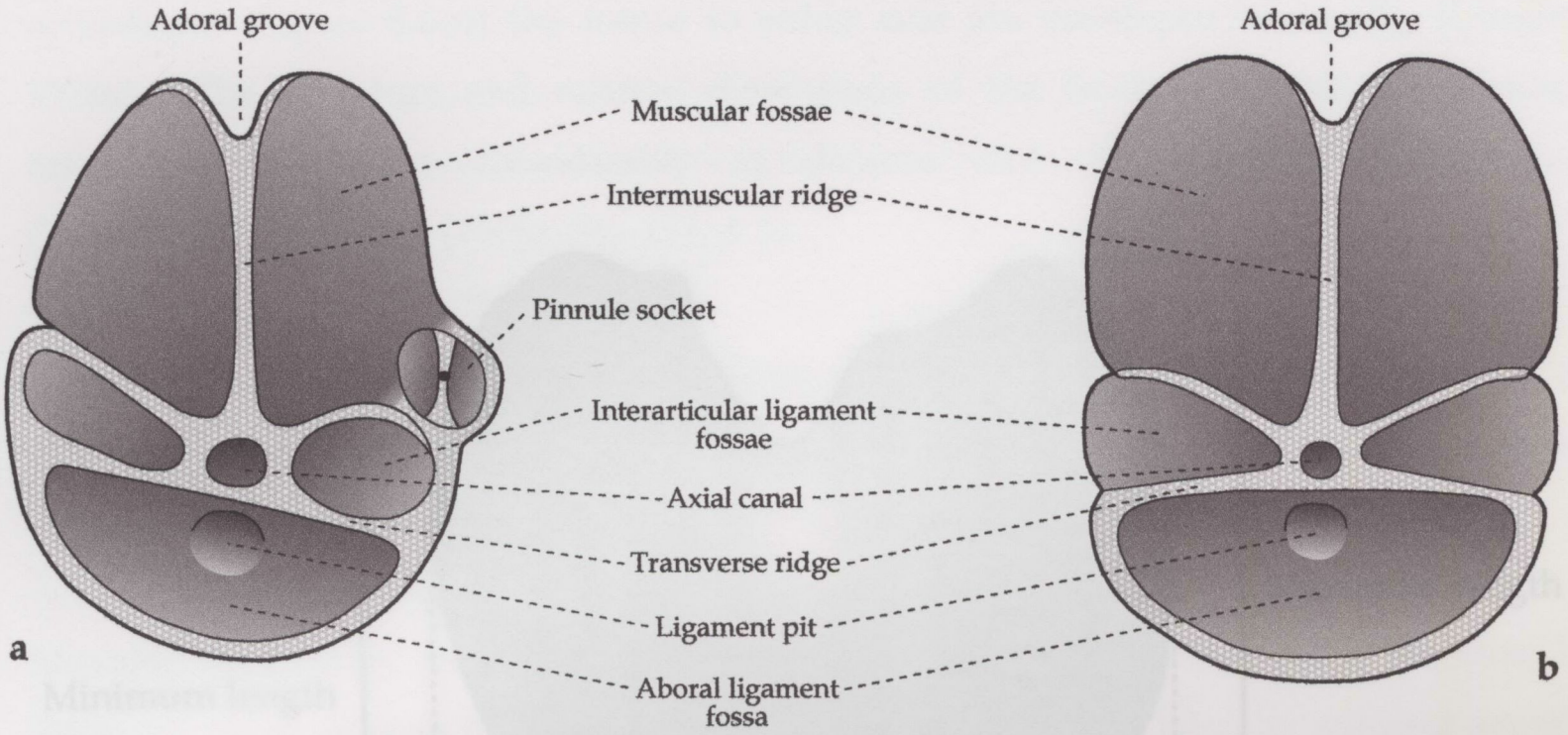
Synostosial articulation is rare, especially amongst Carboniferous genera, and in modern crinoids is found only in the radicular cirri of bourgueticrinids (Donovan 1990). The two adjacent articulating facets have no morphological features of relief, *i.e.* they are simply planar (Ubaghs 1978*a*). Although flexion can occur in all directions, it is minimal (Ubaghs 1978*a*). Donovan (1990) suggested the lack of flexibility provided by a synostosial suture could be improved by the ligament properties and arrangements between the columnals. Unlike symplexy, however, rotation probably occurs around the columnal axis. This would put the small ligaments that unite two apposing facets together under tension and render the stem in danger of breaking. Increased flexibility may be gained by facets that are concave as this creates more surface area for ligamentary fibre attachment between apposing facets. In this instance a narrow articular rim (Ubaghs 1978*a*) occupies the periphery of the columnal. A straight suture line is observed laterally (Ubaghs 1978*a*; Lewis 1980; Donovan 1986*a*). A close suture is created by a zygosynostosis when mobility is virtually non-existent between apposing articular facets due to accreted calcareous deposits. This is rare in stems but common, along with ankylosis, in holdfasts (Ubaghs 1978*a*).

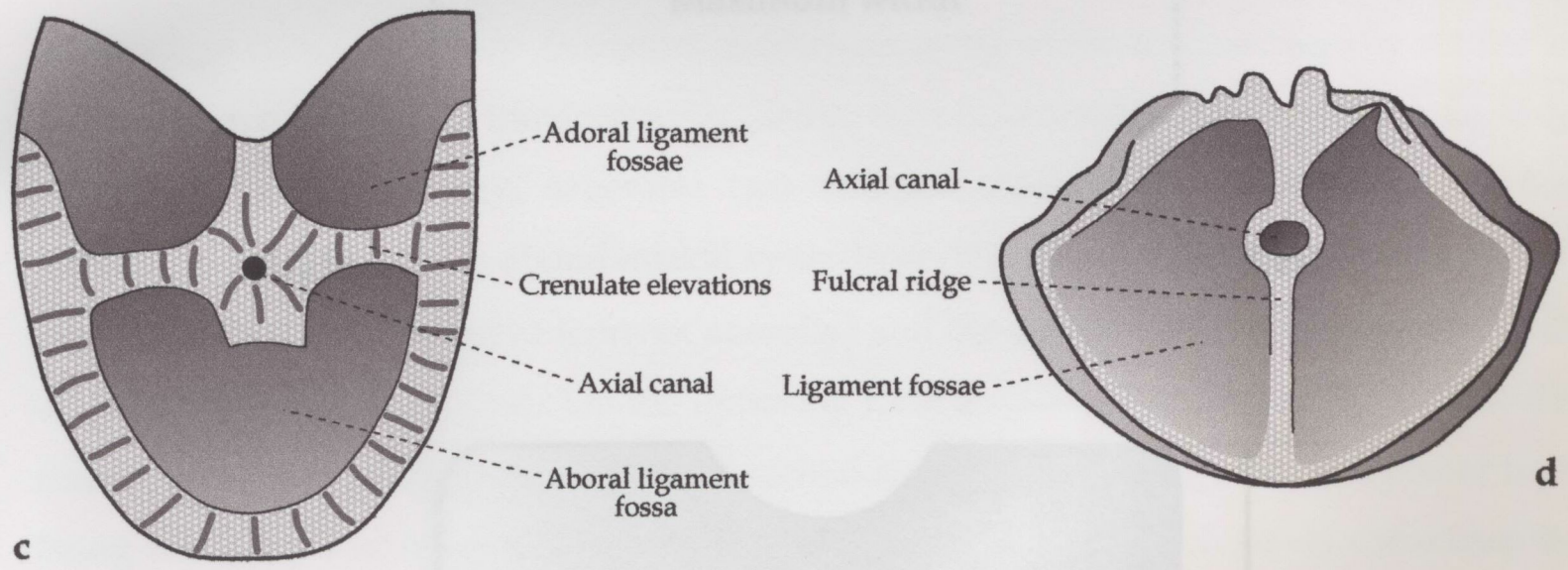
5.2.2.4. Articulations between brachials

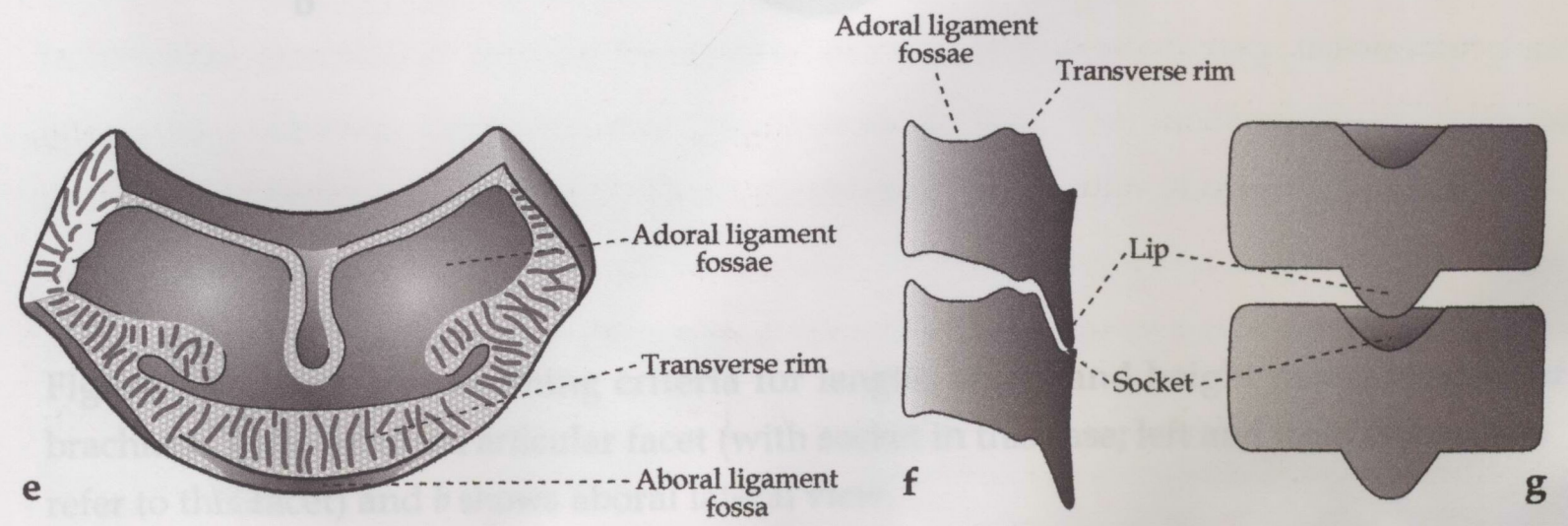
Brachial articulations between each other and the arm facet with which they articulate may be muscular (Figure 5.6.*a*,*b*), involving both muscular and ligamentary tissues, or ligamentary (Figure 5.6.*c*-*g*) which involves only the latter.

In general the surface of a muscular facet has a prominent fulcral ridge, extending horizontally or obliquely across, with a somewhat central axial canal and five fossae. Ligaments are attached to the aboral ligament fossa which occupies the area on the aboral side of the fulcral ridge and which may possess a deeper ligament pit. Two interarticular ligament fossae lie adorally to the fulcral ridge on either side of the axial canal. An intermuscular ridge extending from the axial canal to the adoral groove separates two adoral muscular fossae. If the fulcral ridge is perpendicular to the adoral-aboral axis of the facet (straight muscular articulation (Figure 5.6.*b*)) the left and right sides of the facet are essentially symmetrical, but if the ridge is at an angle to the axis (oblique muscular

Figure 5.6.*a-g*. Diagrams of brachials displaying various forms of articular facet articulations. *a*. Schematic oblique muscular articulation (from Ubaghs 1978*a* (Fig. 134, *2*) after Clark 1915). *b*. Schematic straight muscular articulation (from Ubaghs 1978*a* (Fig. 134, *1*) after Clark 1915). *c*. Trifascial articulation on secundibrachial of *Paradichocrinus polydactylus* (Casseday and Lyon) (from Ubaghs 1978*a* (Fig. 139, *4*) after Van Sant and Lane 1964). *d-g*. Synarthrial articulation. *d*. *Himerometra bassleri* Gislén (from Ubaghs 1978*a* (Fig. 140, *1*) after Gislén 1934), an example of transverse synarthry. *e-g*. *Forbesiocrinus nobilis* De Koninck and Le Hon, an example of aboral-adoral synarthry. *e* shows distal facet of primibrachial, *f* and *g* show two articulated brachials in aboral aspect and in medial longitudinal section (following Ubaghs 1978*a* (Fig. 141, *1*, *3*, *2*) after Springer 1920).


Adoral groove
Muscular fossae
Intermuscular ridge
Pinnule socket
Interarticular ligament fossae
Axial canal
Transverse ridge
Ligament pit
Aboral ligament fossa
a
Adoral groove
b


Adoral ligament fossae
Crenulate elevations
Axial canal
Aboral ligament fossa
c
Axial canal
Fulcral ridge
Ligament fossae
d


Adoral ligament fossae
Transverse rim
Adoral ligament fossae
Transverse rim
Aboral ligament fossa
e
Lip
Socket
f
g

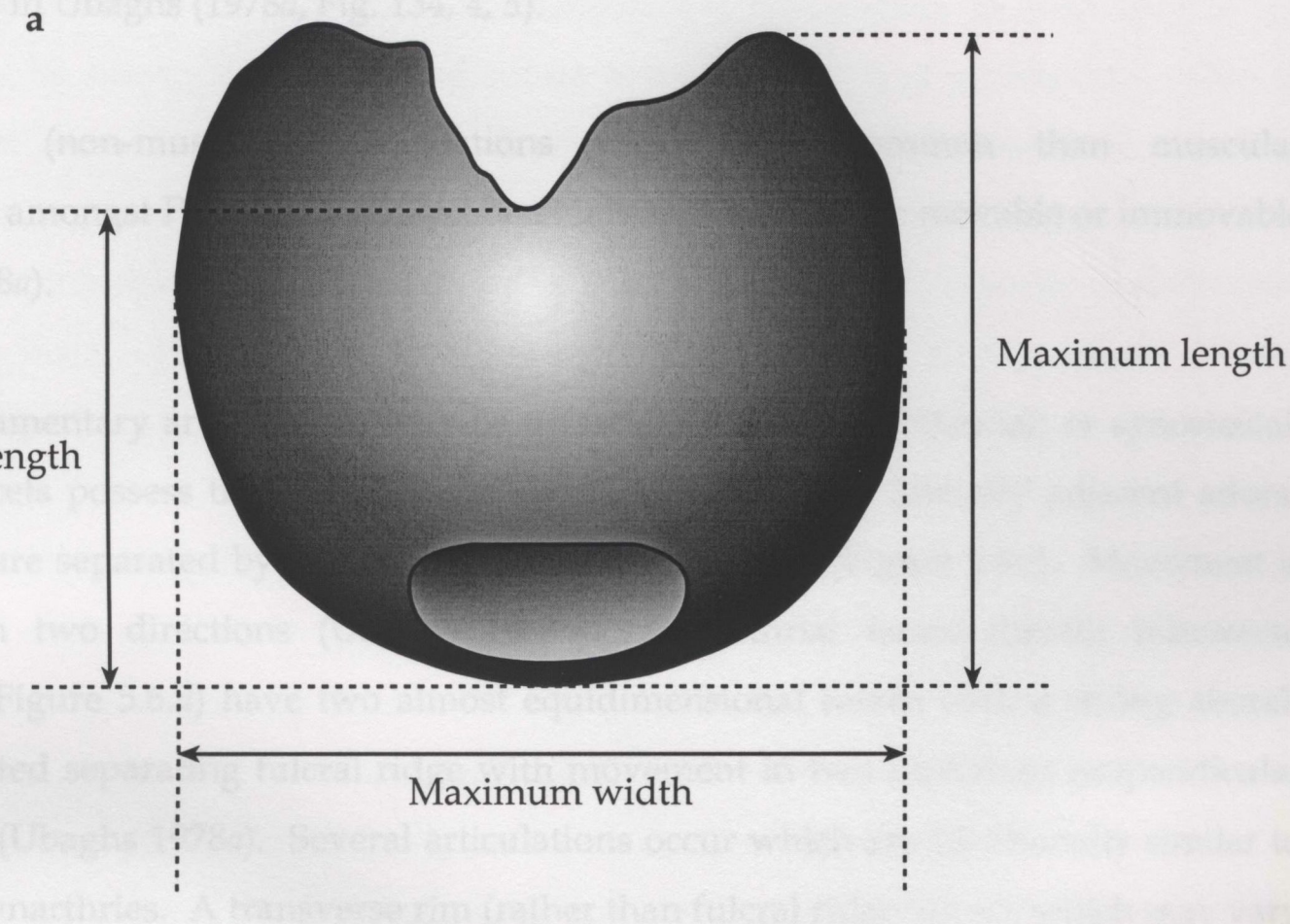


Figure 5.7. Diagrams outlining criteria for length, width and height measurements of brachials. *a* shows distal articular facet (with socket in this case; left and right orientation refer to this facet) and *b* shows aboral lateral view.

articulation (Figure 5.6.*a*)) the fossae to either side are developed unequally (Ubaghs 1978*a*). The sculpture and relative dimensions of the facets involved in muscular articulation can vary considerably as demonstrated in *Marsupites testudinarius* (Schlotheim) in Ubaghs (1978*a*, Fig. 134, *4*, *5*).

Ligamentary (non-muscular) articulations were more common than muscular articulations amongst Palaeozoic crinoid brachials and were either movable or immovable (Ubaghs 1978*a*).

Movable ligamentary articulations may be trifascial, synarthrial (bifascial) or synostosial. Trifascial facets possess three fossae, one aboral fossa and two laterally adjacent adoral fossae, that are separated by sometimes crenulate elevations (Figure 5.6.*c*). Movement is moderate in two directions (Ubaghs 1978*a*). Synarthrial facets (herein transverse synarthry) (Figure 5.6.*d*) have two almost equidimensional fossae with a strong aboral-adoral oriented separating fulcral ridge with movement in two directions perpendicular to the ridge (Ubaghs 1978*a*). Several articulations occur which are functionally similar to transverse synarthries. A transverse rim (rather than fulcral ridge *per se*), which may vary greatly in its morphology, separates two unequal shallow fossae that may have a crenulated margin (herein aboral-adoral synarthry) (Figure 5.6.*e*). The transverse rim on many flexible brachials curve (convex aborally) and the aboral fossa inclines downwards very steeply to form a socket. On the opposing facet a rounded process or lip fits into the aboral socket of the apposing proximal brachial facet (Figure 5.6.*e-g*), the margins of both being crenulated which restricts any movement laterally. On such facets there may be only one adoral fossa. Brachials with synostosial articulation have slightly concave facets which may be smooth or rugose and which may have a surrounding crenulate rim. A small amount of movement is permitted in all directions.

Immovable articulation may be by zygosynostosis, symplexy, syzygy, symmorphy or ankylosis. During the Palaeozoic zygosynostosy was the most common type of articulation between brachials. Their facets are essentially planar, but often with indistinct strengthening crenulae or vermiculae, or sometimes a low ridge that fits into a groove on the apposing facet. Although a very small amount of movement is permitted by such brachial facets the arms which they compose may have a multitude of small brachials to slightly increase overall flexibility. In some camerates crenulae interlock on

apposing brachial facets to give a symplectial articulation that, laterally, produces a crenulate suture. Movement is very slight, but again overall flexibility of the arm may be increased by having a high number of low brachials. If the crenulae of apposing brachial facets do not interlock *i.e.* culmina meet culmina, the articulation, as seen only in the articulates, is by syzygy and the lateral suture is seen as a ring of perforations. One or two toothlike projections or ridges may fit into corresponding depressions on apposing facets of symmorphially articulating brachials. Crenulae may also be present. Ankylosis occurs by varying amounts of stereom being deposited between vertically and laterally adjacent brachials. The joint produced is completely rigid. [See also Figure 5.7 for measurement criteria.]

5.2.3. LONGITUDINAL SECTIONS OF COLUMNALS

Longitudinal cross-sections are important in distinguishing between those columnals that appear to be homomorphic (by their lateral and articular facet morphologies) belonging to homeomorphic stems, but which, in fact, are heteromorphic. Narrow, low columnals, which cannot always be seen laterally, are also disclosed in longitudinal section. The width of the axial canal is observed, as is the outline of the inner boundary of the claustrum. The difference in the stereom microstructure can also be observed longitudinally (Plate 12).

5.2.4. COLUMNAL AND PLURICOLUMNAL MORPHOMETRICS

Various heights and diameters of columnals, their morphological features and pluricolumnals are measured in microns under the SEM, or in millimetres under the binocular microscope (Section 3.3). Comparing these measurements as mathematical indices means that it is possible to compare different facets and this may even be used in the diagnosis of a columnal morphospecies (the ratio from the comparison of two features is multiplied by 100 to give a whole number, *i.e.* the index or percentage) (Moore *et al.* 1968; Ubaghs 1978*a*; Donovan 1986*a*). Only relevant and important indices for each columnal morphospecies are utilised (Moore *et al.* 1968). These data are especially useful when looking at ontogenetic changes (Section 5.3.1). [See Figure 5.8 for symbols used in equations and Figure 5.9 for diagrams accompanying Section 5.2.4.]

5.2.4.1. Facetal indices

Once articular facetal boundaries have been deciphered each morphological feature is

A	areola	K	columnal
Ai	areolar index	KH	columnal height
C	crenularium	KHi	columnal height index
Ci	crenularial index	KSi	columnal shape index
CL	claustrum	L	lumen
CLi	claustral index	Li	luminal index
D	diameter	N	nodal
E	epifacet	Ni	nodal index
Ei	epifacetal index	NT	noditaxis
F	articular facet	P	perilumen
Fi	facetal index	Pi	periluminal index
FSi	facetal shape index	R	radius
FL	flange	Z	zygum
FLi	flange index	Zi	zygal index
H	height index	y	maximum diameter, height or ratio
IN	internode	x	minimum diameter, height or ratio
INi	internodal index		

Figure 5.8. Symbols used for columnal and pluricolumnal indices and measurements (modified after Moore *et al.* 1968).

measured for its radii or diameter. When columnals[1] have non-circular outlines in any parts of their morphologies it is necessary to calculate a mean (Moore *et al.* 1968). This is also necessary if a columnal has been deformed to create an irregular outline or, for instance, the crenularium is wider on one side of the facet than the other. The method used herein differs slightly to that suggested by Moore *et al.* (1968), Ubaghs (1978*a*) and Donovan (1986*a*), and applied in Moore and Jeffords (1968) and Donovan (1986*a*; 1989*a*), where only two measurements are taken from features with a pentaradiate symmetry, *i.e.* the minimum (x) and maximum (y) radii or diameters. This has been found to be unsatisfactory in the present study since a pentagonal lumen is often irregular in its outline and the lobes of pentalobate lumina in certain columnal morphotypes, e.g. members of Columnal Group A, are of different dimensions. For a columnal possessing a pentalobate lumen it is necessary to take five diameter measurements, one from each angle to the extremity of each appropriate opposite lobe, and the mean calculated (Figure 5.9.*a*). Of course, a pentaradiate lumen means that it is necessary for the surrounding areola, for example, to have an inner outline of the same shape. The average areola radius is calculated by taking the mean of ten measurements, *i.e.* the five maximum and minimum radii measurements. For elliptical outlines two measurements are taken, *i.e.* the

[1] When measuring cirrals the word cirral may be substituted for columnal in an equation where this is appropriate.

maximum and minimum radii (or diameters for columnal or lumen outlines), and the mean calculated (Figure 5.9.*e*) (Moore *et al.* 1968). Ovate columnals are measured as on Figure 5.9.*h* where the mean articular facet diameter is found by measuring FD*y* across the longest axis of the facet and FD*x* across the minimum true diameter of the facet. This smaller axis usually coincides with that of the lumen and other features of the articular facet. It may be necessary to take means of apparently circular facetal features and facets themselves as often they are not exactly so. When measuring columnals with tetrameral symmetry (Figure 5.9.*g*) the diameter/radius of facetal features is taken halfway along the long side and perpendicular to it. Measurements through the diagonal are not used. Moore *et al.* (1968) did not mention, or did not use, deformed columnals. However, the use of such specimens is sometimes necessary.

To exemplify the methods of Moore *et al.* (1968) and Ubaghs (1978*a*) the following equation was used to find the crenularial index;

Crenularial Index = *Ratio of total width (diameter) of crenularium to that of columnal articulum (facet)* x 100

or, in short,

Ci = 2CR/FD x 100 (circular or regularly-shaped crenularium)

Ci = (CR*x* + CR*y*)/FD x 100 (non-circular or irregularly-shaped crenularium and a regularly-shaped articular facet) and so on...

Donovan (1986*a*) modified this slightly to,

Crenularial Index, Ci = $\frac{\text{(Total width (i.e. diameter) of crenularium, CD)}}{\text{(Total width of articular facet, FD)}}$ x 100

since 2CR is equal to CD.

Taking into account the above discussion the following indices formulas, used herein, are modified after Moore *et al.* (1968), Ubaghs (1978*a*) and Donovan (1986*a*) to include mean measurements of all outlines and shapes of articular facets and their morphological

features. An equation for the claustral index has been devised. However, since the claustrum is included as part of the articular facet herein its total mean diameter is not compared with that of the lumen as was suggested by Moore *et al.* (1968), but with the remainder of the articular facet. When discussing elliptical facets, such as those of columnals that belonged to *Platycrinites*, the bifascial fields may be interchanged with the term areola and peripheral rim with crenularium for ease of insertion into equations. The sum of all indices over a particular columnal facet must equal 100 (Moore *et al.* 1968). The zygal index is a reciprocal of the luminal index (Moore *et al.* 1968).

Crenularial Index = *Ratio of total mean diameter of crenularium to that of articular facet* x 100

Ci = (2 x mean CR)/(mean FD) x 100

Areolar Index = *Ratio of total mean diameter of areola to that of articular facet* x 100

Ai = (2 x mean AR)/(mean FD) x 100

Claustral Index = *Ratio of total mean diameter of claustrum to that of articular facet* x 100

CLi = (2 x mean CLR)/(mean FD) x 100

Periluminal Index = *Ratio of total mean diameter of perilumen to that of articular facet* x 100

Pi = (2 x mean PR)/(mean FD) x 100

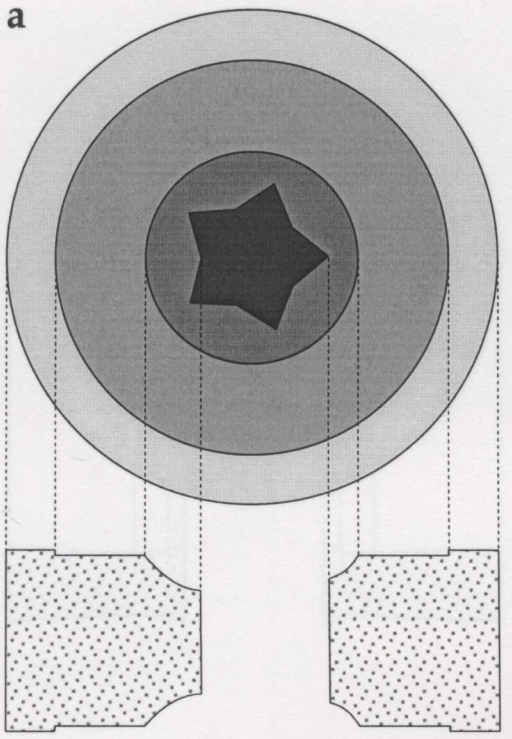
Luminal Index = *Ratio of mean diameter of lumen to that of articular facet* x 100

Li = (mean LD)/(mean FD) x 100

Zygal Index = *Ratio of total mean diameter of zygum to that of articular facet* x 100

Zi = (2 x mean ZR)/(mean FD) x 100

a



Ci = (2 x mean CR)/(mean FD) x 100
Ci = (2x5.0)/49.0 x 100
Ci = 20.4

Ai = (2 x mean AR)/(mean FD) x 100
Ai = (2x9.0)/49.0 x 100
Ai = 36.7

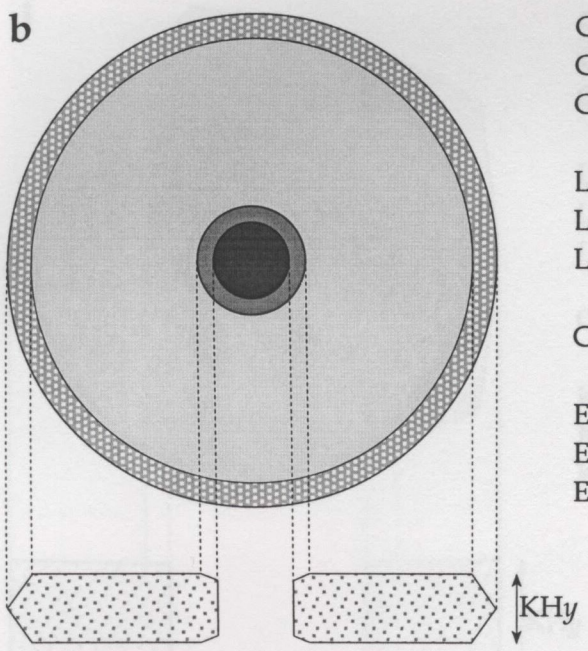
CLi = (2 x mean CLR)/(mean FD) x 100
CLi = (2x4.0)/49.0 x 100
CLi = 16.3

Li = (mean LD)/(mean FD) x 100
Li = 13.0/49.0 x 100
Li = 26.5

Ci + Ai + CLi + Li = 20.4 + 36.7 + 16.3 + 26.5 = 100.00

KHi = KH*y*/(mean KD) x 100
KHi = 18.0/49.0 x 100
KHi = 36.7

b



Ci = (2 x mean CR)/(mean FD) x 100
Ci = (2x16.5)/44.0 x 100
Ci = 75.0

CLi = (2 x mean CLR)/(mean FD) x 100
CLi = (2x1.5)/44.0 x 100
CLi = 6.8

Li = (mean LD)/(mean FD) x 100
Li = 8.0/44.0 x 100
Li = 18.1

Ci + CLi + Li = 75.0 + 6.8 + 18.2 = 100.00

Ei = (2 x mean ER)/(mean KD) x 100
Ei = (2x2.5)/49.0 x 100
Ei = 10.2

KHi = KH*y*/(mean KD) x 100
KHi = 7.0/49.0 x 100
KHi = 14.3

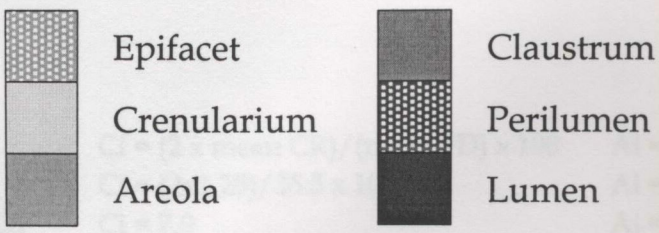
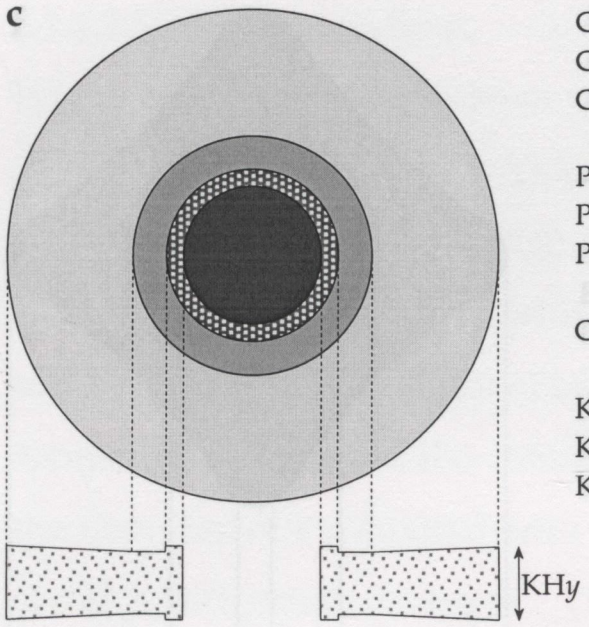


Figure 5.9. *a-h.* Hypothetical columnal facets, with medial longitudinal sections, to exemplify morphometrics of facetal features and latera and how they can be used to produce indices (diagrams and equations modified after Moore *et al.* (1968) and Donovan (1986*a*)). [All measurements are approximate in mm at printed size.]

c



Ci = (2 x mean CR)/(mean FD) x 100
Ci = (2x12.5)/49.0 x 100
Ci = 51.0

Ai = (2 x mean AR)/(mean FD) x 100
Ai = (2x3.5)/49.0 x 100
Ai = 14.3

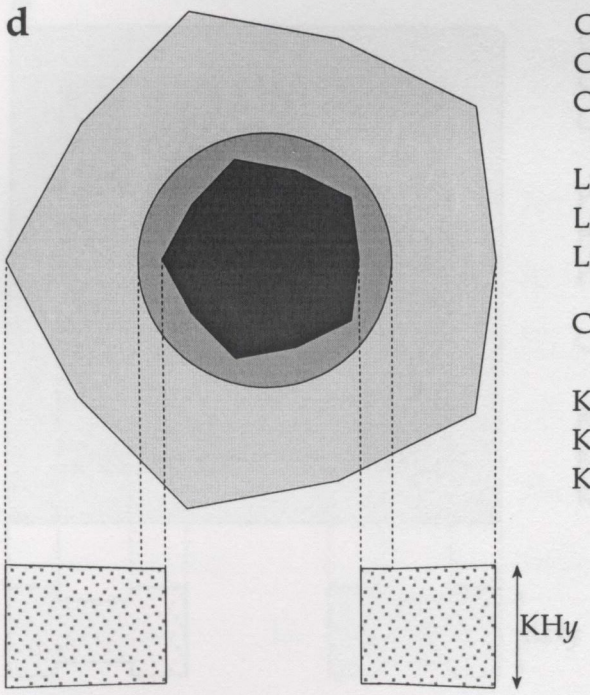
Pi = (2 x mean PR)/(mean FD) x 100
Pi = (2x1.5)/49.0 x 100
Pi = 6.1

Li = (mean LD)/(mean FD) x 100
Li = 14.0/49.0 x 100
Li = 28.6

Ci + Ai + Pi + Li = 51.0 + 14.3 + 6.1 + 28.6 = 100.00

KHi = KH*y*/(mean KD) x 100
KHi = 7.5/49.0 x 100
KHi = 15.3

d



Ci = (2 x mean CR)/(mean FD) x 100
Ci = (2x11.75)/49.0 x 100
Ci = 48.0

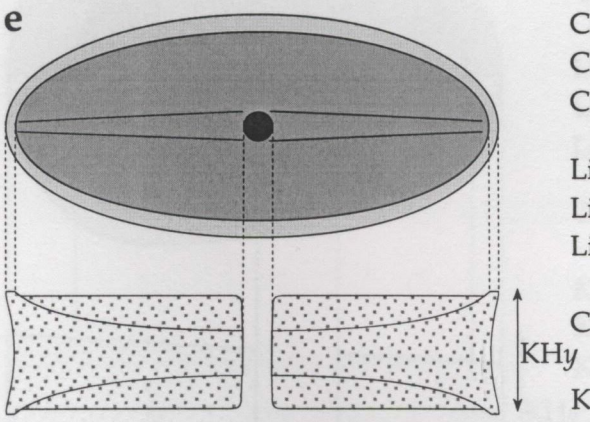
Ai = (2 x mean AR)/(mean FD) x 100
Ai = (2x2.75)/49.0 x 100
Ai = 11.2

Li = (mean LD)/(mean FD) x 100
Li = 20.0/49.0 x 100
Li = 40.8

Ci + Ai + Li = 48.0 + 11.2 + 40.8 = 100.00

KHi = KH*y*/(mean KD) x 100
KHi = 12.0/49.0 x 100
KHi = 24.5

e



Ci = (2 x mean CR)/(mean FD) x 100
Ci = (2x1.25)/35.5 x 100
Ci = 7.0

Ai = (2 x mean AR)/(mean FD) x 100
Ai = (2x15.0)/35.5 x 100
Ai = 84.5

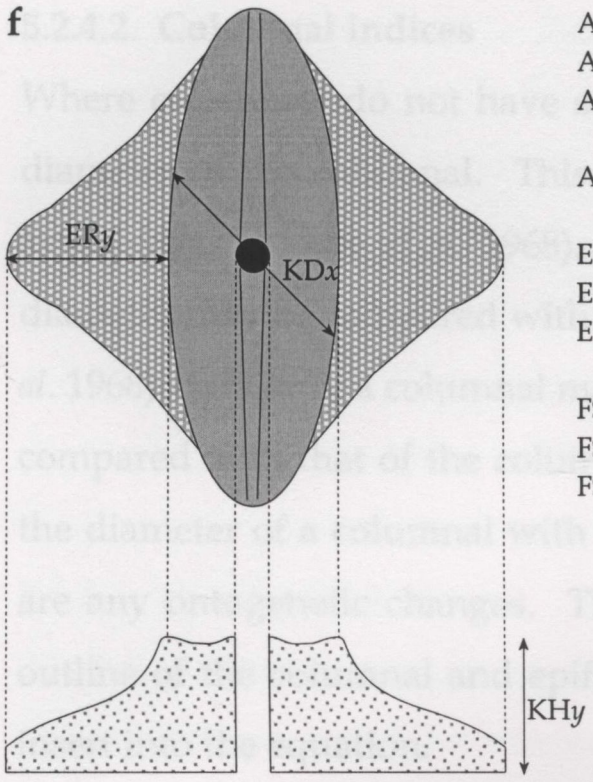
Li = (mean LD)/(mean FD) x 100
Li = 3.0/35.5 x 100
Li = 8.5

Ci + Ai + Li = 7.0 + 84.5 + 8.5 = 100.00

KHi = KH*y*/(mean KD) x 100
KHi = 12.0/35.5 x 100
KHi = 33.8

FSi = FD*x*/FD*y* x 100
FSi = 22.0/49.0 x 100
FSi = 44.9

f



Ai = (2 x mean AR)/(mean FD) x 100
Ai = (2x15.0)/33.0 x 100
Ai = 90.9

Li = (mean LD)/(mean FD) x 100
Li = 3.0/33.0 x 100
Li = 9.1

Ai + Li = 90.9 + 9.1 = 100.00

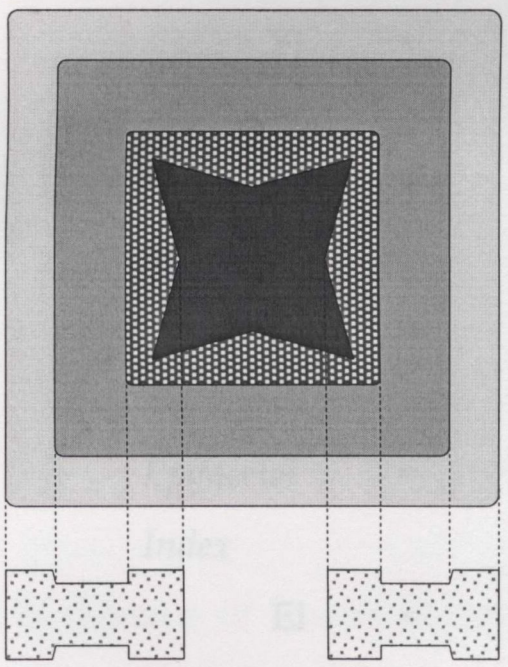
Ei = (2 x mean ER)/(mean KD) x 100
Ei = (2x8.0)/36.0 x 100
Ei = 44.4

KHi = KH*y*/(mean KD) x 100
KHi = 14.5/36.0 x 100
KHi = 40.3

FSi = FD*x*/FD*y* x 100
FSi = 17/49 x 100
FSi = 34.7

KSi = KD*x*/KD*y*
KSi = 11.5/24.5
KSi = 46.9

g



Ci = (2 x mean CR)/(mean FD) x 100
Ci = (2x5.0)/49.0 x 100
Ci = 20.4

Ai = (2 x mean AR)/(mean FD) x 100
Ai = (2x7.0)/49.0 x 100
Ai = 28.6

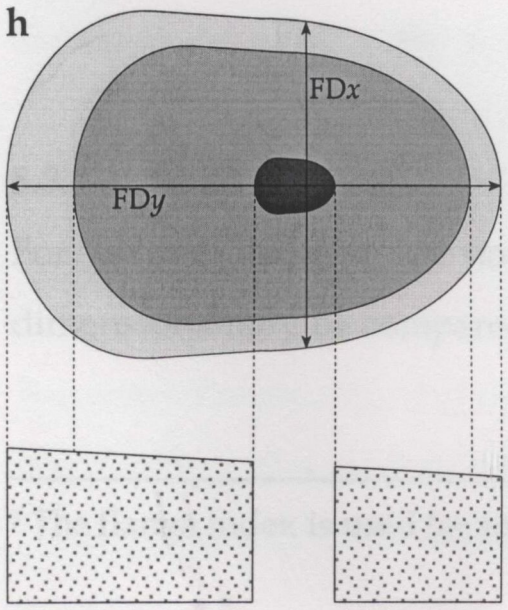
Pi = (2 x mean PR)/(mean FD) x 100
Pi = (2x5.5)/49.0 x 100
Pi = 22.5

Li = (mean LD)/(mean FD) x 100
Li = 14.0/49.0 x 100
Li = 28.6

Ci + Ai + Pi + Li = 20.4 + 28.6 + 22.5 + 28.6 = 100.00

KHi = KH*y*/(mean KD) x 100
KHi = 8.75/49.0 x 100
KHi = 17.9

h



Ci = (2 x mean CR)/(mean FD) x 100
Ci = (2x3.95)/40.7 x 100
Ci = 19.4

Ai = (2 x mean AR)/(mean FD) x 100
Ai = (2x13.15)/40.7 x 100
Ai = 64.6

Li = (mean LD)/(mean FD) x 100
Li = 6.5/40.7 x 100
Li = 16.0

Ci + Ai + Li = 19.4 + 64.6 + 16.0 = 100.00

KHi = KH*y*/(mean KD) x 100
KHi = 15.0/40.7 x 100
KHi = 36.9

FSi = FD*x*/FD*y* x 100
FSi = 32.0/49.5 x 100
FSi = 64.7

5.2.4.2. Columnal indices

Where columnals do not have straight, or almost straight latera, this increases the total diameter of the columnal. This can be compared with the facetal diameter to give the *facetal index* (Moore *et al.* 1968). A columnal may have a distinct epifacet, whose total diameter may be compared with that of the columnal to give the *epifacetal index* (Moore *et al.* 1968). Similarly a columnal may have an enlarged flange[5] whose total diameter may be compared with that of the columnal to give the *flange index*. It can be useful to compare the diameter of a columnal with its maximum height as indices, especially to see if there are any ontogenetic changes. This is the *height index* (Moore *et al.* 1968). Again, if the outline of the columnal and epifacet are non-circular then a mean must be calculated to insert into the equation.

Facetal Index = *Ratio of total mean diameter of articular facet to that of columnal* *x 100*

Fi = (mean FD)/(mean KD) x 100

Height Index = *Ratio of maximum columnal height to total mean columnal diameter* *x 100*

KHi = KH*y*/(mean KD) x 100

Epifacetal Index = *Ratio of total mean diameter of epifacet to that of columnal* *x 100*

Ei = (2 x mean ER)/(mean KD) x 100

Flange Index = *Ratio of total mean diameter of flange to that of columnal* *x 100*

FLi = (2 x mean FLR)/(mean KD) x 100

5.2.4.3. Shape indices

For columnals that are non-circular, *i.e.* elliptical or ovate, minimum to maximum dimensions may be compared mathematically to give shape indices (Moore *et al.* 1968).

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[5] The flange index is used for any lateral structure such as a ridge.

Columnal Shape Index	=	*Ratio of minimum columnal diameter to maximum columnal diameter*	*x 100*
KSi	=	KD*x*/KD*y* x 100	
Facetal Shape Index	=	*Ratio of minimum articular facet diameter to maximum articular facet diameter*	*x 100*
FSi	=	FD*x*/FD*y* x 100	

5.2.4.4. Noditaxial indices

The height of nodals and internodes can be expressed and compared as indices. The *nodal index* is a reciprocal of the *internodal index* and therefore total 100 (Moore *et al.* 1968).

Nodal Index	=	*Ratio of maximum height of nodal to that of noditaxis to which it belongs*	*x 100*
Ni	=	NH*y*/NTH*y* x 100	
Internodal Index	=	*Ratio of total maximum height of internode to that of noditaxis to which it belongs*	*x 100*
INi	=	INH*y*/NTH*y* x 100	

5.3. CLASSIFICATION OF DISARTICULATED CRINOID MATERIAL

In the case of crinoids naming and classification is usually carried out on the basis of the arrangement of the plates in the crown (Section 5.1). [Presumably this excludes the stem of crinoids since this part is commonly lacking and not fully described. However, when columnals, or pluricolumnals, are found associated with their respective crowns they are assigned the same name that the crown has been given.] Since crinoids have skeletons made up of many individual elements which disarticulate following death this method of classification is not easy to apply to the majority of crinoid fossils because articulated specimens are rare.

For some Palaeozoic, and many Mesozoic and Cenozoic, crinoid genera and species, the morphology of a stem or of its component columnals can be diagnostic (Ubaghs 1978*a*). However, this is rarely the case and since stems and columnals are rarely found attached

to their respective crowns establishing their taxonomic identity is usually almost impossible. It appears that for most crinoid taxa described in the literature from well-preserved crowns: 1) the morphology of the stem is not well preserved or seen, or 2) preserved and a) not formally described, or b) described insufficiently. Indeed, only a small percentage of taxa described in the *Treatise* (Moore and Teichert 1978*a*) make any reference to the morphology of the stem. There is a list of dissociated crinoid ossicles in the *Treatise* (Jeffords 1978), but again there are no descriptions of their morphologies. This is a source of more problems since there is no well illustrated and fully described list of disarticulated crinoid ossicles. A columnal described in detail by one author may have previously been only briefly described in conjunction with its crown by another author, so that the first author is unaware that the taxon has already been described and named.

In the past authors have assigned Linnaean binomina to individual disarticulated crinoid elements, usually with reference to the morphology of the ossicle itself. Rules of the International Code of Zoological Nomenclature (ICZN 1985) exclude the use of Linnaean binomina for disarticulated material of uncertain taxonomic origin. If disarticulated material can be identified as having been derived from a unique whole organism taxon, then it can serve as a type and can be assigned a Linnaean binomen. This is clearly not the case for much disarticulated crinoid material. For example, the distinctive columnals of the proxistele of allagecrinid microcrinoids cannot be identified to the level of genus or species unless the thecae are associated with them (G. D. Sevastopulo, pers. comm. 2000). Thus it would be impossible to identify the theca of a new genus based on a type species represented by stem ossicles alone. For this reason names proposed by the authors referred to above have not been validated. This highlights the problems in these methods of naming and classifying disarticulated material and another method must be used.

Moore (1939) stated that if an isolated ossicle with a name were subsequently found as part of a more complete specimen the name given to that ossicle would become invalid as it would be synonymous with the name of the complete crinoid. He reached the conclusion that it would be impractical to apply the rules of zoological nomenclature to isolated crinoid ossicles. His first suggestion to overcome this problem was by designation of groups by Roman letter with further subdivisions by Greek letter, for example, Columnals-A-alpha. The system did not conform with the strict rules of the code; the names that were given to the isolated ossicles were descriptive. Moore

recognised that two identical ossicles could come from two different real species, but they would still be placed in the same group in terms of isolated material. *"Description and cataloguing of ossicles does not require distinction according to zoological orders and families"*.

There are similar problems of taxonomic nomenclature amongst other fauna and flora including other echinoderm groups, conodonts and fish microvertebrates and plants. Moore (1939) noted that different generic/specific names of conodonts were given to individual elements rather than to the conodont animal itself and that different generic and/or specific names had been given to different parts of a single tree or plant. This latter method is, in fact, permitted by the International Code of Botanical Nomenclature which effectively validates the use of parataxa (Section 5.3.5).

Conodont taxonomy has been problematical in the past with different Linnaean binomina being assigned to similar individual conodont elements because they were not found with the conodont animal itself. When the individual elements were arranged as apparatuses, or later found together in the mouth of a conodont animal itself, it was found that several elements with different Linnaean binomina were found in a single mouth. Also, some individual elements, which had been assigned Linnaean binomina occurred vicariously in different multi-element taxa. 'Multi-element taxonomy', based on the entire conodont apparatus, has taken over from 'form taxonomy' (Section 5.3.4), which was based on the morphologies of individual elements (Duncan 1999), in conodont taxonomy.

Similar problems to those of conodonts have been encountered in the nomenclature of dissociated fish microvertebrates (Duncan 1999). Several types of teeth can occur in a single mouth with differing dentitions. Recognising their origin from the same species could be difficult without the availability of an entire specimen.

5.3.1. ONTOGENETIC CONSIDERATIONS

In some crinoid species the morphology of columnals may change throughout ontogeny (Simms 1989*a*). This can occur by growth in height and width and by development of the articular facet, especially with reference to the increase in the number of crenulae of the crenularium (Jeffords and Miller 1968). In several isocrinids columnals in the larval stage show synarthrial articulation whilst more mature specimens show pentaradiate symplectial articulation (Simms 1989*a*). Mistakes could be made by assigning different

names to columnals of different ontogenetic stages of a single species if their morphological traits are very different and it is not known that they are, in fact, conspecific. The same mistakes could be made when describing complete specimens.

5.3.2. DIFFERENT TAXA - VS - XENOMORPHIC STEMS

Different species of crinoid belonging to the same genus, or family, may have indistinguishable, or very similar, columnal morphologies. Likewise, columnals obtained from totally unrelated taxa may have similar columnal morphologies. It is likely, therefore, that some specimens of columnal morphospecies that have been put into the same group actually belonged to unrelated biological species. Because these specimens have been found independently of their calyces it is not possible to distinguish specifically between them. Ultimately, this could lead to an underestimate in crinoid diversity. And if fragmentary remains are ignored altogether this will also lead to an underestimate in crinoid diversity.

Columnals obtained from different portions of xenomorphic stems may have completely different morphologies, for example the Recent *Annacrinus wyvillethomsoni* (Section 4.3.1). This could lead to the inference that some groups of morphospecies have been obtained from different taxa when, in fact, they are conspecific. Assigning such morphospecies into different groups could lead to an overestimate in crinoid diversity. However, as soon as longer portions of columns are obtained, such errors will be corrected (S.Donovan, pers. comm. 2000).

5.3.3. INTRATAXON AND INTERTAXON MORPHOLOGICAL VARIATIONS

Problems in recognising whether columnals originate from the same or different species.

Simms (1989*b*) erected a new species, *Shroshaecrinus obliquistriatus*, on the evidence of only disarticulated ossicles. Columnals were used as part of the diagnosis. He remarked on and illustrated (Plate 14, Figs 18-22), "*the range and variation in development and configuration of crenulae*" on the articular facets of several columnals. Whether these columnals came from the same species maybe questioned since a long length of articulated stem was not found, the longest pluricolumnal comprising only four ossicles. Simms stated that the rationale for proposing a new species was because of differences in the sculpture of the crown, and that *S. obliquistriatus* is very closely related to *S. shroshaensis* and is probably ancestral to it. However it is possible that the columnals

could have come from an already described species of *Shroshaecrinus* rather than from a new one. If these columnals were indeed to be treated as originating from a single species, there would be interesting comparisons to be made with the changes in the pattern of the crenulae seen on facets of columnals belonging to Columnal Plesion A. In *S. obliquistriatus* the size and pattern of the crenulae of the perilumen alter, as do those of the crenularium, but not exactly the same changes seen in Columnal Plesion A. The changes in Columnal Plesion A could suggest that Columnal Types 1a to 1c could have originated from a stem of the same species. However, these changes are also sufficient to suggest that they could have derived from different species.

The problem of whether different columnal taxa are conspecific, and therefore from a xenomorphic stem, or are from different biological species is paramount in this study. As demonstrated above, there really is no reliable way to decipher the origins of two different columnals without a full length of stem. The history of palaeontology is full of such problems (the case of cf. *Anomalocaris* for example) (S. Donovan, pers. comm. 2000).

5.3.4. FORM TAXONOMY

Form taxa were described by Jeppsson and Merrill (1982) as being "*recognised solely on morphology without recourse to their phylogenetic relationships to any other organisms*". This implies a taxonomy of forms classified on the basis of morphological categories (Bengtson, S. 1985). Form taxa are useful taxonomic entities, different in their morphologies, but are not acceptable for nomenclature and classification as true genera and species (Moore, Jeffords and Miller 1968, p. 26). Biologically, "taxonomy" implies classification on phylogenetic relationships and S. Bengtson (1985) suggested "form classification" as a more appropriate term. The ICZN (1985) makes no allowance for the classification of these taxonomic entities.

5.3.5. PARATAXONOMY

There are discrepancies in the literature as to what a parataxon actually is and several definitions have been given in the past. Moore and Sylvester-Bradley (1957) proposed the term for a zoological classification and nomenclature set up specifically for dissociated parts of animals. Sylvester-Bradley's (1958) explanation was: "*Parataxa are artificial taxa, based on material deemed, by the ICZN, to be inadequate for diagnosis of natural taxa, and classified on arbitrary morphological grounds, without regard to relationships.*" This definition

excludes biological taxonomy bringing the concept closer to form taxonomy. In his description of parataxonomy, Melville (1979) implied that the status of parataxa or orthotaxa is directly related to the completeness of the material: "*[A parataxon is] a taxon based on a fragment or detached organ of an animal which can be classified at genus-group and species-group levels by comparison with other fragments or detached organs, but which cannot be assigned to the same taxa at those levels as the whole to which they belong.*" On distinguishing between conceptual biological taxa, he gave the following descriptions:

(Ortho)taxon - A conceptual taxon, which belongs to the unified taxonomic system that forms the core of biological systematics. Unless it is used relating to "parataxa", it may be called "taxon".

Sciotaxon - A (conceptual ortho)taxon, which represents an identical real taxon as another (conceptual ortho)taxon recognised on material of a different nature. [This replaces "parataxon" where the term had previously been used incorrectly.]

Parataxon - A conceptual taxon that belongs to a taxonomic system, which by formal decision, is outside the orthotaxonomic system covering the same group of organisms. It is based on a particular sort of material, *i.e.* a fragment or incomplete specimen.

A literal translation of "parataxonomy" was given by S. Bengtson (1985) as: "*A taxonomy existing outside an established orthotaxonomic system*".

From the point of view of their biostratigraphical use columnals could be artificially classified as parataxa. Several workers (Moore 1939; Yeltyschewa 1956; Moore and Jeffords 1968) (Section 5.1) have attempted a classification system using Linnaean binomina, but they have been rejected by the ICZN (1985) (Moore, Jeffords and Miller 1968, p. 26) since parataxa are not accepted as valid and thus Linnaean nomenclature should not be used.

5.3.6. MORPHOTYPES

Columnal Plesion A herein, for example, contains four Columnal Taxa (Numbers 1a, 1b, 1c and 1d). These four taxa have similar morphological traits as explained in the text. Within each taxon there are also slight variations in relative sizes of articular facet morphology and each specimen represents a morphotype. Morphotypes have the same overall gross morphology with only slight variations and, thus, are not given different group names. Every specimen described in this thesis, therefore, is a morphotype.

5.3.7. THE USE OF OPEN NOMENCLATURE

Open nomenclature is used by the taxonomist to remark on the identity of a specimen that cannot be determined absolutely (Bengtson, P. 1988). Since fossil material is generally incomplete, open nomenclature is used widely amongst palaeontologists. Richter (1943, 1948) (*fide* Matthews 1973 and Bengtson, P. 1988) stressed that if a specimen were assigned to a known genus without the certainty that it should be there, taxonomic information may be distorted and information would be wrongly incorporated into the literature. If no name were assigned to the specimen at all then important information could be ultimately lost. There is no standard as to the use of open nomenclature by the ICZN (1985), but several symbols are in use described by Matthews (1973) and P. Bengtson (1988); the suggestions of the latter are used herein. These symbols are explained below:

cf. (compare to) indicates a provisional identification:

cf. *Agenus aspecies*	a provisionally assigned genus
Agenus **cf.** *aspecies*	a provisionally identified species
cf. *Agenus* **cf.** *aspecies*	both a provisionally assigned genus and a provisionally identified species

A question mark (**?**) after the name indicates an uncertain identification, but is less uncertain than cf.:

*Agenus***?** *aspecies*	genus uncertain
*Agenus aspecies***?**	species uncertain
*Agenus***?** *aspecies***?**	both genus and species uncertain

aff. has affinities with a named taxon, but is definitely not conspecific/congeneric with it:

aff. *Agenus aspecies*	a new genus
Agenus **aff.** *aspecies*	a new species
aff. *Agenus* **aff.** *aspecies*	a new genus and new species

sp. following a genus name indicates that specific identification is impossible or not been attempted:

Agenus **sp.**

In this thesis, open nomenclature also refers to the method of categorising columnals and other dissociated crinoid ossicles by number. These numbers can subsequently be replaced by Linnaean binomina where that becomes possible (see below). Outside of this study, each author would have their own numbered columnal taxon, *i.e.*, Columnal Taxon

Number n Mannifield, 2001 and Columnal Taxon Number n Smith, 2002.

In some cases the taxonomic origin of a crinoid columnal may be known to a certain extent. Nevertheless, use of a Latin name for it would be inappropriate since this would imply that more is known of the origin of the columnal than actually is (Jeppsson and Merrill 1982). Using columnals with elliptical articular facets from the Palaeozoic for an example in this study: it is known that these columnals originate from the stem of a crinoid belonging to the family Platycrinitidae. There are several genera that belong to this family, so using the suggestion of Jeppsson and Merrill (1982, p. 1492) and Bengtson, P.(1988) the columnal could be referred to as gen. et sp. indet. Platycrinitidae-Type Columnal 1. This method can be applied to dissociated ossicles derived from other parts of the crinoid skeleton such as basals and brachials.

Since crinoid material is commonly found disarticulated and its taxonomic origin unknown, Linnaean binomina are not acceptable. The best solution for the naming of dissociated crinoid ossicles seems to be the use of open nomenclature, a letter or numbering system, e.g. Plesion A, Columnal Taxon Number 1, or. This leaves open the option for a columnal, or any ossicles from other parts of the skeleton, to be assigned their correct generic and/or specific names if they are subsequently found articulated with their crown. [Plesion is used when it is not known which taxonomic rank is being represented. It does not alter the rank in question (Patterson and Rosen 1977) (*fide* Smith 1994, p. 96).] This method prevents unnecessary Linnaean binomina being incorporated into the literature and causing subsequent problems. On reading a description of the fossil, it still informs us of the morphology, and differences in morphology and stratigraphical occurrence of each group still gives us a basis to work from for biostratigraphical analysis.

5.4. SUMMARY

Naming and classification of dissociated columnals herein take into account the following details:

- transverse outline of the articular facet and its morphology, including articulation
- columnal outline
- latus morphology
- indices

Herein the naming system used is open nomenclature based on form classification; even though a descriptive name is not allocated the diagnosis is descriptive. Each type of columnal form described is a morphospecies. Several slightly different morphotypes may occur within each morphospecies. This means that for each subsequent discovery of any of these columnal forms attached to a crown, the correct Linnaean binomina can be applied to them.

CHAPTER 6

SYSTEMATIC PALAEONTOLOGY

6.1. INTRODUCTION

In the following chapter, tables labelled '*Columnal morphometrics, measurements in units*' the columns with headings such as *CLR* or *KHi* are fully explained in Section 5.2.4 and in Figures 5.8 and 5.9. Columns headed *No. crenulae touching facetal feature* may be one or two in number. If there is one column, this implies that crenulae are only simple on the crenularium. If there are two columns, e.g. the table for Columnal Taxon Number 10, this implies that crenulae are peripherally intercalated or bifurcating, as well as being simple on the crenularium. Where the number of crenulae is entered as 'about 35' this means that some of the articular facet is missing or that detail is reduced. An average number is reached by multiplying the number of crenulae on a quarter of the facet by four, or, by multiplying the number of crenulae on half of the facet by two. Some tables have a last column headed *Extras*. This contains 'SEM:' or 'Bin:' sometimes followed by '?', 'IN' or 'N'. 'SEM' signifies that the measurements in the column were taken on the SEM and 'Bin' that the measurements were taken under the binocular microscope with camera lucida attachment. 'N' signifies that the columnal measured was a nodal, 'IN' that it was an internodal and '?' that it is not known what noditaxial order the column belonged to. Where * is inserted into a table next to the noditaxis order of a columnal it means that cirrus-related structures occur on that particular columnal.

The description of the stereom microstructure follows recommendations by Smith (1980).

Where specimens are listed under *Material*, there are further specimens available in the bulk sample from which they were extracted.

6.2. DESCRIPTIONS OF CROWNS AND ENTIRE SPECIMENS

Since the *Treatise on Invertebrate Paleontology* (Moore and Teichert 1978*a*) was produced several workers, including Donovan (1988*a*), Sevastopulo and Lane (1988), Simms (1994) and Ausich (1996; 1998), have carried out phylogenetic work on crinoids with most of the discussion concentrated on the position of the cladids and disparids. Crinoid

classification herein follows Simms and Sevastopulo (1993).

Class CRINOIDEA J. S. Miller, 1821

Subclass CAMERATA Wachsmuth and Springer, 1885

Diagnosis. (After Ubaghs 1978*b*, p. T410.) Rigid sutures generally unite thecal plates; calyx monocyclic or dicyclic; radials not compound; posterior side of calyx usually differentiated by supplementary plates positioned in *A* ray and *CD* interray, with no definite relationship to *C* ray, radianal lacking; proximal brachials generally incorporated in theca by aboral or adoral plates or both, rays divide at least once, free arms uniserially or biserially arranged, brachials monopinnulate or hyperpinnulate, imperforate; interbrachials usually present; ambulacrals comparable to fixed brachials incorporated in tegmen or below it; mouth and proximal portion of food grooves (except very rarely) covered by tegminal pavement; anus opens directly through tegmen or as anal tube.

Order MONOBATHRIDA Moore and Laudon, 1943

Diagnosis. (After Ubaghs 1978*b*, p. T440.) Monocyclic calyx.

Suborder GLYPTOCRININA Moore, 1952

Diagnosis. (After Ubaghs 1978*b*, p. T487.) Pentagonal basal circlet; radials of circlet all join.

Superfamily PLATYCRINITACEA Austin and Austin, 1842

Diagnosis. (After Ubaghs 1978*b*, p. T509.) Calyx comprises only basals and radials, three unequal basals smallest usually in *AE* interray, or fused; posterior side of calyx slightly or not distinct in calyx; brachials and interbrachials few and small in calyx, proximal brachials distinct from radials, but firmly joined to calyx, tegmen or both by interradially positioned plates.

Family PLATYCRINITIDAE Austin and Austin, 1842

Diagnosis. (After Ubaghs 1978*b*, p. T515; Moore and Laudon 1943, p. 101; Burdick and Strimple 1983, p. 166.) Calyx monocyclic comprising three unequal, sometimes fused basals and five large radials; anal plate does not interrupt or alter radial circlet; tegmen multiplated, orals distinct; ambulacrals and interambulacrals important tegminal elements, absent in younger genera; anus opens directly through tegmen; primibrachials *1* typically axillary, arms entirely free, biserial and pinnulate; stem transversely circular proximally, but elliptical and twisted thereafter, articulation synarthrial, fulcral ridge coincides with longest diameter of columnals, axial canal small and circular.

Genus PLATYCRINITES J. S. Miller, 1821

1836 *Platycrinus* Agassiz, p. 179.

1843 *Centrocrinus* Austin and Austin, p. 6.

1842 *Atocrinus* M'Coy in Griffith, p. 11.

Type species. *Platycrinites laevis* J. S. Miller, 1821, p. 74, by subsequent designation of Meek and Worthen, 1865, p. 160.

Other species. There are too many to be named individually, but see Bassler and Moodey (1943) and Webster (1973, 1977, 1991 and 1993).

Diagnosis. (After Ubaghs 1978*b*, p. T515; Donovan and Westhead 1987, p. 211.) Calyx bowl-shaped; three unequal basals, azygous basal usually in AE interray, or fused with other two of equal size; radials large, upper articular facets angustary, or broad; tegmen flat or pyramidal, comprises numerous plates, orals distinct; anus eccentric, opens directly through tegmen, or through short or long anal tube; fixed proximal brachials like those of free arms, primibrachials *1*, rarely primibrachials 2, axillary, axillaries distinct supporting two equally sized brachials, arms divide further one to five times heterotomously, uniserial proximally, become biserial above highest axillary of branches and pinnulate; one to three interradial plates on tegmen between proximal brachials fixing them to tegmen; stem transversely circular in proxistele with symplectial articulation, elliptical columnals with synarthrial articulation comprise mesistele and dististele; attached by

cirriferous runner.

Stratigraphical range. ?Upper Silurian; Lower Devonian to Upper Permian (Europe - N. Am. - N. Africa - Indonesia (Timor.) - Aus. (Queensland, New South Wales)).

Platycrinites expansus (M'Coy), 1844

Plate 13, figs a, b

1844 *Platycrinus expansus* M'Coy, p. 175, pl. 25, figs 18, 19.

1943 *Platycrinites expansus* (M'Coy), Bassler and Moodey, p. 620.

1955 *Platycrinites expansus* (M'Coy), Wright, p. 284, pl. 69, figs 17-20; pl. 70, figs 7, 10, 11.

1969 *Platycrinites expansus* (M'Coy), Sevastopulo, p. 45, pl. 6, figs 1-4.

Material. Specimens TCD.35957 and TCD.35958, two calyces that are squashed, the former with some brachials still articulated. The specimens were collected by Professors G. D. Sevastopulo and N. G. Lane in 1972 from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595. This is the type locality.

Emended diagnosis. (Modified after M'Coy 1844, p. 175; Wright 1955, p. 284.) Calyx twice as wide as high; basal circlet wide and flat, tripartite sutures deep; radials very large, wider than high, distal articular facet large, prominent; anal opening eccentric on tegmen surface; terminal plates numerous, tuberculate; coarse granular to vermiculate sculpture on all plates of crown.

Description. Although the specimens are somewhat squashed it is apparent that the calyces are very wide compared with their heights. Sculpture is seen as raised ridges, on the calycal plates, which follow the plate sutures. There are only one or two 'circuits' of ridges per plate.

The basal circlet is very low, almost flat, with deep, wide tripartite sutures. The three basals are uneven in their sizes with two large ones and a third smaller one. The stem facet is depressed below the level of the basal plane. Radials appear to be of equal widths in each calyx, although some are slightly asymmetrical. They are wider than high

(20:11). Their radial arm facets are crescentic in outline and slightly concave. They are long because the plates are very thick, but they occupy only the central 30% of the width of the upper plate. Their articular surface morphology is unclear, but it appears that there are very fine, uneven crenulae radiating inwards from the outer boundary. They are angled away from the aboral surface at about 45°. The radial:basal and radial:radial sutures are deep.

Primibrachial *1* of two of the arms on specimen TCD.35957 are present. On one of these arms, it is seen that this is axillary and gives rise to a single secundibrachial on either of its shoulders. Laterally these brachials are moderately convex.

The tegmen is not seen.

The stem facet at the base of the calyx is observed on specimen TCD.35957. Its outline is circular or elliptical, but this is unclear owing to the specimen being crushed. However, articulation here is symplectial since a narrow crenularium can be seen.

Remarks. The reasoning behind the assignment of these specimens to this species is that the radials are low and wider at the top than the bottom, both characteristics M'Coy noted in his original description. However, other species described and figured by Wright (1955) also have fairly wide calyces and wider than high radials. It is stressed, therefore that the present taxonomic positioning is very tentative.

Wright (1955) mentioned that M'Coy's description of *P. expansus* was based solely on the evidence from calyces, as in the present study. The three specimens that Wright described were more complete. His information on the tegminal plates is added to the diagnosis in the present study.

Stratigraphical range. Lower Carboniferous (Arundian) - Ireland.

Subclass DISPARIDA Moore and Laudon, 1943

Emended diagnosis. (Modified after Moore and Laudon 1943, p. 24; Moore, Lane *et al.* 1978, p. T520.) Simple crown, tendency towards bilateral symmetry; monocyclic calyx composed of tightly sutured plates, generally steep-sided and conical; radials main calyx components; anal plates often present in aboral calyx; orals main tegmen components; arms free above radials, slender, uniserial, may branch several times or not at all, non-

pinnulate; interbrachials usually lacking; mouth sub-tegminal.

Remarks. Some additional diagnostic characters, which were listed under the 'Inadunata', have been appended to this diagnosis.

Superfamily ALLAGECRINACEA Carpenter and Etheridge, 1881

Emended diagnosis. (Modified after Moore and Strimple 1973, p. 16; Moore, Lane *et al.* 1978, p. T537.) Crown slender, moderately tall, bilateral symmetry often well developed through *E* ray and *BC* interray (homocrinoid bilateral symmetry) in some genera; calyx conical to bowl-shaped; basals fused to one, or up to five; radials upflaring, almost equally sized, or with *A* and *D* radials much larger than others, larger radials generally with multiple arm facets; anal tube tall, cylindrical, comprising brachial-like plates; arms uniserial, non-bifurcating, generally long, thin, rarely less than five in mature specimens, or armless; stem generally circular in transverse section.

Remarks. Moore, Lane *et al.* (1978) stated that the members of this group should possess a stem, which is circular in transverse section. However, since they later described the family Allagecrinidae as possessing round or slightly elliptical stems (p. T537), the diagnosis of the current group has been emended and now states that stems should generally be circular transversely.

Family ALLAGECRINIDAE Carpenter and Etheridge, 1881

Emended diagnosis. (Modified after Moore and Strimple 1973, p. 16; Moore, Lane *et al.* 1978, p. T537.) Very small, often microscopic crinoids, crown tall, slender; calyx mainly conical (microcrinoids), medium high or low bowl-shaped, summit truncate, transverse outline circular, slightly elliptical, pentalobate or pentasteroidal, base horizontal almost or entirely covered by proximal columnal; basals five, or fused to three or one, sometimes visible laterally; radials five, sloping steeply upwards, or rounded to bulbous longitudinally, upper articular facet gently concave or deeply excavate, one to thirty-four in number on a single radial, but usually only *A* and/or *D* radials multifaceted, facets narrow and elongate longitudinally and lacking transverse ridge or distinct muscle areas, oral circlet often domed; *C* radial may be developed as an aniradial, anal X often present;

anal tube tall, erect comprising very thick brachial-like plates in linear series following anal X, may extend higher than arms; arms cylindrical, well rounded aborally, grooved adorally, non-bifurcating, but few to many, may be closely spaced and erect; brachials elongate, articular facets smooth, planes normal to arm axis; arms non-pinnulate; orals; stem circular or slightly elliptical in transverse section, homeomorphic or moderately heteromorphic, tapering distally.

Genus LITOCRINUS Lane and Sevastopulo, 1982

1982 *Litocrinus*, Lane and Sevastopulo, p. 258.

1988 *Litocrinus*, Sevastopulo and Lane, p. 246.

1999 *Litocrinus*, Webster and Jell, p. 262.

Type species. *Kallimorphocrinus punctatus* Lane and Sevastopulo, 1981, by original designation.

Other species. *L. angulatus* (Strimple and Koenig, 1956), *L. extensus* (Wright, 1952), *L. indicus* (Gupta and Prokop, 1978), *L. pristinus* (Peck, 1936), *L. puteatus* (Peck, 1936), *L. scoticus* (Wright, 1932), *L. tintinabulum* (Strimple and Koenig, 1956).

Diagnosis. (After Lane and Sevastopulo 1982, p. 258; Sevastopulo and Lane 1988, p. 246; Moore, Lane *et al.* 1978, p. T539 (adapted from *Kallimorphocrinus*).) Small allagecrinids, aboral calyx typically high to medium cone-shaped, sides nearly vertical to evenly expanded, generally higher than wide, round to asteroidal in aboral view and pentaradiately symmetrical; radials of equal width, upper articular facets with little or no aboral ligament area; basals three or fused; no anal series; oral circlet moderately domed, retained in maturity, lacking anal notch; mature specimens with none, three, four, or rarely five arms, uniserial, brachials two to several; stem comprising circular columnals; plates smooth or with coarsely pitted sculpture.

Remarks. The genus *Litocrinus* was erected by Lane and Sevastopulo (1982) following their description of *Kallimorphocrinus punctatus* (1981), which would become the type species of the new genus. It was provided to accommodate several species, which had previously been assigned to the genus *Kallimorphocrinus*. These species were moved because they

lack an anal notch, which *Kallimorphocrinus* possesses, and because they have three, or fused, basals as opposed to five. *Litocrinus* includes all Mississippian species previously described and *Kallimorphocrinus* the Pennsylvanian species. They also mentioned that since immature *Litocrinus* and *Allagecrinus* individuals are virtually indistinguishable (Gutschick 1968) (as are *Allocatillocrinus* (Moore, Lane *et al.* 1978)), some of the species, which they placed in the genus *Litocrinus*, may be found to be representative of *Allagecrinus* in future.

A *Litocrinus* sp. has recently been described as the first specimen of the genus from the Australian Carboniferous (Webster and Jell 1999).

Stratigraphical range. Lower Carboniferous - Scotland, ?India; Mississippian (Kinderhookian to Osagean) - USA (Missouri, New Mexico, Tennessee, Oklahoma); Viséan - Aus. (QLD).

Litocrinus sp.

Plate 14, figs a, b

Material. Specimen number TCD.35956, a single reasonably preserved specimen comprising the calyx and orals only. The specimen was collected by Professors G. D. Sevastopulo and N. G. Lane in 1972 from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Additional material. Eleven further calyces, under specimen number TCD.35956, remain undescribed. They are from Bed BD:L10, a wackestone, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8197 5919.

Description. The calyx is medium cone-shaped. In aboral view, it is pentagonal in outline. All the plate boundaries are indistinct. There is no sculpture on the surface of the calyx. The base of the basal circlet is smooth. Radials are about twice as high as wide. They flare out directly above the basals, then become almost vertical just over halfway up their heights. The arm articular facets are fully developed in all rays and are mostly horseshoe shaped and deep. Detail of the facets is not discernible.

The five plates of the oral circlet are preserved and in lateral view they are

moderately domed and rounded. Ridges delineate the interoral sutures. There is no anal notch, but the *CD* interray is wider than other interrays.

Caly

Calyx morphometrics (maximum dimensions), measurements in microns.

Basal height	*Radial height*	*Aboral calyx height*	*Thecal height*	*Thecal width* (CD *to* A)	*Thecal width* (CB *to* DE)
about 180	about 820	about 940	about 1230	?	about 1050

The arms are not preserved.

None of the stem is preserved.

Remarks. The lateral profile of the calyx is not unlike that of *L. scoticus* (Wright, 1932). However, there is no 'frosted' or finely granulate sculpture present on the surface of the theca. To place the specimen into a particular species would not be appropriate with what little evidence can be gathered from it.

Lane and Sevastopulo (1981) mention that specimens of *K. punctatus* with five arm facets are rare, yet the only calyx found in this study has five arm facets.

The additional material was immersed in 3.6% hydrofluoric acid for one weekend and the specimens are apparently not damaged or cracked.

Stratigraphical range. Lower Carboniferous (Viséan) - Ireland (Arundian); Mississippian (early Osagean) - USA (Tennessee).

Subclass CLADIDA Moore and Laudon, 1943

Emended diagnosis. (Modified after Moore and Laudon 1943, p. 24, 32; Moore, Lane *et al.* 1978, p. T520, T578.) Dicyclic aboral calyx composed of tightly sutured plates; up to four anal plates in calyx, prominent anal sac; arms simple or branched, free above radials, interbrachials usually lacking, pinnulate or non-pinnulate; mouth sub-tegminal; stem generally circular in transverse section.

Remarks. Additional applicable diagnostic characters previously listed under 'Inadunata' have been appended to the above diagnosis. Moore, Lane *et al.* (1978, p. T578) state "*mostly three, two or one anal plates in cup but a few lacking any*". The superfamily Agassizocrinacea, which belongs to this subclass, contains the genus *Agassizocrinus* that

has four anal plates in the calyx (see Moore and Laudon 1943, p. 48). Although Moore, Lane *et al.* (1978) specify this feature at all lower levels down to genus, their diagnosis of the order is clearly incorrect.

'stem-group cladids'

Plesion POTERIOCRININA Jaekel, 1918

Diagnosis. (After Moore, Lane *et al.* 1978, p. T630.) Calyx high conical to patelliform; radial articular facets angustary to plenary, sloping to planar, transverse ridge, ligament pits, fossae and muscle fields usually distinct; up to four anal plates in calyx; anal sac cylindrical and tall; arms usually predominantly pinnulate, commonly biserial; stem generally circular in transverse section.

Remarks. 'Stem-group cladid' is the informal grouping together of the former suborders Poteriocrinina and Dendrocrinina by Simms and Sevastopulo (1993). They stress that further work should be carried out on this matter.

Superfamily SCYTALOCRINACEA Moore and Laudon, 1943

Diagnosis. (After Moore and Laudon 1943, p. 59; Moore, Lane *et al.* 1978, p. T638.) Generally tall crown; calyx conical to truncate bowl-shaped; infrabasals visible in lateral view; radial articular facets plenary; isotomously branching arms; stem circular in transverse section.

Family SCYTALOCRINIDAE Moore and Laudon, 1943

Emended diagnosis. (Modified after Moore and Laudon 1943, p. 59; Moore, Lane *et al.* 1978, p. T639.) Crown tall, slender; calyx conical to bowl-shaped; five infrabasals visible laterally; radial articular facets plenary, bearing transverse ridge and ligament pits; three anal plates in calyx, anal sac tall, slender; arms branch isotomously on primibrachial *1*, *2*, *3* or unbranched, predominantly uniserial; pinnulate.

Remarks. To accommodate the newly erected genus *Bundoranocrinus* the diagnosis of the

family now states that branching may occur on primibrachial *1*, *2* or *3*, as opposed to only primibrachial *1* or *2*, as stated in Moore, Lane *et al.* (1978.), or primibrachial *1*, as stated in Moore and Laudon (1943).

Genus BUNDORANOCRINUS gen. nov.

Etymology. From 'Bundoran', the type locality of the Bundoran Shale Formation from where the type, and only, specimen was found.

Type species. Bundoranocrinus vermiculatus gen. et sp. nov., by monotypy.

Diagnosis. Entire lateral surface of skeleton covered with vermiculate sculpture; calyx conical, approximately as high as wide, thickly plated; infrabasals as high as wide, prominent in lateral view, widening slightly distally; basals hexagonal, highest and largest plates of calyx; radials pentagonal, equal in height to infrabasals, upper articular facets slightly concave and plenary, radial of *A* ray narrower than others; anal series unknown; anal tube plates cog-like transversely, full anal sac structure unknown; arms long, slender, branch only once isotomously on primibrachial *1*?, *2* or *3*, *A* ray atomous, number of arms unknown; brachials uniserially arranged, strongly cuneate proximally and almost as high as wide on highest side, become lower and less cuneate distally, transversely almost round, articular surfaces weakly crenulate or smooth, adoral groove V-shaped with nadir expanded and rounded; arms non-pinnulate proximally, medial pinnules as unsegmented spines pointing proximally, distal pinnules unknown, pinnule facets concave, concavity increasing distally; stem heteromorphic, nodals higher than internodals, proxistele widening rapidly slightly towards calyx, columnals transversely circular, articulation symplectial.

Remarks. The newly erected genus *Bundoranocrinus* has confidently been placed in the family Scytalocrinidae because its morphological attributes (except for the number of primibrachials - see remarks below) most closely resemble those outlined by this family. The new genus and species are based on a single specimen.

The type specimen bears very similar morphological features to those of the genera *Bollandocrinus* and *Hypselocrinus*, and especially the species *Bollandocrinus erectus* Wright, 1951*b* and *Hypselocrinus hoveyi* (Worthen, 1875). Differences are seen in the

relative sizes of the calycal plates, the upper articular facets of the radials, the number of arms, the shapes of the brachials, and in the arrangement of the columnals of the stem (a full list of generic similarities and differences can be compared in Figure 6.1). However, the reasoning behind erecting a new genus for this particular crinoid, and not simply a new species of either *Bollandocrinus* or *Hypselocrinus*, is that it has a very distinct sculpture, which the other two genera lack, and that arm branching may occur on primibrachial *3*.

The type specimen has only two primibrachials in the *B* ray, but clearly three primibrachials in the *E* ray, the most distal one being an axillary. In Wright (1951*b*, p. 62), the diagnosis of the genus *Bollandocrinus* specifies that primibrachials are invariably two in number and that the most distal one in each ray is axillary. The diagnosis for the family Scytalocrinidae, Moore and Laudon, 1943 also states that primibrachials be no more than two in number.

The number of primibrachials in genera of advanced cladids with conical calyces is commonly specified in their diagnoses. However, Kammer and Ausich (1992) have shown that the number of primibrachials in *Hypselocrinus hoveyi* is variable between one and two in number, as it is in other members of the genus. This brings into question the validity of such a diagnostic attribute, even at the level of family. Where branching occurs, especially at higher levels of the arms and anywhere from secundibrachials and upwards, the number of brachials in a brachitaxis often changes from specimen to specimen, and even in different branches of a single specimen. This is clearly demonstrated in the type specimen of *Bundoranocrinus* where, although bifurcation only occurs once, there is a discrepancy in the number of primibrachials. The number of primibrachials *alone* is not enough to distinguish between genera.

There are several other differences between the proposed genus *Bundoranocrinus* and the other genera under discussion. Specimen TCD.35950 clearly has strongly cuneate brachials which are not "much wider than high" as specified by Wright for *Bollandocrinus*. In fact, on their highest side these brachials are only just wider than their height and are also strongly cuneate as opposed to slightly cuneate as in Wright's description. They are also transversely more round in their outline than those in the figured specimens of Wright (1951*b*).

The description of brachials in the literature as a whole is fairly poor. When describing crinoid species the morphology of brachial articular surfaces, outlines and dimensions are usually neglected in the same way as columnals of the stem are, while the calyx is usually fairly well described. On discerning the differences in brachial

Figure 6.1. Table outlining morphological differences between the genera *Hypselocrinus* Kirk, 1940, *Bollandocrinus* Wright, 1951 and *Bundoranocrinus* gen. nov. herein. The diagnoses for *Hypselocrinus* and *Bollandocrinus* are emended after Wright (1951*a*; 1951*b*), Moore *et al*. (1978*a*) and Kammer and Ausich (1992).

	Hypselocrinus	*Bollandocrinus*	*Bundoranocrinus*
Crown	very tall, slender	tall	very tall, slender
Aboral calyx	narrowly cone-shaped, high	cone-shaped, moderately large, medium height, height:width ratio about 1:1, thickly plated, sutures slightly grooved	narrowly cone-shaped, high, height:width ratio about 1:1, thickly plated
Infrabasals	rather high, prominent in lateral view, form lower 25% of calyx wall	high, prominent in lateral view, form appreciable part of calyx wall, sides almost straight or steeply upturned distally	as high as wide, prominent in lateral view, form lower 33% of calyx wall, widening distally
Basals	large, higher than IBB and RR	large, high, higher than IBB and RR	large, as high as wide, higher than IBB and RR
Radials	large, slightly crescentic in outline, upper articular facet straight, plenary	large, moderately high, slightly crescentic in outline, upper articular facet straight, plenary with strong transverse ridge and deep ligament furrow	large, equal in height to IBB, upper articular facet slightly concave, plenary
Arms	very long, slender, branch only once isotomously, but *A* ray may be atomous and *B* ray may branch once more, nine, ten, or rarely eleven arms	stout, branch only once isotomously, ten arms	long, slender, branch only once isotomously, or *A* ray may be atomous, probably nine or ten arms
Brachials	rather high, cuneate, may become more rectangular and lower distally, typically IBr_1, but rarely IBr_2, axillary	much wider than high, slightly cuneate to rectangular, rounded, IBr_2 always axillary and low	almost as high as wide and strongly cuneate proximally, becoming slightly lower, narrower and less cuneate distally, transversely rounded, IBr_2 (high) or IBr_3 (low) axillary
Pinnules	long, slender	long, slender	medially as spines, distally unknown
Anal area	three plates in calyx, RA high on shoulders of *BC* and *CD* BB, anal X large, RX within calyx limits	three plates in calyx, RA, lower part of anal X and RX within calyx limits	unknown
Anal sac	long, slender, six or seven times height of calyx, composed of ten or more vertical series of hexagonal plates	unknown	unknown in whole, but cog-like tube plates show height to be at least four times height of the calyx
Stem	transversely circular, heteromorphic, nodals prominent	transversely circular, heteromorphic, nodals not very nodose, columnals with pentalobate lumen	transversely circular, heteromorphic, difference between nodals and internodals in height only, symplectially articulated
Sculpture	plates smooth, or with pits at plate corners	plates smooth	vermiculate sculpture on entire lateral surface (?except anal sac)
Range	*L. Carb. (Viséan)*, Eur. (Isle of Man, Scotland); *L. Miss. (late Osagean - early Meramecian)*, USA (Indiana, Missouri)	*L. Carb. (late Tournaisian - early Viséan)*, Eur. (northern England, Northern Ireland); *L. Miss. (late Osagean)*, USA (Illinois)	*L. Carb. (Viséan)*, Eur. (Ireland)

morphologies between the genera under current discussion, the importance of a full description of such a feature has been demonstrated.

The occurrence and amount of gape between the upper facet of a radial and its respective primibrachial *1* should probably not be used as a diagnostic feature. During life a reasonable amount of movement, and therefore gape, was achieved between the radial and primibrachial *1*. Therefore, the gape in a fossil specimen is surely a process of initial taphonomy, *i.e.*, immediately post-mortem. This can be demonstrated firstly on the type specimen of *Bundoranocrinus* where the *A* ray is clearly gaping, but the adjacent *B* and *E* rays are not - their first primibrachials have simply slipped inwards sometime between death and diagenesis. The said articulation for *Hypselocrinus* Kirk, 1940, has been diagnosed by Wright (1951*a*) as slightly gaping and by Moore, Lane *et al.* (1978) as not gaping. The figured specimens of both authors display both gaping and non-gaping articulations, usually with a combination of both within individual specimens. In their descriptions of several *Hypselocrinus* species Kammer and Ausich (1992) correctly do not use gaping as a diagnostic feature as is demonstrated by several of their figured specimens of the genus which display both gaping and non-gaping articulations. However, they make no mention of the exclusion of the gape as a diagnostic feature.

The diagnosis of the stem of *Hypselocrinus*, as correctly stated in Wright (1951*a*), is heteromorphic. However, in their descriptions of *H. hoveyi* (Worthen 1875), *H. arcanus* (Miller and Gurley 1890) and *H. vansanti* Kammer and Ausich, 1992, Kammer and Ausich (1992) stated that the stems are homeomorphic. It can clearly be seen in their figured specimens USNM S3799 (Figure 5.13, p. 473) and FMNH UC6398 (Figure 5.16) that the stems are, in fact, heteromorphic with differences in heights of columnals for both specimens and differences in diameters in the latter.

It is apparent that the use of the arrangement of calycal plates to erect or characterise a genus/species is not sufficient alone. Both the morphologies and arrangement of columnals and brachials are as, if not more, important.

Bundoranocrinus vermiculatus gen. et sp. nov.

Plate 15, figs a-f; Figures 6.1, 6.3, 6.4

Etymology. From the characteristic vermiculate sculpture that covers the entire lateral surface of the crinoid.

Holotype. Specimen number TCD.35950 is exceptionally preserved showing the most proximal part of the stem, the anterior part of the calyx, a number of articulated and disarticulated portions of at least six arms, a few plates of the anal tube and a distinct vermiculate sculpture over the entire lateral surface. The specimen was collected by Professors G. D. Sevastopulo and N. G. Lane in 1972 from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Material. A sinlge paratype, specimen TCD.35961, a well-preserved calyx with a distinct sculpture over the entire lateral surface. Collected from the same locality as the holotype.

Diagnosis. As for genus.

Description of holotype. The entire lateral surface of the skeleton has a distinct vermiculate sculpture.

The crown is very tall (at least 130 mm high) and slender. The calyx is a narrow cone shape, high at approximately 15 mm and is as high as wide. It is dicyclic, thickly plated and the anterior side is seen revealing the *B*, *A* and *E* rays. Three infrabasals of presumably five are prominent in lateral view. They are rather high forming approximately 33% of the lower calyx wall. Laterally, they appear subequally pentagonal in outline, widen slightly distally and are slightly higher than wide (5:4.7)[6] at their extremes. They point distally and their upper two sloping shoulders are slightly concave across their facets. The proximal facets with the stem are slightly convex. Four basals of presumably five can be seen in lateral view, but only the *EA* and *AB* basals are seen fully. They are subequally hexagonal in outline and have points directed proximally and distally, but the nadir of each basal is discrete. They are as high as wide (7:7) at their extremes and are the largest plates in the calyx. They widen slightly distally. The *AB* basal is slightly narrower (7:5.5) than the *EA* basal. Three radials of presumably five can be seen fully, and these are positioned in the *B*, *A* and *E* rays. They are subequally pentagonal and slightly crescentic in outline. They are wider than high, and the *A* ray is slightly narrower than the *B* and *E* rays (6:5.3 (*A* radial) and 8.5:5 (*B* radial)). Longitudinally, they are slightly convex and point proximally. The nadir of the *A* radial is

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[6] The numbers in ratios are equal to millimetre measurements taken.

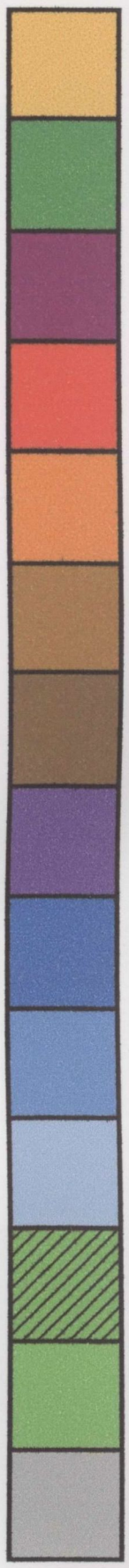
skewed towards the *AB* interray. The upper articular facets are slightly concave and plenary. No anal plates of the posterior calyx are seen.

Six uniserial, pinnulate arms are seen of presumably nine or ten, belonging to the right *C* ray, left and right *B* ray, the *A* ray and the left and right *E* ray. They are long and slender, the longest articulated section reaching 110 mm above the summit of the calyx, and taper only slightly distally in as much as is seen. They are free above the radials and appear to branch isotomously only once, except for the *A* ray which is atomous. Primibrachial *1* of the *B* ray is wider than high (8.5:4), primibrachial *2* is also wider than high (7.5:5.5) and is axillary. The arm of the *A* ray comprises only primibrachials as no branching occurs. Primibrachials *1* and *2* of the *E* ray have approximately the same dimensions as primibrachial *1* of the *B* ray. Primibrachial *3* is axillary, wider than high, but much lower (4 mm) than the axillary primibrachial of the *B* ray. All axillary primibrachials have very steeply sloping shoulders on which secundibrachials sit. At their extremes, secundibrachials (and all but the most proximal primibrachials of the *A* ray) are almost as high as wide, and are strongly cuneate proximally. They become relatively slightly narrower, lower and slightly less cuneate distally. They are transversely essentially circular with a V-shaped adoral groove which reaches the centre of the articular surface, and which has a rounded, expanded nadir. The pinnules are mostly unknown. However, on the right *C* ray arm about 40 mm from the summit of the calyx two spine-like, unsegmented pinnules are seen on the adoral surface of two secundibrachials. Beyond this, pinnule sockets are seen that are laterally ovate in outline and concave with concavity increasing distally. It appears there are no pinnule sockets on primibrachials or the more proximal secundibrachials, and the adoral side of the *A* ray is not seen so it not known if this arm is pinnulate at all.

The anal structure is not known. However, several small anal tube plates of just over 2 mm diameter are visible to the left of the left *E* ray and approximately 50 mm from the calyx summit. They appear circular in outline and possess several cog-like teeth around their exteriors. They are wider than they are high.

The tegmen is not seen.

Approximately 77 mm of the stem is preserved, with a further 27 mm long external mould in the shale matrix. The columnals that form the stem are circular in outline and are symplectially articulated, the crenulate suture being regular and



Infrabasal

Basal

Radial

Primibrachial

Secundibrachial

Tertibrachial

Quartibrachial

Pinnule

Interprimibrachial

Intersecundibrachial

Intertertibrachial

Anal X

Anal sac plate

Identification of plate undetermined

Figure 6.2. Legend for plates of the crown in figures 6.3, 6.7, 6.8, 6.9 and 6.11.

Figure 6.3. Plate diagram for *Bundoranocrinus vermiculatus* sp. nov. (drawn using camera lucida); specimen number TCD.35950 (see Figure 6.2 for plate legend).


2cm

	A ray	*AB* interray	*B* ray	*BC* interray	*C* ray	*CD* interray	*D* ray	*DE* interray	*E ray*	*EA* interray	TOTAL
Infrabasal	1	-	1	-	x	-	x	-	1	-	3
Basal	-	1	-	1	-	x	-	1	-	1	4
Radial	1	-	1	-	1	-	x	-	1	-	4
Primibrachial	17	-	2	-	x	-	x	-	3	-	22
Secundibrachial	x	-	9,8	-	26	-	x	-	36,26	-	105
TOTAL	19	1	21	1	27	0	0	1	67	1	**138**

Figure 6.4.*a.* Table displaying types and numbers of crown plates in specimen TCD.35950 of *Bundoranocrinus vermiculatus* gen. et sp. nov.

	A ray	*AB* interray	*B* ray	*BC* interray	*C* ray	*CD* interray	*D* ray	*DE* interray	*E ray*	*EA* interray	TOTAL
Infrabasal	1	-	1	-	1	-	1	-	1	-	5
Basal	-	1	-	1	-	1	-	1	-	1	5
Radial	1	-	1	-	1	-	1	-	1	-	5
TOTAL	2	1	2	1	2	1	2	1	2	1	**15**

Figure 6.4.*b.* Table displaying types and numbers of crown plates in specimen TCD.35961 of *Bundoranocrinus vermiculatus* gen. et sp. nov.

moderately coarse. However, the full morphology of the articular facet is unknown. The stem is heteromorphic, nodals being higher than internodals, and all latera are straight. The noditaxis is approximately 212N (Type II) proximally to 3231323N (Type III) distally. The proxistele rapidly widens a small amount towards the base of the calyx. The most proximal columnal has at least one longitudinally orientated suture located below the *E* ray infrabasal and about 0.5 mm from the anterior edge of it. This columnal has sinuous proximal and distal articular facets sagging below, and in harmony with, the convex base of each basal, and it thins slightly in the areas around the suture. Moving distally, the next columnal below varies in thickness. It also has a sinuous proximal articular facet, which fits the columnals above. It has at least one apex pointing into a thinner area of the columnal above, *i.e.* below the longitudinal sutures. However, the distal articular facet of this columnal is horizontal, and all columnals below this have horizontal both proximal and distal articular facets. The most distal 23 mm of the preserved stem portion lacks the vermiculate sculpture. As far as is seen the stem is non-cirriferous.

Description of paratype. The entire lateral surface of the skeleton has a distinct vermiculate sculpture. The vermiculae become as long as and aligned with the edges of the plates.

The calyx is a narrow cone shape with a height of approximately 27 mm. All plates of all rays can be seen, but some of them are cracked or sunken behind others due to compaction. The five infrabasals are high and form approximately 33% of the lower calyx wall. They are all about as high as wide with the following ratios;

A	*B*	*C*	*D*	*E*
9.5:8.5	-	8.5:9	10.5:9	9.5:8

The *B* ray infrabasal cannot be measured precisely as it is partially covered, and the *A* ray infrabasal has a horizontally orientated crack across the entire plate, so this measurement is also slightly imprecise. Five basals are fully seen. They are subequally hexagonal in outline, except for the *CD* basal, which is distally truncate and is therefore heptagonal, and they widen slightly distally. They are higher than wide at their extremes with the following ratios:

AB	*BC*	*CD*	*DE*	*EA*
14:12	15:12.5	15.5:14.5	16:13	-

Five radials are seen fully, but the *D* radial is broken. They are subequally pentagonal

and crescentic in outline, and are much wider than high with the following ratios:

A	*B*	*C*	*D*	*E*
8.5:11	7:13	7.5:13	-	8:12.5

The upper articular facets are slightly concave and plenary. The morphologies of the distal articular facets are unclear, but it can be seen that there is a straight transverse ridge across each. No anal plates are preserved.

Articulation of the stem was probably symplectial since crenulae are seen on the proximal facets of the infrabasals where the stem would have been articulated.

Remarks. The narrow *A* radial in both specimens would support the inference that this ray was atomous. The other visible rays are wide enough to accommodate an axillary primibrachial which gives rise to two arms.

It is not known whether the loss of sculpture on the distal portion of the stem is through a process of taphonomy or was a feature of the stem before burial.

That this specimen could have been classified as a *Bollandocrinus* or *Hypselocrinus* species if only the calycal plates were known is a distinct possibility since the arrangement of the calycal plates in both are similar. However, the distinct vermiculate sculpture of the calycal plates, and the entire specimen surface, is a characteristic that neither of the other two genera has. It is unlikely that, if there were such an sculpture on the lateral surface of either of the other two genera, it would not have been preserved on *any* of the many described specimens.

Stratigraphical range. Lower Carboniferous (Viséan) - Ireland (Arundian).

Superfamily CROMYOCRINACEA Bather, 1890

Diagnosis. (After Moore and Strimple 1973, p. 21; Moore, Lane *et al.* 1978, p. T690.) Calyx bowl-shaped, basal concavity may be present; radial articular facets plenary; two or three anal plates in calyx; anal sac inconspicuous; arms five to twenty or more, branch only on primibrachials *1* or secundibrachials *1*, uniserial or biserial; stem circular in transverse section.

Family PHANOCRINIDAE Knapp, 1969

Diagnosis. (After Knapp 1969, p. 351; Moore, Lane *et al.* 1978, p. T690; Burdick and Strimple 1983, p. 54) Crown tall, narrow; calyx low bowl-shaped, truncate, medium high or low, proximally invaginated or with subhorizontal base; infrabasals not visible laterally; basals visible in lateral view; upper radial facets wide and near horizontal; three anal plates within calyx limit, but may be less; anal sac slender, shorter than arms; arms five to ten, branch isotomously on primibrachials *1* only, generally uniserial, but later forms may become biserial with flattened sides and gently convex outer surfaces, arms apposed, pinnulate; stem transversely circular.

Remarks. In Knapp's (1969) original description of the family it was stated *"basal cavity deep"*. This was correctly omitted in the diagnosis in Moore, Lane *et al.* (1978) as it can be variable.

Genus PHANOCRINUS Kirk, 1937

Type species. Zeacrinus formosus Worthen, *in* Meek and Worthen, 1873, p. 549, by original designation.

Emended diagnosis. (Modified after Kirk 1937, p. 602; Sutton and Winkler 1940, p. 551; Moore and Laudon 1943, p. 60; Burdick and Strimple 1969, p. 9; Knapp 1969, p. 347, 351; Moore, Lane *et al.* 1978, p. T692; Burdick and Strimple 1983, p. 54.) Calyx low bowl-shaped, never less than twice as wide as high, constricted at summit, basal invagination narrow or wide and deep or shallow, or essentially absent, plates may be swollen, plate sutures moderately impressed; infrabasal attitude dependent on basal concavity of calyx, may be visible outside most proximal columnal, may be steeply downflared; basals pentagonal except *BC* basal, which is always hexagonal, and *CD* basal which is sometimes distally truncate and hexagonal to support anal X; radials wider than high and shovel-shaped, curved upwards from basal plane, but not vertically; arrangement of anal plates variable, but usually three in which case radianal, anal X and third anal plate interrupt radial circlet and within calyx limit; secundibrachials short, parallel sutures to slightly cuneate, primibrachial *1* axillary, pentagonal in outline, much wider than high; arms usually ten, rarely nine, well rounded, uniserial, or biserial in younger species; pinnules

long and stout; anal sac slender with single elongate spine at distal end; stem circular, lumen pentalobate, distinctly heteromorphic; outer surface of plates may possess sculpture of various types.

Remarks. In the original description of the genus *Phanocrinus* Kirk, 1937, forms possessing five to ten-arms were placed in the genus. A new genus *Pentaramicrinus* was erected by Sutton and Winkler (1940) to include forms similar to *Phanocrinus*, but which possessed only five arms. *Pentaramicrinus* was subsequently modified by Burdick and Strimple (1969) to include forms that had erect lateral calyces (vertical) with no distal constriction, but with no stipulation on the number of arms, although five, nine and ten arms are known to occur. Some illustrated specimens of *Phanocrinus* and *Pentaramicrinus* are not dissimilar in the shape of the calyx and the specimens under discussion have affinities to some species of both genera. However, overall the specimens hold more affinities to the genus *Phanocrinus* than to *Pentaramicrinus,* so they are placed in the former, and tentatively compared with the species *Phanocrinus calyx* (M'Coy).

Stratigraphical range. Lower Carboniferous (Viséan) - Scotland (Brigantian), Ireland (Asbian), Morocco; Upper Mississippian (Genevievian to Chesterian) - USA (Kentucky, Alabama, Oklahoma, Illinois, Indiana, Iowa, Georgia, Tennessee, Texas, ?Nevada (Webster 1991)).

Phanocrinus cf. *calyx* (M'Coy, 1849)

Plate 13, figs d-f

1849 *Cupressocrinus calyx* M'Coy, p. 244.

1851 *Cupressocrinus calyx* M'Coy, p. 117, pl. 3D, fig. 1.

1854 *Cupressocrinus calyx* M'Coy, p. 105.

1854 *Poteriocrinus calyx* (M'Coy), de Koninck and Le Hon, p. 90, pl. 1, figs 6a-d.

1878 *Zeacrinus calyx* (M'Coy), Sladen, p. 249.

1881 *Hydreionocrinus calyx* (M'Coy), de Koninck and Le Hon *in* Wachsmuth and Springer, p. 131.

1912 *Hydreionocrinus* sp. Wright, p. 52, pl. 5, fig. 2.

1912 *Eupachycrinus*? *calyx* (M'Coy), Bather, p. 74, text-fig. 13.

1918 *Eupachycrinus* No. 1 sp. Wright, p. 376, text-figs 1-6.

1924 *Eupachycrinus*? *calyx* (M'Coy), Wright, p. 276, pl. 16, fig. 4.

1925 *Eupachycrinus calyx* (M'Coy), Wright, p. 277.

1926 *Eupachycrinus calyx* (M'Coy), Wright, p. 145, pl. 15; pl. 17, figs 4, 5; text-figs 1-60.

1927 *Eupachycrinus calyx* (M'Coy), Wright, p. 364.

1937 *Phanocrinus calyx* (M'Coy), Kirk, p. 603.

1939 *Phanocrinus calyx* (M'Coy), Wright, p. 22, pl. 5, figs 1, 4; text-fig. 15.

1943 *Phanocrinus calyx* (M'Coy), Bassler and Moodey, p. 607.

1945 *Phanocrinus calyx* (M'Coy), Wright and Strimple, p. 226.

1948*a* *Phanocrinus calyx* (M'Coy), Strimple, p. 113.

1948*b* *Phanocrinus calyx* (M'Coy), Strimple, p. 490, text-figs 1-4.

1951*b* *Phanocrinus calyx* (M'Coy), Wright, p. 94, pl. 17, figs 15, 21; pl. 18, figs 1-19, 22, 23, 29; pl. 33, figs 6, 14.

1969 *Phanocrinus calyx* (M'Coy), Burdick and Strimple, p. 9.

1973 *Phanocrinus calyx* (M'Coy), Webster, p. 205.

1977 *Phanocrinus calyx* (M'Coy), Webster, p. 133.

Material. Two well preserved specimens collected by two German undergraduate students, B. Kaufmann and C. Michel, during their mapping of the area in the summer of 1999. Specimen number TCD.28140 is an almost complete calyx and was collected from approximately GR 7668 5082 (see Figure A.23.), the northern side of Tievebaun Mountain (near localities TM1 and TM2), Co. Sligo. Specimen TCD.28141 comprises a calyx and several associated arms and was collected from approximately GR 7520 4224, near Meenaphuill, about 1 km south of Glencar Lough, Co. Leitrim. The rocks at both of these localities are probably representative of the Glencar Limestone Formation.

Emended diagnosis. (Modified after Wright 1951*b*, p. 94.) Calyx low-bowl shaped; infrabasals very small, sunken into basal concavity and downflaring, distal corners extend outside stem, not seen laterally; basals large; anal plates three, generally within calyx, variable in size and shape; single primibrachial, generally axillary; arms nine or ten, stout, tapering gradually distally, generally uniserial; pinnules short, pinnulars seven to ten; plates generally smooth, may have very fine tuberculate sculpture.

Description. The crown is tall (at least 55 mm high in specimen number TCD.28141) and

all of its component plates have either a smooth or ?finely tuberculate outer surface. The calyx is a low bowl-shape, slightly constricted at its summit; the sutures of all of its component plates are impressed. It is over twice as wide as high in both specimens. The calyx of specimen TCD.28141 measures about 6 mm in height and 14 mm in width from the left to right lateral margins, and that of specimen TCD.28140 measures about 6 mm in height and 16 mm in width across the same diameter. The base of the calyx of specimen TCD.28140 has an apparently shallow, narrow concavity. Infrabasals are seen in the *A* and *B* rays, but are concealed by stem remnants and matrix in the other rays. The entire infrabasal circlet is smaller than the smallest basal plate. The basals are all pentagonal in outline with the exception of the *BC* basal, which is hexagonal in outline for the reception of the radianal on its posterior side. The *DE*, *EA* and *AB* basals are all of roughly the same dimensions (4.2:4.5), but the *DC* basal is higher and slightly wider (6:5). Their distal halves are seen in lateral view. Specimen TCD.28141 reveals partly what are interpreted as the *E*, *A*, *B* and *C* radials, and specimen TCD.28140 reveals the *D*, *E*, *B* and *C* radials with the *A* radial being entirely missing. They are pentagonal in outline and shovel-shaped, except for the two posterior radials, which are unevenly pentagonal owing to the presence of the anal plates that interrupt the radial circlet. They are the largest plates in the calyx and are all wider than high (7:9 (*E* radial)). Overall, they are slightly swollen. Their lateral curvature is discrete proximally, but it increases distally, towards the summit, where it recurves. The upper articular facets of the radials are slightly concave and plenary. They have a very slightly curved transverse ridge separating an aboral ligament area and a gently concave inner muscular area. Sculpture cannot be deciphered further than this. It can be seen where the *A* radial is missing that the articular facets with the adjacent basals and radials have a finely crenulate rim surrounding an area with what appear to be very low, wide and irregularly shaped depressions, presumably for connective tissue. Specimen TCD.28140 shows three plates in the anal area. The radianal is unevenly pentagonal in outline and is as large as the *CD* basal. It rests on the *BC* and *CD* basals and has its longest side touching the *C* radial. On its distal left shoulder, it supports the anal X, which is less than half its size, and on its short distal right shoulder, it supports the third and smallest anal plate of the calyx. The leftmost corner of the radianal touches the *D* radial, thus is separating the *CD* basal from the anal X.

Specimen TCD.28141 reveals six uniserial, pinnulate arms out of (presumably) ten, the others being occluded by the matrix. The arms are free and branch isotomously only once as seen on the proximal part of the ?*A* ray and the visible portions of the remaining

arms. A single axillary primibrachial is seen in the ?*A* ray. It has been fractured so has a section broken away and its edges are occluded by matrix. However, it can be seen that it is as wide as the distal radial facet across its proximal margin and then tapers gradually. It has two equally sized, steeply sloping shoulders, which presumably house the lowermost few secundibrachials, but these cannot be seen. Some of the secundibrachials have parallel sutures and others are slightly cuneate, but still wider than they are high (1.5:3.5). Pinnules are not seen.

The anal structure is not seen.

The tegmen is not seen.

A small portion of the proximal stem is preserved in specimen TCD.28141, although not the most proximal portion, and it measures about 7 mm in length and does not appear to taper or widen either proximally or distally. The component columnals are circular in outline, symplectially articulated and have a regular, fine crenulate suture with rounded apices and troughs and a high amplitude. The morphology of the articular facet cannot be seen as the broken distal end is fractured and broken away, but the latera are straight to slightly convex. The stem is heteromorphic with higher orders being of a greater height and slightly more laterally convex. The inferred noditaxis is approximately $(32)_3 31 (32)_3 3N$. Measurements, in mm, of all columnals of specimen TCD.28141 and their inferred noditaxial orders are inserted in the following table:

KH	0.9	0.3	0.6	0.4	0.6	0.3	0.6	0.3	0.7
Order	N	3	2	3	2	3	2	3	1

As far as can be seen the stem is non-cirriferous.

Remarks. The noditaxis of the stem is a variation on a Type III pattern (of Webster 1974).

The arrangement of the anal plates in the calyx of specimen TCD.28140 could be described as the *"Normal Type"* (Wright 1918), which is the equivalent of *"Extreme Type"* or *"Development Trend B"* (Strimple 1948*b*, almost attained in his Fig. 4) (not *"Development Trend C"* as mentioned in Strimple 1948*a*), and *"Advanced Type"* of Wright (1927) and Strimple (1948*a*). The description of this condition in the latter was; *"Where the radianal has a direct connection with left posterior radial and anal X is entirely separated from posterior basal"*.

Two of the arms definitely belong to the ?*A* ray, but it is unclear as to which rays the remaining arms belong to as their proximal articulations cannot be seen.

Stratigraphical range. Lower Carboniferous (Viséan) - Scotland (Brigantian), Ireland (Asbian).

Infraclass FLEXIBILIA Zittel, 1895

Diagnosis. (After Moore 1978, p. T765.) Globose to ovoid crown composed mainly of tightly spaced arms, which may or may not be distinct from remainder of calyx and which are joined by ligaments rather than by solid union; infrabasals three in number, often hidden by stem; five subequal basals and radials; radianal commonly present, anal X plate interrupting posterior radials; arms non-pinnulate, uniserial, bifurcating isotomously or both isotomously and heterotomously, rarely atomous, incurved and tapering distally; interbrachials present or lacking, disposed interradially and/or perradially between arm branches; flexible tegmen lacks anal sac, mouth disclosed, many small interambulacral plates; stem generally transversely circular, columnals very low, non-cirriferous.

Order SAGENOCRINIDA Springer, 1913

Diagnosis. (After Moore 1978, p. T775.) Plates of the crown usually tightly united; calyx low bowl shaped; basals and radials large, upflaring gently to steeply distally; anal X usually large reaching beyond radials, but may be small or lacking, anals tightly united to basals, radials and brachials; arms usually wide, rounded slightly externally, composed of low, wide, uniserially arranged brachials which are laterally closely united with brachials of adjacent arms or interbrachials; stem tapers distally.

Superfamily SAGENOCRINITACEA Roemer, 1854

Diagnosis. (After Moore and Strimple 1973, p. 16; Moore 1978, p. T794.) Globose to elongate ovoid crown, many closely united arms with intercalated interradially and perradially positioned interbrachial plates; calyx stout; one to several anal plates posteriorly, interlocking with adjacent brachials, rarely lacking; tegmen concealed by distally strongly incurving arms; stem transversely circular, large.

Family EURYOCRINIDAE Moore and Strimple, 1973

Diagnosis. (After Moore and Strimple 1973, p. 16; Moore 1978, p. T808.) Calyx thickly plated, extends higher than arms; infrabasals, basals and radials not distinct from remainder of calyx formed by closely sutured brachials, interbrachials and anals; infrabasals always and basals generally concealed by proximal columnals, except posterior basal which interrupts radial circlet; anal X supported by posterior basal, additional anal plates may follow; arms stubby, free, generally bifurcating isotomously on primibrachial 2, but sometimes primibrachial 3.

Genus AMPHICRINUS Springer, 1906

1906 *Amphicrinus* Springer, p. 518.

1913 *Amphicrinus* Springer, Zittel, p. 205.

1914 *Amphicrinus* Springer *in* Wright, p. 161.

1920 *Amphicrinus* Springer, Springer, p. 261.

1939 *Amphicrinus* Springer, Strimple, p. 4.

1943 *Amphicrinus* Springer, Bassler and Moodey, p. 297.

1943 *Amphicrinus* Springer, Moore and Laudon, p. 74.

1944 *Amphicrinus* Springer, Moore and Laudon, p. 179.

1948 *Amphicrinus* Springer, Cuénot, p. 67.

1953 *Amphicrinus* Springer, Ubaghs, p. 755.

1964 *Amphicrinus* Springer, Arendt and Hecker, p. 94.

1971 *Amphicrinus* Springer, Strimple and Moore, p. 39.

1971 *Paramphicrinus* Springer, Strimple and Moore, p. 40.

1973 *Amphicrinus* Springer, Webster, p. 49.

1973 *Paramphicrinus* Springer, Moore and Strimple, p. 37.

1977 *Amphicrinus* Springer, Webster, p. 37.

1977 *Paramphicrinus* Springer, Webster, p. 125.

1978 *Amphicrinus* Springer, Moore, p. T809.

1978 *Paramphicrinus* Strimple and Moore, Moore, p. T811.

1986 *Amphicrinus* Springer, Webster, p. 56.

1986 *Paramphicrinus* Springer, Webster, p. 235.

Type species. *Amphicrinus scoticus* Springer *in* Wright, 1914, by subsequent monotypy.

Other species. *A. carbonarius* Springer, 1920, *A. luberculatus* Yakovlev, 1961, *Amphicrinus*? sp. Wright, 1954, *A. oklahomaensis* Strimple, 1939 [=*Paramphicrinus oklahomaensis* (Strimple, 1939)], *A. poundi* Strimple, 1939 [=*Paramphicrinus poundi* (Strimple, 1939)].

Emended diagnosis. (Modified after Springer 1920, p. 337; Moore 1978, p. T809, p. T811.) Crown ovoid to round; bowl-shaped, strong calyx forms lower half of crown, expanding upward from radials; infrabasals entirely within circlet of basals, diminutive tripartite (?or fused), entirely covered by stem; basals covered by stem, distal extremities sometimes seen as small triangles in ?juvenile specimens, posterior basal mostly exposed; radials mostly covered by stem, those of *C* and *D* rays smaller than others and asymmetrical seen laterally; radianal lacking, anal X on truncate extremity of *CD* basal, followed by further plates in single, double or triple series, interlock laterally with fixed brachials, reach height of highest interradial interbrachials; closely abutting, parallel, small free arms form upper half of crown, incurving at summit so that numerous (up to one-hundred) arm tips almost converge, proximally broad comprising two primibrachials, followed by usually three, sometimes four secundibrachials, first bifurcation slightly heterotomous, three to four further bifurcations becoming distinctly heterotomous distally, also tapering, sutures between brachials strongly arcuate, becoming more pronounced distally, commonly with patelloid processes at level above primibrachials; first interradially positioned interprimibrachial rests on distal shoulders of radials, single (immature), double or triple (adult) vertical series of few to over twenty plates follow reaching up to height of distal tertibrachials, perradially positioned interbrachials initiating between secundibrachials and tertibrachials may occur in more mature specimens, but fewer in number, interbrachitaxes taper both proximally and distally; stem about 10 mm diameter proximally, tapering gradually distally, curving gently toward *DE* interray, most proximal columnals less than 0.5 mm high on convex side, lower on concave side, sinuous and symplectially articulating, articular facets with peripheral crenularium with many fine crenulae, areola smooth, wide and planar, lumen pentasteroidal to pentalobate in outline.

Remarks. An incomplete flexible specimen comprising only a bundle of arms from the level of secundibrachials upwards from the Namurian of northern England was

designated as *Amphicrinus*? sp. by Wright (1954, p. 151). It was tentatively placed in this genus, since it held closest resemblance to this than any other flexible genus. It is not known whether this represents another species of *Amphicrinus*, or if it even belongs to *Amphicrinus* at all. Therefore, the range of the genus should not include the Namurian.

Springer (1920) described another species of *Amphicrinus*, which he named *A. carbonarius*. The specimen comprises only the arms from the level of secundibrachials upward. He stated that he had not described it previously "because the parts preserved are not sufficient to determine its generic characters". However, after seeing Wright's (1914) *Amphicrinus* specimens he assigned the specimen to the same genus because it fitted in well stratigraphically, but an entire specimen was not found to confirm this inference. The only diagnostic specific character that he noted was that the narrow distal arms were "rather angulated". The other characters described are generic such as the brachial sutures being strongly arcuate and the arms being closely abutting. This angulation of the distal arms is not sufficient to characterise a new species, especially when the arms of many genera also have this attribute, which is accentuated when the brachial sutures become more strongly arcuate. Taking the above into account this specimen should be classified as cf. *Amphicrinus* sp. rather than *Amphicrinus* n. sp. because it does resemble the species *A. scoticus*, so is probably not a new species, but the generic positioning is also doubtful.

Little work has been carried out on the ontogeny of flexible crinoids since Springer (1920) and, hence, little is known about their post-larval ontogeny. It is known that infrabasals, basals, radials and plates of the posterior interray change little in number or relative proportion, simply growing in size at the same rate as the stem and the arms (Lane 1978). The calyx, therefore, retains the same overall outline (with the exception of *Homalocrinus parabasilis* Angelin (Springer 1920)).

There is an increase in the number of crown plates by the addition of interbrachial plates in all rays, except the posterior interray, which served to enlarge the calyx. The calyx was enlarged by intercalation and subsequent growth in height and width of interbrachials so that it could accommodate the increasing volume of the visceral mass of the crinoid (Lane 1978) (see Figure 4.2, p. 49, for a full explanation of interbrachial terminology). Accommodation was also made by the tegminal area becoming progressively wider and

	Amphicrinus	*Paramphicrinus*
Crown	sub-round	round, medium sized
Aboral calyx	strong, forms majority of lower part of crown	strong, bowl-shaped, forms lower half of crown
Infrabasals	covered by stem	covered by stem
Basals	covered by stem, except distal extremity of posterior basal	covered by stem, except posterior basal, sub-horizontal in attitude
Radials	mostly covered by stem, *C* and *D* radials smaller than others and asymmetrical	distal edges not covered by stem, *C* and *D* radials smaller than others and asymmetrical
Arms	wide proximally, strong, branch four or five times isotomously, tendency towards heterotomy distally, small distal arms free and tapering, but closely laterally abutting	wide proximally, strong, branch isotomously on IIBrr, thereafter branching distinctly heterotomous (bi-endotomous type), eighty to one-hundred closely abutting free arm tips at crown summit curve inward and taper distally
Brachials	arcuate sutures, getting stronger distally, commonly with patelloid processes above IBrr, IBr_2 axillary	sutures mostly arcuate and getting stronger distally, IBr_2 and $IIBr_3$ axillary
Interbrachials	interradial iIBrr rest on shoulders of RR, polygonal, first interradial iIBr large, about eleven further iBrr up to iIIBrr follow in two series; central perradial iIIBrr and iIIIBrr total up to four, arranged in a single series, left and right perradial iIIIBrr few in number arranged in a single series, all interradial areas taper distally	interradial iIBrr rest on shoulders of RR, polygonal, first interradial iIBr large, fifteen to twenty further iBrr up to iIIIBrr follow in two or three series; central perradial iIIBrr and iIIIBrr total about ten, arranged in double series following first iIIIBr, highest iIIIBr reaching almost to height of highest IIIBr, left and right perradial iIIIBrr three to five in number in single or double series, all interradial areas taper distally
Anal area	RA lacking, anal X rests on truncated posterior basal, further anals in single to double series reach almost to height of highest interradial iBr	RA lacking, moderately large anal X on truncate extremity of posterior basal, followed by sixteen to twenty higher anals in double series which reach almost to height of highest interradial iBrr
Stem	large, proximally comprises very low circular columnals, tapers gradually distally and curves gently away from calyx, articular facet with peripheral crenularium and pentasteroidal axial canal	large, proximally comprises very low circular columnals, tapers gradually distally and curves gently away from calyx toward *DE* interray or *A* ray, articular facet with peripheral crenularium and pentasteroidal or pentalobate axial canal
Sculpture	none	none
Range	*L. Carb. (Viséan)*, Eur. (Scotland, England, Ireland), USSR, USA (Oklahoma)	*L. Penn. (Morrowvian) - U. Penn. (Missourian)*, USA (Oklahoma, Arkansas, Illinois, Kansas)

Figure 6.5. Table outlining morphological similarities between the genera *Amphicrinus* Springer, 1906 and *Paramphicrinus* Strimple and Moore, 1971. The diagnoses are emended, *Amphicrinus* after Wright (1954) and Moore (1978) and *Paramphicrinus* after Strimple and Moore (1971) and Moore (1978).

higher in its position in the crown (Lane 1978). As demonstrated by Springer (1920) for *Forbesiocrinus multibrachiatus* Lyon and Casseday, interradially positioned interbrachials increase in number in small to large specimens from one to about twenty; Springer noted a similar pattern in all flexibles for which he had suitable material. These plates held the proximal arm portions together. As their numbers increased and they grew in size, the overall height of the interbrachitaxis increased so that a larger portion of the arms were laterally united by them. This provided increased support for the highly flexible free, more distal arms when they moved (Lane 1978). However, it restricted the overall movement of the proximal arms and, therefore,the calyx, and this meant that organs of the body cavity were not damaged (Lane 1978).

Paramphicrinus Strimple and Moore, 1971, is inferred, herein, to represent mature individuals of the genus *Amphicrinus* Springer, 1906. Several lines of evidence suggest that the two genera are the same and represent different stages of ontogeny of *Amphicrinus* (Figure 6.11.*a-f*). The number of interbrachials appears to be the main, if not only, difference between the two genera. In the diagnosis of *Amphicrinus* (Moore 1978, p. T809), there is no indication as to the number of interradially positioned interbrachials. The diagnosis of *Paramphicrinus* (Strimple and Moore 1971; Moore 1978, p. T811), however, specifies that there should be sixteen to twenty interradial interbrachials. From figured specimens of *P. oklahomaensis*, it is observed that these interbrachials are arranged: either in a double series, whose numbers fall within sixteen to twenty (hypotype, specimen number IGS42P61, in Strimple and Moore (1971), Fig. 18, Pl. 22, fig. 2*a-d* (*BC*, *EA* interrays)); or are less than sixteen (holotype, specimen number USNMS4031, in Strimple and Moore (1971), Fig. 17, Pl. 23, fig. 3*a* (all rays, except posterior) (note that at mid-height the interbrachitaxis may occur as a single series)); or in a triple series, whose numbers exceed twenty (Strimple and Moore (1971), Fig. 18, Pl. 22, fig. 2*b* and *c* (*AB*, *DE* interrays) (Fig. 17 (*BC* interray) which shows a triple series at mid-height of the interbrachitaxis, but does not show how many plates are in the interbrachitaxis in total)). Since the interbrachials both exceed twenty and are less than sixteen in different specimens of *Paramphicrinus*, the number of interbrachials does not appear to be a good discriminator between *Amphicrinus* and *Paramphicrinus*. Exceeding twenty and falling short of sixteen interradially positioned interbrachials means that this diagnostic feature is incorrect. Specimens TCD.35951 and TCD.35953 have interradially positioned interbrachials comparable in number to those observed in figured specimens of *Amphicrinus* in Wright

(1954) and Moore (1978), *i.e.* about twelve, and they are more or less in a double staggered series. However, specimen TCD.35952 has much fewer interprimibrachials and they are arranged in a single series. The latter specimen is smaller than the former two, therefore this single series is likely to be an early or immature ontogenetic feature.

In the description of *P. oklahomaensis* (Strimple, 1939) (Strimple and Moore 1971) central perradially positioned interbrachials are said to occur in a double series. In the holotype (specimen number USNMS4031) (Strimple and Moore 1971, Fig. 17), it can be seen that in fact they occur as a single series, except in the *A* ray. The number of central perradially positioned interbrachials (primi- and secundi-) in the three current specimens is comparable to that of previously figured specimens of *Amphicrinus* (about three) rather than *Paramphicrinus* (about ten in a double series (*P. oklahomaensis* (Strimple, 1939) hypotype, specimen number IGS42P61 (Strimple and Moore 1971))), although the holotype of *P. oklahomaensis* (Strimple, 1939) (specimen number USNMS4031) (Strimple and Moore 1971) has only about four of these plates. Left or right perradially positioned interbrachials should occur in a single series in *P. oklahomaensis* (Strimple, 1939). In the hypotype (specimen number IGS42P61) (Strimple and Moore 1971, fig. 18), these plates occur in a single to double series and in the holotype it appears that they do not occur at all, except for a single left perradially positioned intertertibrachial in the *D* ray. Specimen TCD.35951 clearly has at least two left perradially positioned intertertibrachials in the *C* ray, and a single central one, which are not seen in any figured specimens of *Amphicrinus*, but, as mentioned, are seen in figured specimens of *Paramphicrinus*, the number in each being about three to five. The presence of left and right perradially positioned intertertibrachials indicates a more mature specimen. It is likely that no interbrachials initiate intercalation at a higher order since the arms are free and strongly heterotomous above the most distal tertibrachials. Using this morphological feature the holotype of *P. oklahomaensis* (Strimple, 1939) is more akin to a species of *Amphicrinus*.

It is inferred that intercalation of interbrachials initiates with a single series of interradially positioned plates (Figure 6.11.*a*). These gradually increase in number, plates being added distally to the interbrachitaxis. This gradually increases to a double series (Figure 6.11.*c-e*), and in very mature specimens to a triple series. Initially, perradially positioned interbrachials are intercalated as a single series (Figure 6.11.*a-e*). Again, their numbers may increase distally and finally a double series may occur (Figure 6.11.*f*). In very mature specimens, left and right perradially positioned interbrachials may be

intercalated in a single series. The higher in the calyx the interbrachitaxis, the fewer the number of plates and the later it is initiated.

The anals are specified to appear as a double series in *Paramphicrinus*. However, *P. oklahomaensis* (*in* Strimple and Moore 1971, fig. 17) shows that at mid-height the anitaxis is a single plate across and distally there are three plates across in a series. Therefore, this feature is also incorrectly described in the diagnosis of *Paramphicrinus* of Strimple and Moore (1971).

Like interbrachials, anal plates probably initiate as small, irregularly shaped plates, which later ankylose to form larger, more regularly shaped plates. These then form part of a clearly developed series, whether the series be single, double or triple.

There is an increase in the number of arm branches per ray throughout ontogeny (Springer 1920), although the mechanism for the increase is not known. It is possible that they autotomised distal portions of the arms, replacing them firstly with an axillary brachial with the subsequent related brachitaxis following, as do extant comatulids (Lane 1978). The number of arms at the summit of the crown is unknown in previously figured specimens of *Amphicrinus* and there is no mention of the number in the diagnosis of the genus. However, it does mention that following the first bifurcation on primibrachial 2 there may be another three or four bifurcations with a tendency towards heterotomy in the distal portions (Moore 1978). This potentially has a maximum outcome of one-hundred-and-sixty arms. According to Strimple and Moore (1971) and Moore (1978) in the original description of *P. oklahomaensis* (Strimple, 1939) there should be at least eighty, possibly up to one-hundred, arm tips at the crown summit in well preserved specimens, again tending towards heterotomous branching. Unfortunately, neither previously figured specimens nor the specimens in the current sample of *Amphicrinus* show the summit of the crown. It is therefore unknown how many arms can occur in *Amphicrinus*. It is inferred that the more mature the specimen (*i.e., Paramphicrinus*), the more bifurcations occur and therefore the greater the number of arms.

From what can be seen of the stem in specimens TCD.35952 (Figure 6.8) and TCD.35951 (Figures 6.6, 6.7), the smaller of the two specimens (TCD.35952) has about five columnals in the first mm and the larger (TCD.35951) has about four columnals in the first mm of the proxistele. This is further evidence for Springer's (1920) inference that columnals of the proxistele in flexible crinoids increase in height during ontogeny.

The genus *Paramphicrinus* Strimple and Moore, 1971, is herein considered an invalid

junior synonym of *Amphicrinus*, whose members should be considered as belonging to the genus *Amphicrinus*, the senior synonym. The species *P. oklahomaensis* (Strimple, 1939), and *P. poundi* (Strimple, 1939), should be returned to their originally designated genus of *Amphicrinus*, and therefore their names should be *A. oklahomaensis* Strimple, 1939 and *A. poundi* Strimple, 1939. [Although there is no supporting literature or explanation, *A. poundi* Strimple, 1939 (as seen in Strimple and Moore 1971, Pl. 22, fig. 1*g-h*), is referred to as *P. poundi* (Strimple) in Moore 1978.]

Stratigraphical range. Carboniferous (Viséan; Westphalian) - Scotland (Brigantian), Ireland (Arundian), Russia, ?England; Lower Pennsylvanian (Morrowan) to Upper Pennsylvanian (Missourian) - USA (Oklahoma, Arkansas, Illinois, Kansas, Iowa, Texas).

Amphicrinus scoticus Springer *in* Wright, 1914

Plate 13, fig. c; Plate 16, figs a-c; Plate 17, figs a-c;

Figures 6.5, 6.6, 6.7, 6.8, 6.9, 6.10, 6.11

1793 *Encrinus* Ure, p. 325, pl. 18, fig. 13.

1912 *?Forbesiocrinus* sp. Wright, p. 53, pl. 6, figs 1, 2; pl. 7, figs 1, 2.

1912 *?Euryocrinus* sp. Wright, p. 56, pl. 7, fig. 3.

1914 *Amphicrinus scoticus* Springer *in* Wright, p. 161, pl. 19, figs 3, 4.

1918 *Amphicrinus scoticus* Springer, Wright, p. 381.

1920 *Amphicrinus scoticus* Springer, *in* Springer, p. 338, pl. 40, figs 9-11.

1923 *Amphicrinus scoticus* Springer, Wright, p. 489.

1925 *Amphicrinus scoticus* Springer, Wright, p. 288.

1939 *Amphicrinus scoticus* Springer, Wright, p. 53, pl. 11, figs 1-6.

1943 *Amphicrinus scoticus* Springer, Bassler and Moodey, p. 298.

1946 *Amphicrinus scoticus* Springer, Wright, p. 37, pl. 3, figs 7, 10-12; pl. 4, figs 1-3, 5-7, 10-12.

1954 *Amphicrinus scoticus* Springer, Wright, p. 149, pl. 41, figs 1, 14; pl. 42, figs 8, 9; pl. 43, figs 16-18, 20-23; pl. 47, figs 26, 27.

1978 *Amphicrinus scoticus* Springer, Moore, p. T809, fig. 541, 7; fig. 543, 5*a-c*.

Material. Four moderately complete, well preserved specimens. Specimen number TCD.35951 shows the aboral crown including the most proximal part of the stem (partial)

surrounded by all rays, which are splayed. Specimen TCD.53171 also shows the aboral crown, but is less complete in the way of arms and interbrachial plates. It lies on a piece of shale and several disarticulated plates from the crinoid surround it, but are of indeterminable position. Specimen numbers TCD.35952 and TCD.35953 are laterally compressed showing a good proportion of the arms on one side, but with arms generally lacking on the other. Specimens TCD.35951, TCD.35953 and TCD.53171 were collected by Professors G. D. Sevastopulo and N. G. Lane in 1972 from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595. Specimen TCD.35952 was collected by Anthony Randall in June 1969 from the Bundoran Shale Formation, probably very near to the locality where the other specimens were collected. It was dispatched by the Ulster Museum.

Emended diagnosis. (Modified after Springer 1920, p. 338; Wright 1954, p. 151; (see *Remarks*).) Crown subround, higher than wide (about 40:35), widest point at tertibrachial *3*; calyx small, low; infrabasals very small, lying entirely within basals, sometimes partly or entirely resorbed; basals in larger specimens covered by stem, distal extremities uncommonly visible as small triangles, posterior basal more than twice as large as others and extending above them, truncate, interrupting radial circlet and clearly visible; radials may be covered by up to about half of the stem, *C* and *D* rays smaller than others; anal *X* commonly incomplete or lacking, rests upon posterior basal, followed by single or double series of anal plates; primibrachials *1* larger than radials, widening upward, secundibrachials *1* and *2* as large, secundibrachial *3* widening upward, tertibrachials five or six in number; arms flat, closely abutting and infolding distally, interlock closely with interbrachials by zigzag lines; brachial sutures arcuate, strongly so distally; first interradially positioned interprimibrachial rests on oblique shoulders of radials, larger than anal, angular above for support of about eleven further interbrachials in a double series; perradially positioned interbrachials present, occur in double series in mature specimens; most proximal stem composed of low columnals, tapers distally, stem facet wide, about twice the usual basal circlet diameter, sharply and deeply indented.

Description. The entire lateral surface of the crown has a finely pustulate sculpture.

The calyx is stout and thickly plated. Infrabasals are not seen at all, being completely concealed by the stem, except in specimen TCD.53171 where, as can seen on

Plate 17, fig. c, a small even pentagonal circlet can be deciphered. The infrabasal:infrabasal sutures, however, cannot be seen. The distal extremities of basals of the *BC* and *DE* rays are exposed in specimen TCD.35952, *EA*, *AB* and *BC* rays in specimen TCD.35953, the *BC* ray only in specimen TCD.53171, but they are completely covered in specimen TCD.35951. The infrabasal:basal and basal:basal sutures can be seen at the base of specimen TCD.53171. In all specimens the posterior basal is enlarged interrupting the radial circlet and reaching beyond the summit of it. It is truncated (laterally in specimen TCD.35952) for the reception of the anal X, which, in specimen TCD.35951, lies directly above it. Specimen TCD.53171 has what appears to be a very elongate posterior basal. No suture can be deciphered that would separate it into two smaller plates, *i.e.,* the basal and the anal X. The anal X is not seen in specimens TCD.35952 and TCD.35953. No further plates of the anal series are seen in any specimen. Five radials are seen in all specimens with the exception of specimen TCD.35952 where the *B* radial is missing. They are seen in lateral view, but are also partly concealed proximally by the stem. In outline, they are hexagonal and horizontally elongate. The *C* and *D* radials are asymmetrical, their posterior sides being lower than their anterior sides to accommodate the enlarged posterior basal.

The arms, where fixed, consist of interlocking brachials. They branch isotomously firstly on primibrachial 2, which is axillary, except in the *C* and *D* rays where branching is slightly heterotomous. Usually three, but sometimes four secundibrachials follow with five to nine tertibrachials, and at least eleven quartibrachials. Branching becomes slightly heterotomous on tertaxillaries and thereafter, and branching is not seen at a higher level in any specimen. Radials, primibrachials and secundibrachials have roughly equal widths, but thereafter the widths of brachials are reduced. The arms start to taper distally from the first quartibrachials. Brachial sutures have an arcuate depression on both proximal and distal facets, which becomes more pronounced on distal brachials. The arc is in line with the apex of the axillary of each particular brachitaxis, so where heterotomy occurs the arc is shifted laterally. The two distal shoulders of axillary brachials reduce in the amount they slope distally so that on tertibrachials they are almost horizontal in attitude. Where two shoulders of a single axillary meet there is a raised rounded to pointed process. The posterior sides of *C* and *D* primibrachials alter in both size and shape in response to the anal series. The posterior side of both primibrachials of the *D* ray are laterally elongated. The posterior shoulder only of the axillary is widened and,

Figure 6.6. Aboral view of *Amphicrinus scoticus* Springer, 1906, (specimen number TCD.35951) drawn using camera lucida (same scale as Figure 6.7).

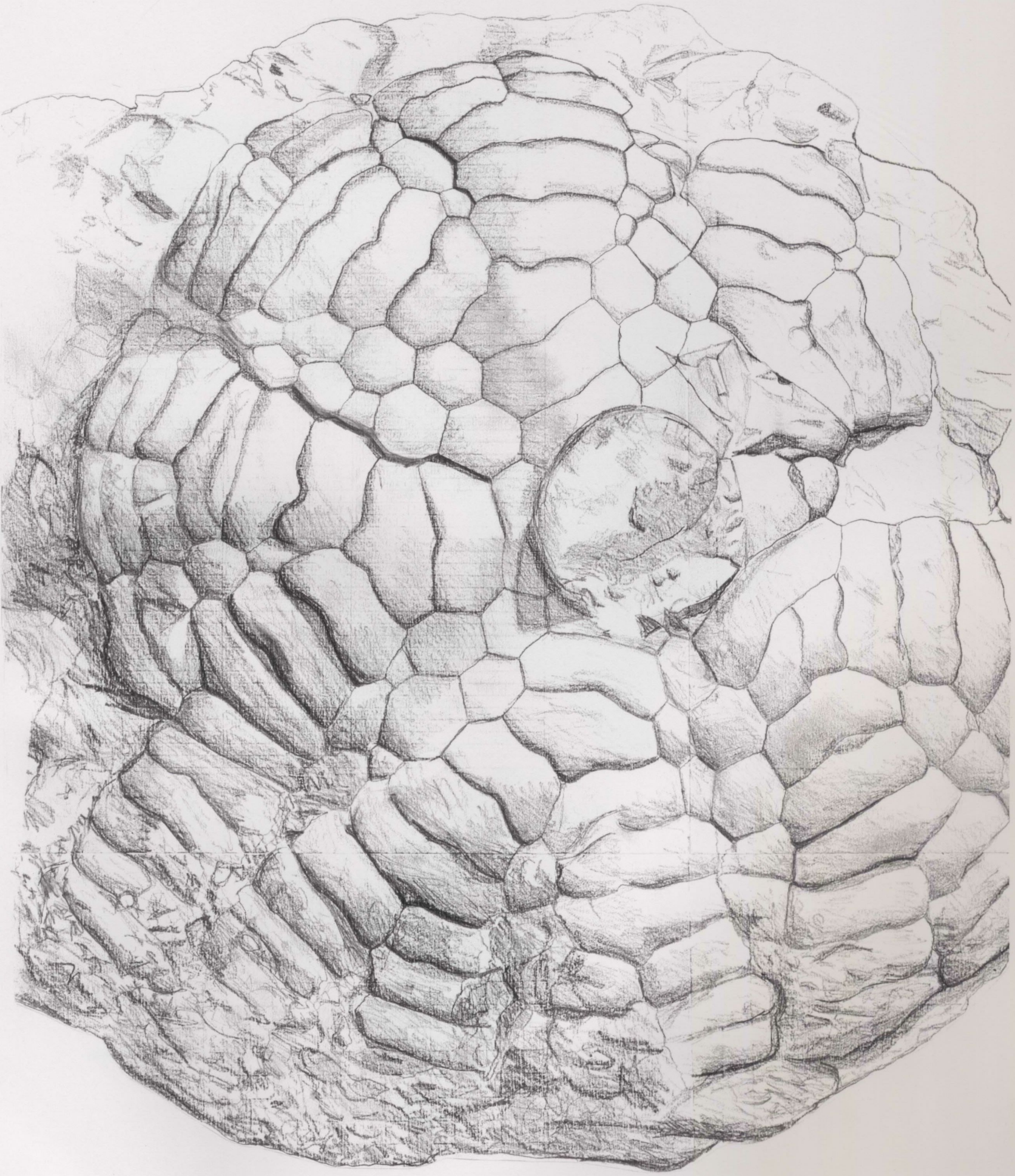
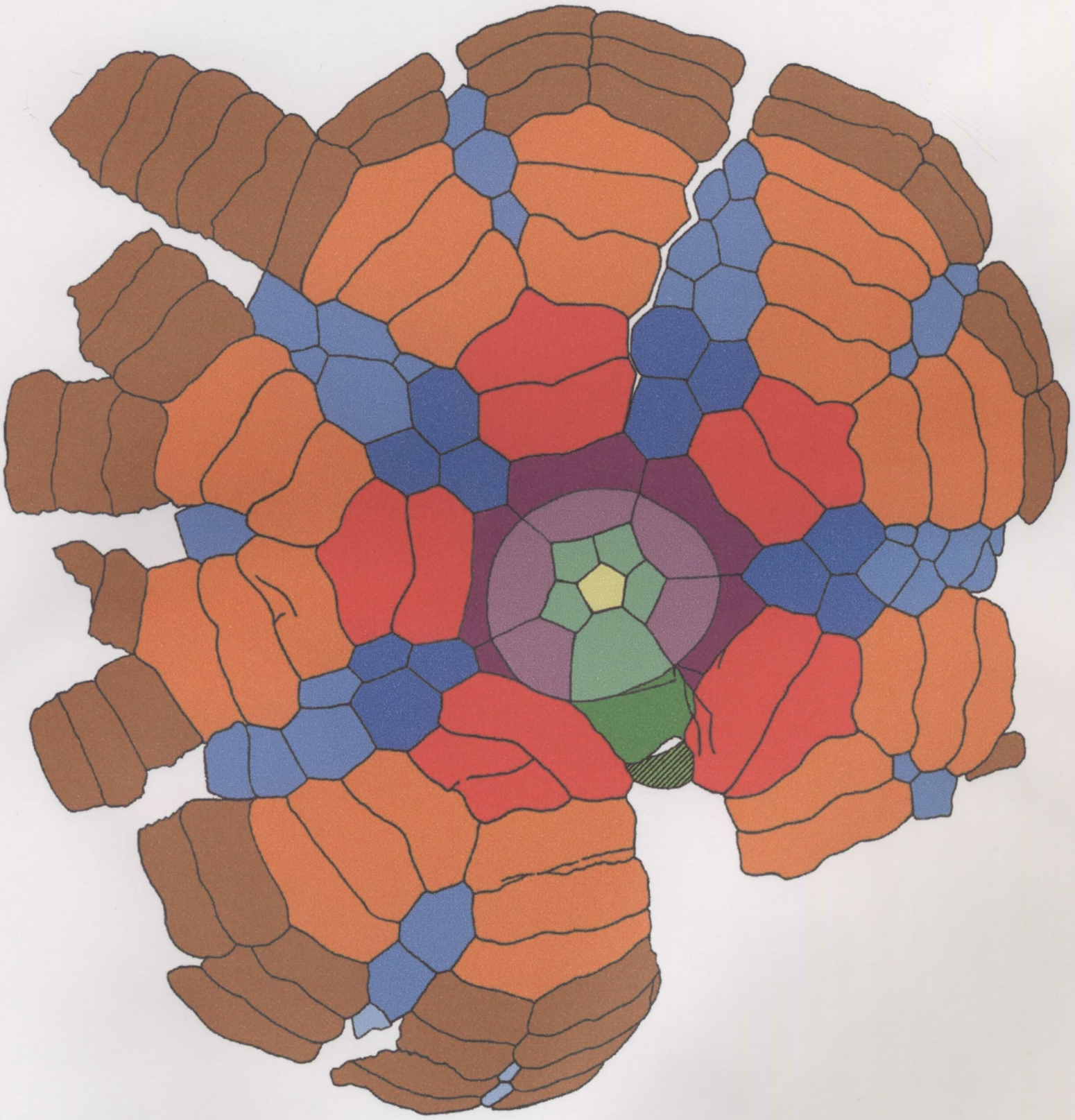


Figure 6.7. Aboral view plate diagram of *Amphicrinus scoticus* Springer, 1906, (specimen number TCD.35951) (see Figure 6.2 for plate legend).



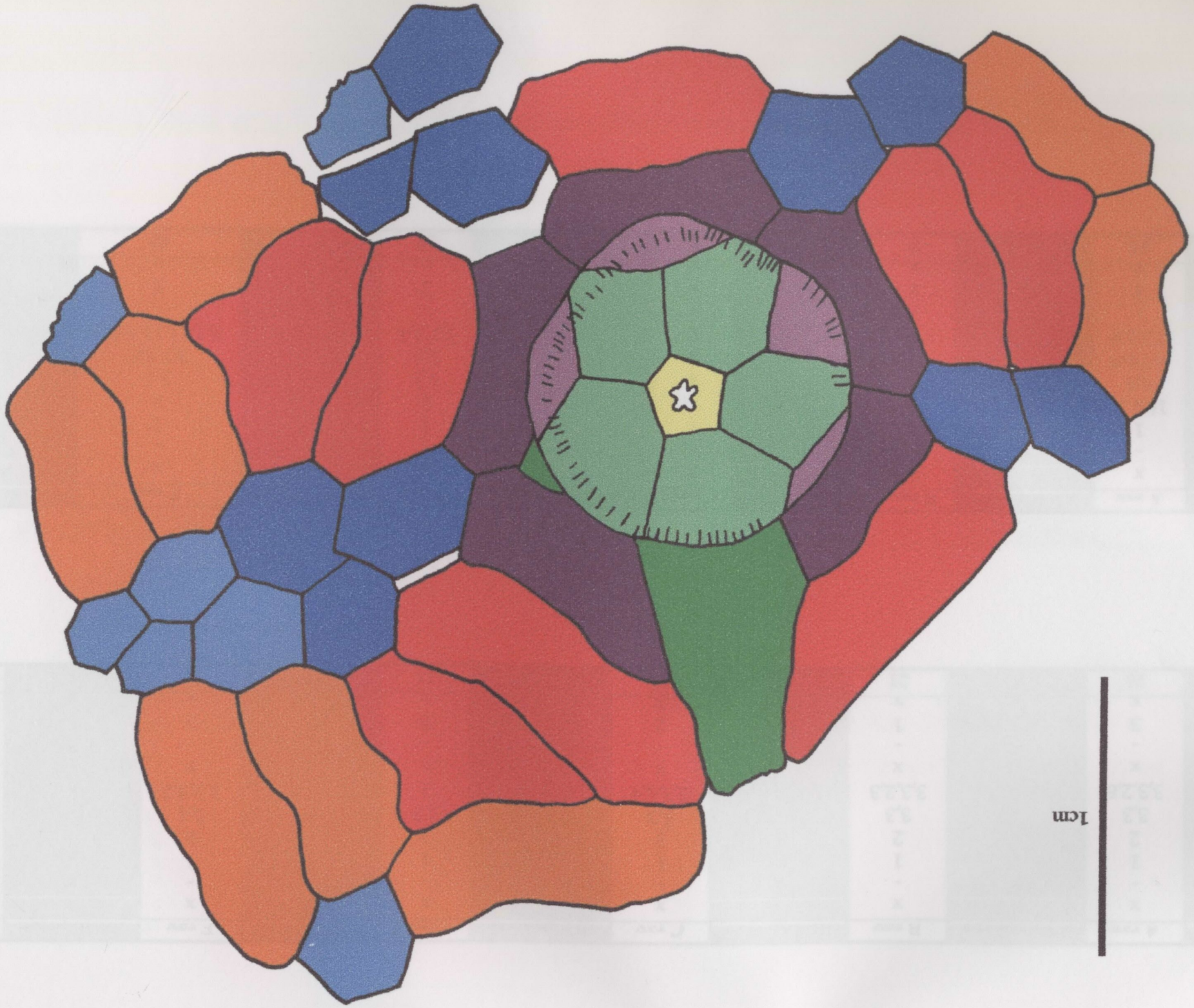
1cm

Figure 6.8. Plate diagram for *Amphicrinus scoticus* Springer, 1906 (drawn using camera lucida); specimen number TCD.35952 (see Figure 6.2 for plate legend). Note tertibrachials of *B* ray, left-hand side of *D* ray and radial plate of *C* ray are seen only laterally on specimen, so plate diagram has been modified to include these plates.



1cm

Figure 6.9. Aboral view plate diagram of *Amphicrinus scoticus* Springer, 1906, (specimen number TCD.53171) (see Figure 6.2 for plate legend).


1cm

	A ray	AB interray	B ray	BC interray	C ray	CD interray	D ray	DE interray	E ray	EA interray	TOTAL
Infrabasal	x	-	x	-	x	-	x	-	x	-	0
Basal	-	x	-	x	-	1	-	x	-	x	1
Radial	1	-	1	-	1	-	1	-	1	-	5
Primibrachial	2	-	2	-	2	-	2	-	2	-	10
Secundibrachial	3,3	-	3,3	-	3,3	-	2,3	-	3,4	-	30
Tertibrachial	3,3,2,6	-	3,3,2,3	-	2,3,4,4	-	1	-	2,2,2,2	-	47
Quartibrachial	x	-	x	-	x	-	x	-	x	-	0
Interprimibrachial	-	3	-	3	-	anal X	-	3	-	3	13
Intersecundibrachial	3	5	1	4	2	x	2	7	3	6	33
Intertertibrachial	x	x	x	x	3	x	x	x	x	x	3
TOTAL	26	8	21	7	27	2	11	10	21	9	142

Figure 6.10.*a*.

	A ray	AB interray	B ray	BC interray	C ray	CD interray	D ray	DE interray	E ray	EA interray	TOTAL
Infrabasal	x	-	x	-	x	-	x	-	x	-	0
Basal	-	x	-	1	-	1	-	1	-	x	3
Radial	1	-	x	-	1	-	1	-	1	-	4
Primibrachial	1(of 2)	-	x	-	x	-	2	-	2	-	6
Secundibrachial	4,4	-	x	-	x	-	1,3	-	3,4	-	17
Tertibrachial	9,7,6,8	-	8	-	x	-	5,8	-	8,7,8,8	-	82
Quartibrachial	5,5,6,8	-	x	-	x	-	2,7,3,4	-	3,1,11,10,4,4,6	-	79
Interprimibrachial	-	x	-	x	-	(anal X missing)	-	1(of 2)	-	1(of 2)	2
Intersecundibrachial	1	x	x	x	x	x	2	1	2	1	7
Intertertibrachial	x	x	x	x	x	x	x	x	x	x	0
TOTAL	64	0	8	1	1	1	38	3	82	2	200

Figure 6.10.*b*.

	A ray	AB interray	B ray	BC interray	C ray	CD interray	D ray	DE interray	E ray	EA interray	TOTAL
Infrabasal	x	-	x	-	x	-	x	-	x	-	0
Basal	-	1	-	1	-	1	-	x	-	x	3
Radial	1	-	1	-	1	-	1	-	1	-	5
Primibrachial	2	-	2	-	2	-	2	-	2	-	10
Secundibrachial	4,4	-	4,4	-	4,4	-	3,3	-	2,3	-	35
Tertibrachial	5,7,9	-	7,7,6,8	-	4,5,4,4	-	x	-	3,3	-	72
Quartibrachial	8,6,7,8	-	5,5,3	-	4	-	x	-	x	-	46
Interprimibrachial	-	3	-	2	-	(anal X missing)	-	1	-	1	7
Intersecundibrachial	3	4	3	4	3	-	x	4	2	x	23
Intertertibrachial	x	x	1	x	x	-	x	x	x	x	1
TOTAL	64	8	56	7	35	1	9	5	16	1	202

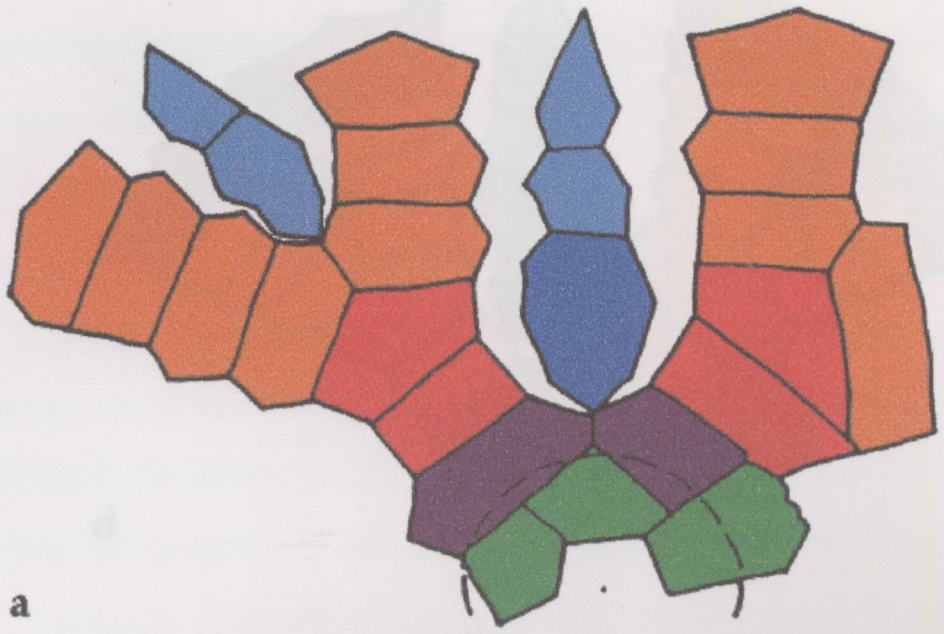
Figure 6.10.*c*.

	A ray	AB interray	B ray	BC interray	C ray	CD interray	D ray	DE interray	E ray	EA interray	TOTAL
Infrabasal	x	-	x	-	x	-	x	-	x	-	0
Basal	-	x	-	1	-	1	-	x	-	x	2
Radial	1	-	1	-	1	-	1	-	1	-	5
Primibrachial	1	-	2	-	2	-	1	-	2	-	8
Secundibrachial	x	-	1,2	-	2,1	-	x	-	1,1	-	8
Tertibrachial	x	-	x	-	x	-	x	-	x	-	0
Quartibrachial	x	-	x	-	x	-	x	-	x	-	0
Interprimibrachial	-	3	-	3	-	(anal X missing)	-	2	-	2	10
Intersecundibrachial	x	1	1	4	1	x	x	x	x	x	7
Intertertibrachial	x	x	x	x	x	x	x	x	x	x	0
TOTAL	2	4	7	8	7	1	2	2	5	2	40

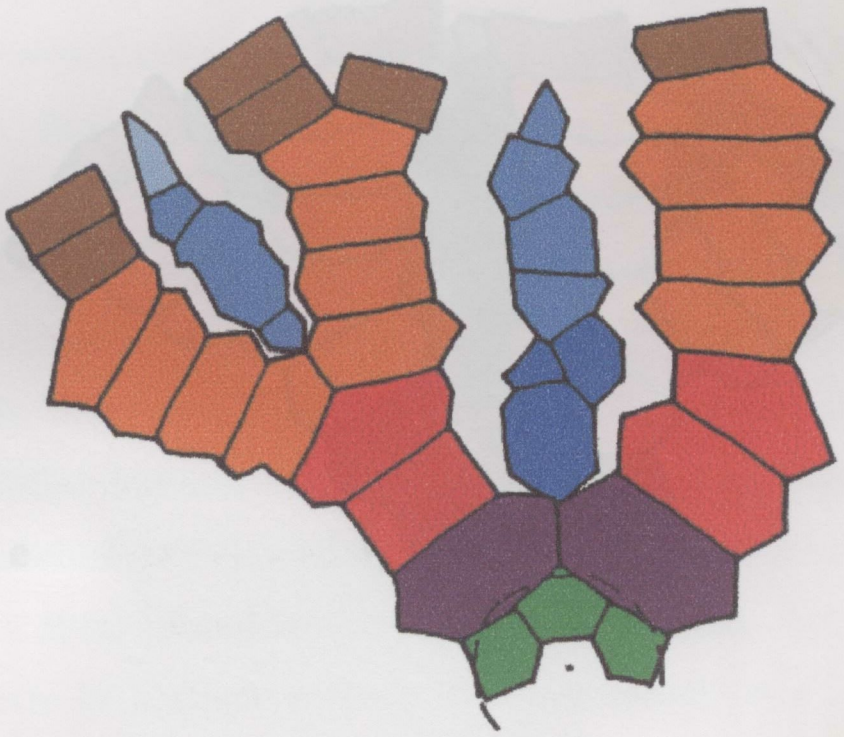
Figure 6.10.*d*.

Figures 6.10.*a-d*. Tables displaying types and numbers of crown plates in specimens TCD.35951, TCD.35952, TCD.35953 and TCD.53171, respectively, of *Amphicrinus scoticus* Springer, 1906.

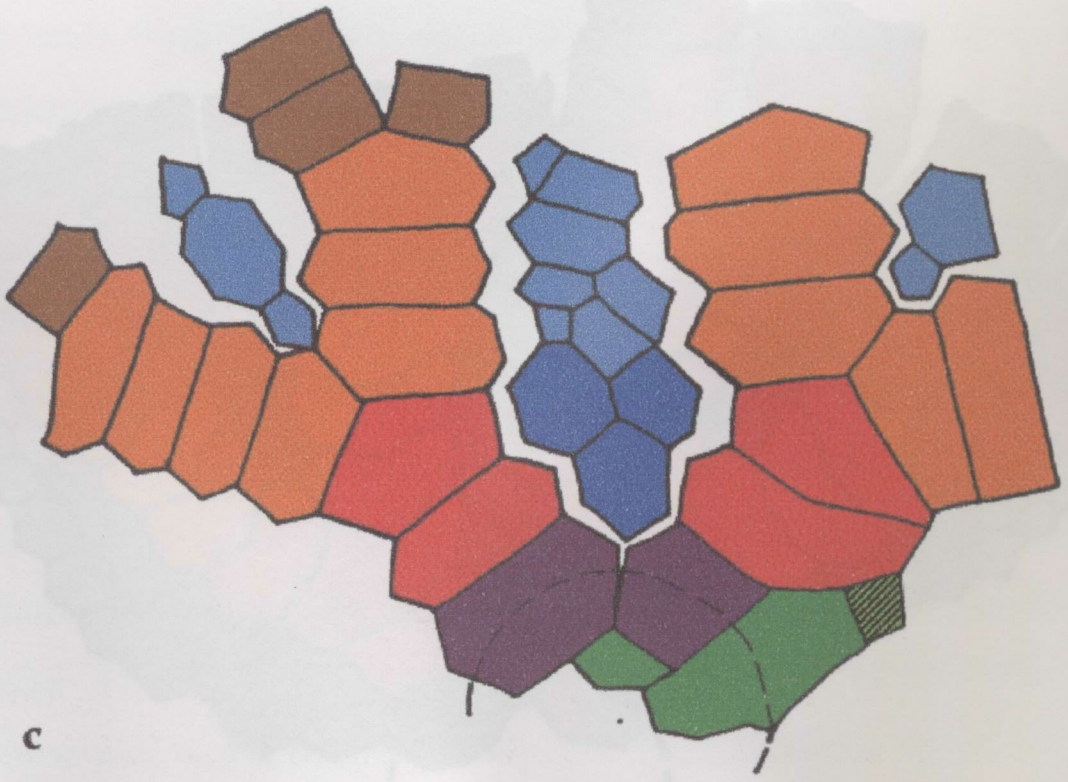
Figure 6.11.*a-f.* Inferred ontogenetic sequence of interradial interbrachials for *Amphicrinus* Springer, 1906. Notice number, arrangement and size of interbrachials. The plate diagrams are not to scale, although specimens increase overall in size from *a* through to *c* (specimen numbers TCD.35952, TCD.35953 and TCD.35951 respectively) (*d-f* all modified, *d* after Springer 1920, p. 337, Fig. 4.5., *e* and *f* after Strimple and Moore 1971, Fig. 17 and Fig. 18 respectively) (see Figure 6.2 herein for plate legend).



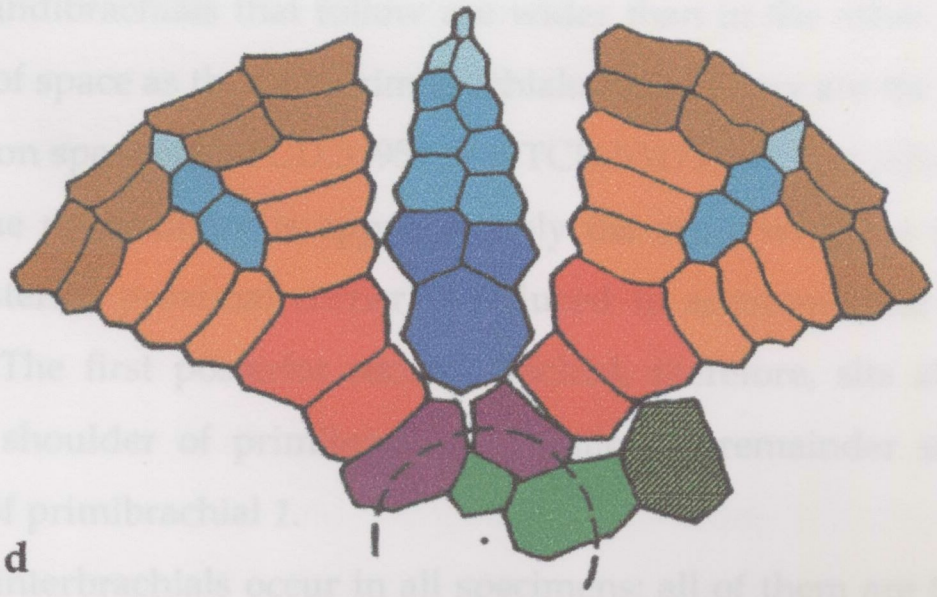
a



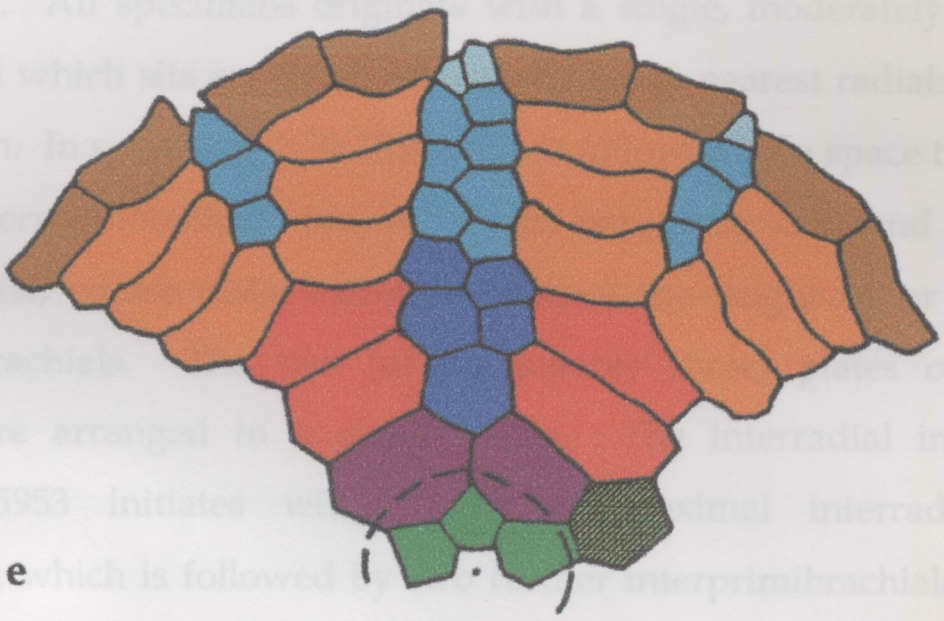
b



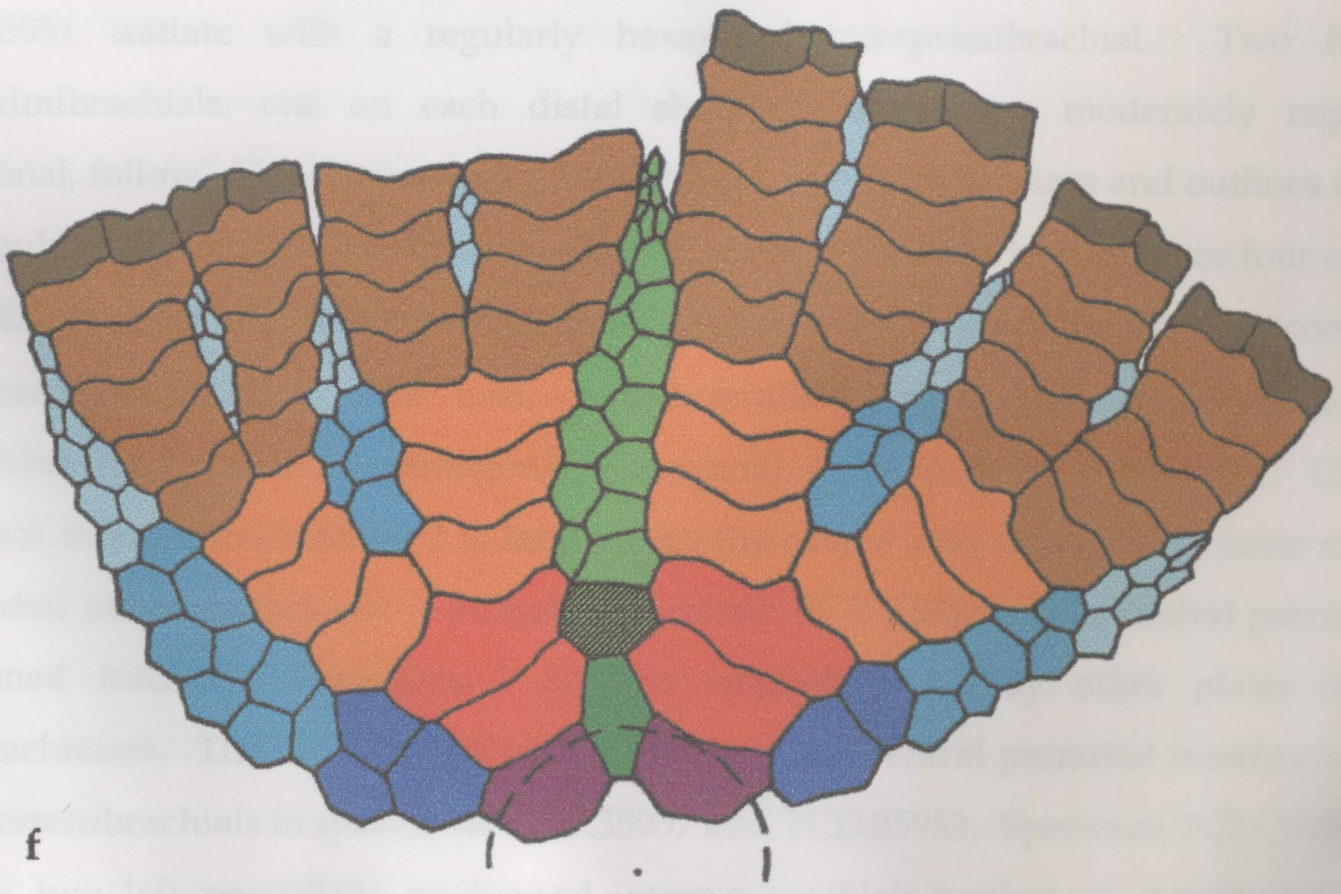
c



d



e



f

therefore, the secundibrachials that follow are wider than in the other rays. Occupying the same amount of space as the two primibrachials of the *D* ray are the primibrachials of the *C* ray, as seen on specimens TCD.35951 and TCD.53171. This is achieved in a slightly different way. The primaxillary is approximately the same width as in the other rays. However, the posterior proximal corner is reduced to accommodate for the enlarged primibrachial *1*. The first posterior secundibrachial, therefore, sits about 60% on the posterior sloping shoulder of primibrachial *2* while the remainder sits on the upper posterior portion of primibrachial *1*.

Polygonal interbrachials occur in all specimens; all of them are tightly sutured to their adjacent brachials. The arrangement of interradially positioned interbrachials varies in each specimen. All specimens originate with a single, moderately large interradial interprimibrachial which sits on the shoulders of its two nearest radials, but which does not interrupt them. In specimen TCD.35952 this is followed by a space that was occupied by a second interprimibrachial, but which is not preserved, and finally a single intersecundibrachial, whose distal extremity reaches the height of, or just beyond, the highest secundibrachials. The two (of presumably three) plates of the interradial interbrachitaxis are arranged in a single series. The interradial interbrachitaxis of specimen TCD.35953 initiates with the most proximal interradially positioned interprimibrachial, which is followed by two further interprimibrachials, one on each of its two uneven distal shoulders. This is followed by about five unequal intersecundibrachials in a single series. The interradial interbrachitaxes of specimen TCD.35951 initiate with a regularly hexagonal interprimibrachial. Two further interprimibrachials, one on each distal shoulder, which are moderately regularly hexagonal, follow. Up to seven intersecundibrachials of various sizes and outlines follow in a double staggered series. In all specimens, a single series of two, three or four central perradially positioned interbrachials occurs in each ray, except in the less complete specimen TCD.53171. The first, intersecundibrachial *1*, sits on shoulders of secundibrachials *1* and is pentagonal, hexagonal or heptagonal in outline. Central perradial intersecundibrachial *2* is larger than the others, and is about the same size as interradial interprimibrachial *1*, except in specimen TCD.35952 whose central perradially positioned intersecundibrachials *2* are the smallest and only other plates in the interbrachitaxis. The ultimate one or two plates of the central perradial interbrachitaxis are intertertibrachials in specimens TCD.35951 and TCD.35953. Specimen TCD.35951 has at least two left perradially positioned intertertibrachials resting on the shoulders of

tertibrachials 2 of the left *C* ray which are much smaller than all other initial interbrachials of the other rays and interrays. It cannot be seen whether specimen TCD.35953 has any equivalent plates, and specimen TCD.35952 has none. The widths of all interbrachitaxes narrow distally overall.

The most proximal portion of the stem is preserved in specimens TCD.35951 and TCD.35952, which can be seen to taper very rapidly away from the calyx. It comprises very low, sinuous circular columnals of which up to seven are seen and it is circular in its outline. The latus is very convex and rounded. On specimen TCD.53171, an impression of the most proximal columnal articular facet morphology can be seen on its base. The deepest side of the impression is towards the *B* ray of the calyx. Articulation is symplectial. There is a very narrow, circular, peripheral crenularium with may irregularly disposed, non-bifurcating, narrow, short crenulae, a wide, smooth and planar areola and a narrow, slightly raised, crenulate perilumen. The lumen is pentalobate in outline with rounded angles and uneven lobes. The lobes are perradially positioned. The two narrowest are coincident with the *C* and *A* rays and the largest coincident with the *B* ray.

Remarks. The discrepancies in the amount of concealment by the stem of the radials and basals have been amended in the diagnosis of the genus and species. In the diagnoses of both *Amphicrinus,* and its synonym *Paramphicrinus* by various authors, it does not say that any part of the basals (except the posterior basal) is exposed beyond the stem impression. Specimen TCD.35951 clearly has its radials partly concealed by the stem, a diagnostic feature of *Amphicrinus,* but some radials of specimens TCD.35952, TCD.35953 and TCD.53171 are fully exposed and their proximal margins can be seen. When this occurs the most distal extremities of the basals are revealed. [More than the distal extremities of the basals are exposed in *A. poundi* (Strimple, 1939) (Strimple and Moore 1971, Pl. 22, fig. 1*a*), although not as much as the posterior basal, and that this specimen is representative of *Amphicrinus* is doubtful anyway.] This may be a feature of preservation. However, it is more likely that the stem, throughout ontogeny, grew further up the aboral calyx covering a greater surface area. This is the location where new columnals were added so this is a reasonable assumption. As the calyx became wider then so did the supporting structure upon which it rested (it is not clear whether this affected the remainder of the stem, or just the proximal part). This inference is supported by the less mature specimens (TCD.35952 and TCD.35953) in which the apices of at least some of the basals are exposed while the

more mature specimens (TCD.35951 and TCD.53171 and figured specimens of *Paramphicrinus* (very mature *Amphicrinus*)) have their basals completely covered by the stem.

Proximal axillaries have steeply sloping distal shoulders so that the higher brachials, which they accommodate, are almost as wide. This acts to ultimately expand the width of the calyx. The almost horizontal shoulders of more distal axillaries means that the following brachials produce much narrower arms and, although they were free in life, could closely abut when necessary. The slightly uneven widths of the shoulders of axillary primibrachials meant that branching was heterotomous, if only slightly, from the first branch and upwards. The unevenness is more pronounced in all other bifurcations. The diagnosis of *Amphicrinus* states that heterotomy is seen only towards the summit of the crown, and in *Paramphicrinus* that well marked heterotomous branching is seen from tertibrachial axillaries upwards. Strimple and Moore (1971) commented on this observation in their discussion of *A. oklahomaensis*. They provided dimensions of shoulders of axillary secundibrachials proving that they are different, the widest shoulder being on the outer side of each axillary. The diagnosis has been altered to accommodate this observation.

Initial perradial interprimibrachials vary in their outlines in each of the specimens. The relative space occupied by this plate in the *AB* interray in specimen TCD.35953 is almost equivalent to that occupied by all of the primibrachials in any of the interrays in specimen TCD.35951. Consequently, its outline is of a different shape also. This change in shape is also caused by the primibrachials that it abuts which, instead of being elongated hexagonal, are tetragonal in outline. The smaller the number of angles in a plate, the fewer the number of plate sutures that are needed.

The lobes of the lumen coincide with the rays of the calyx. This would suggest there is some connection between the rays of the adoral calyx either internally or externally, but it is not known what this connection could be.

The pustulate sculpture seen on the lateral surface of all three specimens is only weak, so is only seen because the specimens are well preserved. The fact that there is no mention of this in any previous diagnoses is probably because it was not preserved, or not observed at the time, on the described specimens.

Stratigraphical range. Lower Carboniferous (Viséan) - Scotland (Brigantian), Russia (Donetz Basin), USA (Oklahoma); ?Pennsylvanian - USA (Kansas).

Order TAXOCRINIDA Springer, 1913

Diagnosis. (After Moore 1978, p. T768.) Elongate ovoid crown, plates not tightly united; weak calyx, not distinct from remainder of crown; anal X and higher anal plates separated from posterior radials and interbrachials by small-plated flexible peristome rather than being closely sutured; arms well rounded, not abutting next neighbours.

Superfamily TAXOCRINACEA Angelin, 1878

Diagnosis. (After Moore 1978, p. T768.) Unusually elongate crown, rays above radials partly or wholly separated; posterior interray usually with tube-like anal series, not included in calyx; arms branch isotomously and/or heterotomously.

Family SYNEROCRINIDAE Jaekel, 1918

Diagnosis. (After Moore 1978, p. T773.) Isotomous branching of arms on primibrachial 2, distinctly heterotomous branching thereafter.

Genus ONYCHOCRINUS Lyon and Casseday, 1860

Type species. *Onychocrinus exsculptus* Lyon and Casseday, 1860, p. 77, by monotypy (=*Oligocrinus* Springer, 1906, p. 519 (type *Forbesiocrinus asteriaeformis* Hall, 1861a, p. 320, by monotypy). *Origocrinus* Jaekel, 1918, p. 79 (*nom. null.*)).

Emended diagnosis. (Modified after Springer 1920, p. 417; Moore 1978, p. T775; Burdick and Strimple 1983, p. 203.) Low crown characterised by widely separated pentaradiate rays above perradial interbrachials, or round to elongate ovoid; infrabasals low, distal extremities often visible beyond stem; posterior basal elongate, hollowed distally for acceptance of anal X, anal tube follows, radianal sometimes present on distal face of *CD* basal; arms comprise three to six primibrachials, initial arm branch isotomously into two main trunks, further branching as heterotomous ramules on both sides of ten main arm trunks, ramules usually with two to several bifurcations produce characteristic arm structure; interbrachials variable, few to many in number; stem tapers away from calyx.

Stratigraphical range. Lower Carboniferous - Scotland, Germany, Ireland; Lower Mississippian (Osagean) - USA (Iowa, Illinois, Indiana, Kentucky), Canada; Upper Mississippian (Meramecian to Chesterian) - USA (Illinois, Indiana (Borden Group), Kentucky, Alabama, Oklahoma).

Onychocrinus polydactylus (M'Coy, 1844)

Plate 17, figs d, e; Figure 6.12

?1836 *Poteriocrinus egertoni* Phillips, p. 205, pl. iii, fig. 39.

?1841 *Isocrinus egertoni* (Phillips), p. 30.

?1843 *Cladocrinus egertoni* (Phillips), Austin and Austin, p. 197.

?1843 *Taxocrinus egertoni* (Phillips), Morris, p. 59.

1844 *Taxocrinus polydactylus* M'Coy, p. 178, pl. 26, fig. 7 (figured as *Cladocrinus*).

1920 *Onychocrinus ?polydactylus* (M'Coy), Springer, p. 421-439, pl. 64, figs 11-14.

1943 *Onychocrinus polydactylus* (M'Coy), Bassler and Moodey, p. 575.

1954 *Onychocrinus polydactylus* (M'Coy), Wright, p. 172, pl. 66, fig. 4.

1969 *Onychocrinus polydactylus* (M'Coy), Sevastopulo, p. 24, pl. 3, figs 1-7; pl. 4, figs 1-5.

Material. A single topotype, specimen number TCD.35955, a calyx, some arm portions and a small amount of stem. The specimen was collected at locality CP1:4, a very fossiliferous, grey, calcareous, muddy shale interbedded with bioclastic limestone ribs, the basal bed of the Benbulben Shale Formation (Holkerian), Carrickphatrick, western Co. Sligo, G4395 3513. No further specimens were collected for description.

Diagnosis. (After Springer 1920, p. 439; Wright, 1954, p. 172.) Crown very elongate; calyx narrow; infrabasals may be covered by column; basals fully visible, pentagonal in outline; anal region not known; primibrachials four, five or six; arms long, slowly tapering distally, bifurcate isotomously, heterotomous ramules branch on every two to five brachials only on inside of the dichotomy, all arms and ramules are stout; interbrachials few; proximal stem tapers rapidly distally, then gradually, thereafter heterotomous.

Description. The entire external surface has a sculpture of very fine tubercles. Sutures between all plates of the crown are crenulate, the articular facets having crenulae on their

outer parts at least.

The crown is low with the arms well separated. The most distal parts of two infrabasals are just seen, but the remaining parts and three other infrabasals are covered by the most proximal columnals of the stem. The parts that are seen resemble the most proximal columnals. A suture can be seen below and just to the left of the *BC* basal. Five basals are seen. They are very high with the two distal faces sloping down steeply to the nadirs of the radial plates. The *CD* basal is broken, but the distal end can be seen to be truncated for reception of the anal plates. They can all be seen in lateral view. Five radials are fully seen which are crescentic in outline. They are much wider than high (9.5:6) and just less than twice as high as the basals. The *E*, *A*, and *B* radials are heptagonal in outline, but the *C* and *D* radials have fewer sides because they are adjacent to the anal series. Longitudinally they are straight. The upper articular facets are slightly concave and plenary, but their sculpture cannot be seen. No plates of the anal series can be seen.

The proximal portions of five arms can be seen which, in three rays, are branching isotomously at least once. Primibrachials are up to five in number as seen in the *C* ray, which is the only ray where the brachials can be fully deciphered, the fifth one being axillary. They are the same width and are as almost as high as the radials (9.5:5.5). Secundibrachials after the first bifurcation are of the same size so branching here is isotomous. There are at least five secundibrachials in some rays. All brachials are externally well rounded and very robust.

Interbrachial plates are generally lacking except in the *AB* interray where one or ?two small plates can be seen. The most proximal one is resting on the distal shoulders of the *A* and *B* radials and as high as primibrachials *1*.

The most proximal four or five columnals of the stem are visible, but they are broken away for the most part. Their morphology cannot be seen except that they have the same lateral sculpture as the crown. They are very low and uneven.

Remarks. The current specimen was assigned to this species of the genus because of its possessing five primibrachials. Springer (1920), following M'Coy's description of the lectotype (as designated by Sevastopulo, 1969 (N.M.I. G35a: 1968)), agreed that there were a large number of primibrachials, probably at least six. Unfortunately, only one dichotomy is seen herein so the growth habit of the ramules cannot be seen further.

	A ray	*AB* interray	*B* ray	*BC* interray	*C* ray	*CD* interray	*D* ray	*DE* interray	*E ray*	*EA* interray	TOTAL
Infrabasal	1	-	0.5	-	0.5	-	x	-	x	-	2
Basal	-	1	-	1	-	1	-	1	-	1	5
Radial	1	-	1	-	1	-	1	-	1	-	5
Primibrachial	3	-	4	-	5	-	4	-	1	-	17
Secundibrachial	x	-	5,2	-	5,1	-	x	-	x	-	13
Interprimibrachial	-	2	-	x	-	x	-	x	-	x	2
TOTAL	5	3	12.5	1	12.5	1	5	1	2	1	44

Figure 6.12. Table displaying types and numbers of crown plates in specimen TCD.35955 of *Onychocrinus polydactylus* (McCoy, 1844).

According to Sevastopulo (1969), the specimen described by Wright (1934, p. 260, text-fig. 31, pl. 15, fig. 5.) as *Onychocrinus polydactylus* (M'Coy) is probably *O. hibernicus* Wright, 1934, due to its ray structure.

Springer mentioned, from M'Coy's original description, that the lectotype (as later assigned by Sevastopulo 1969) came from part of the Middle Limestone (Calp) at Ballintrillick, near Bundoran. This is representative of the Benbulben Shale Formation and is thus Holkerian in age. The paratype of Sevastopulo (1969 (N.M.I. G35b: 1968)) came from Carrowmably, Easky, but there is no grid reference. This is just to the west of the locality where the current specimen was found and is, in fact, probably referring to the same locality.

The specimen was cleaned by soaking it in water to soften the occluding mud, which was then removed with a needle and a scrub with a soft toothbrush. This process was carried out several times before enough matrix was removed and before the sculpture began to deteriorate.

Stratigraphical range. Lower Carboniferous (?Tournaisian-Holkerian) - Ireland (Arundian-Holkerian).

cf. *Onychocrinus polydactylus* (M'Coy, 1844)

Plate 17, fig. f

Material. Specimen TCD.35959, a specimen showing some of the stem and the basal circlet. The specimen was collected by Professors G. D. Sevastopulo and N. G. Lane in 1972 from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Remarks. The specimen shows about five of the most proximal columnals similar to the ones described in specimen TCD.35955. The infrabasals, however, are not seen. The form of the four basals (the *CD* basal is missing) again is similar to those described above. On the basal plates, it is seen that the sculpture is very finely tuberculate. The size of the specimen is also similar to specimen TCD.35955. All of the morphological features of this specimen are characteristic of *O. polydactylus* and it has been obtained from the type locality. However, owing to the fact that not more of the calyx or crown is available for

description the positioning here is made tentatively.

Stratigraphical range. Lower Carboniferous (Arundian) - Ireland (?Tournaisian).

6.3. DESCRIPTIONS OF DISARTICULATED CRINOID COLUMNALS AND PLURICOLUMNALS

A quick reference table outlining morphological features for the specimens used in the following section can be found in Appendix D.

Subclass CAMERATA Wachsmuth and Springer, 1885

Family PLATYCRINITIDAE Austin and Austin, 1842

Diagnosis. (After Ubaghs 1978*b*, p. T515; Burdick and Strimple 1983, p. 166.) Stem transversely circular proximally with symplectial articulation, but elliptical and twisted thereafter with synarthrial articulation, fulcral ridge coincides with long diagonal of columnals, axial canal small and circular.

gen. et sp. indet. PLATYCRINITIDAE-TYPE COLUMNAL 1

Plate 18, figs a, b

Material. Specimen TCD.35962, a single columnal, taken from a bulk sample from Bed BD:B28, interbedded thin, argillaceous limestones and dark grey, calcareous fissile shales, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8191 5959.

Description. Synarthrially articulating, evenly quadrangular columnal with fulcral ridges of opposing articular facets at exactly 90° to each other. The articular facets have an evenly rounded elliptical outline with somewhat blunt ends, and the facetal shape index is high at 83. A narrow, apparently smooth, peripheral rim can be deciphered on one facet. A straight, rounded fulcral ridge, which has greater relief than the peripheral rim, is coincident with the longest diagonal of the facet. At either end it may 'fan out', but this is unclear. The fulcral ridge separates two smooth, moderately depressed bifascial fields. The lumen cannot be seen.

The inclined latus is smooth and concave.

There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FDx*	*FDy*	*FD*	*2ERx*	*2ERy*	*2ER*	*KDx*	*KDy*	*KD*	*KH*	*Fi*	*Ei*	*KHi*	*FSi*	*KSi*	*Min. angle between two fulcral ridges*	*Extras*
TCD.35962	5.45	6.55	6.00	0.00	1.60	1.60	6.00	6.55	6.28	3.7	96	26	59	83	92	90°	Bin

Stratigraphical range. Arundian (Bundoran Shale Formation).

gen. et sp. indet. PLATYCRINITIDAE-TYPE COLUMNAL 2

Plate 19, figs a, b

Material. Specimen TCD.35963, a single columnal, taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Description. Unevenly quadrangular, synarthrially articulating columnal with fulcral ridges of opposing articular facets at 71° to each other. The outlines of the articular facets are a rounded diamond-shape. The facetal shape index is 70. An apparently smooth peripheral rim is easily deciphered. The fulcral ridge is straight, but apparently split into two parallel ridges each with a vermiculate summit. It has about the same relief as the peripheral rim. On one facet at one end of the fulcral ridge six crenulae appear on the peripheral rim, but it cannot be seen how far around the facet they are deposited. Two smooth, depressed bifascial fields are separated by the fulcral ridge. The lumen is very small, central and circular in outline.

The inclined latus is weakly convex. It has a sculpture of several tubercles, similar in form to the cirri, of which some have broken away. In particular, two are disposed adjacent to the articular rim.

There are high tubercles disposed around the circumference of the latus. They appear to be disposed in positions which would suggest octameral symmetry, one position being unoccupied. They are disposed at columnal mid-height.

Columnal morphometrics, measurements in mm.

Specimen number	*FDx*	*FDy*	*FD*	*CRx*	*CRy*	*2CR*	*ARx*	*ARy*	*2AR*	*LD*	*Fi*	*Ci*	*Ai*	*Li*
TCD.35963	5.30	7.50	6.40	0.50	0.45	0.95	1.95	3.0	5.0	0.50	92	15	78	8

ERx	*ERy*	*2ER*	*KDx*	*KDy*	*KD*	*KH*	*Ei*	*KHi*	*FSi*	*KSi*	*Min. angle between two fulcral ridges*	*Extras*
0.00	1.00	2.00	6.40	7.50	6.95	3.0	29	47	71	85	71°	Bin

Stratigraphical range. Holkerian (Benbulben Shale Formation).

Remarks. The specimen TCD.35963 holds morphological similarities, in its vermiculate sculpture on the summit of its fulcral ridge, to the Lower Jurassic isocrinid species *Balanocrinus quiaiosensis* Loriol as figured in Simms (1989*a*, p. 64, Fig. 2 *E* (late pentacrinoid larval stage columnal)).

The specimen was immersed in 30% by volume hydrogen peroxide until effervescing ceased and was then scrubbed with a toothbrush in a weak solution of household detergent.

Discussion. The genera *Platycrinites* and *Eucladocrinus* both have members with elliptical columnals and twisted stems, and are, for the most part, indistinguishable. The differences between the two genera described in Moore and Jeffords (1968) are as follows; 1) *Platycrinites* columnals are generally smaller than those of *Eucladocrinus*, and 2) *Platycrinites* may be cirriferous where *Eucladocrinus* usually is not. On these facts it is probable that specimen TCD.35963 belongs to *Platycrinites*. Specimen TCD.35962 is of a similar size and could be derived from a species of either genus.

Several species with characteristic lateral sculpture, such as *P. penicillus*, can be recognised by the short spines that radiate outwards as described in Burdick and Strimple (1973, Pl. 2, figs 6, 9 and 13). Neither of these specimens have any distinctly characteristic features, so it would therefore be unwise to assign them to either of these species.

Subclass CLADIDA Moore and Laudon, 1943

Infraclass FLEXIBILIA Zittel, 1895

Diagnosis. (Moore 1978, p. T765.) Stem generally transversely circular, columnals very low, non-cirriferous.

gen. et sp. indet. FLEXIBILIA-TYPE PLURICOLUMNAL

Plate 28, figs f-h

Material. A single specimen, TCD.35960, a pluricolumnal of about eighteen ossicles. The specimen was collected by Professors G. D. Sevastopulo and N. G. Lane in 1972 from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The columnals are circular, or very slightly elliptical, in outline with symplectial articulation. They are extremely low with about three or four per mm of pluricolumnal. The stem portion tapers at one end. At the widest end, the columnals are wider, but the widening does not occur gradually. It only occurs across one linear third end of the columnals. This causes the articular facet to be raised. This raised portion is uneven. The articular facet comprises a peripheral, circular crenularium that is wider in diameter on the narrow terminal columnal than the wide terminal columnal. There are about eighty crenulae on the wide columnal and about sixty on the narrow crenularium. They are tightly spaced and all simple. They are very low with well-rounded apices and troughs. The circular areola is very smooth and especially wide on the wider columnal occupying over 60% of the total columnal diameter. On the narrow columnal, it appears slightly inflated, but on the wider columnal it is planar. The circular perilumen is narrow on both facets. It appears to have a sculpture of small crenula-like ridges and grooves that may be vermiculate. The central lumen is probably circular in outline.

The latus is convex. In lateral view, the columnals have an uneven corrugated appearance because the sutures are so closely spaced longitudinally.

There are no cirrus-related structures.

Columnal morphometrics, measurements are approximate in mm.

Specimen TCD.35960	*FD*	*CR*	*AR*	*PR*	*LD*	*Ci*	*Ai*	*Pi*	*Li*	*No. crenulae*	*Extras*
widest columnal	7.5	0.5	2.3	0.5	0.9	13	61	13	12	about 80	Bin
narrowest columnal	5.5	1.0	1.2	0.3	0.5	36	44	11	9	about 60	Bin

Stratigraphical range. Lower Carboniferous (Arundian).

Remarks. The specimen shows the characteristic morphology of the most proximal part of

the stem in a number of flexible genera, that is that the low columnals taper rapidly just below the stem (Moore 1978, p. T760). To attempt identification of a genus would be almost impossible.

Subclass and lower Plesion UNCERTAIN

COLUMNAL PLESION A pln. nov.

Type species. Columnal Taxon Number 1a. gp. nov.

Other species. Columnal Taxon Number 1b. gp. nov.; Columnal Taxon Number 1c. gp. nov.; Columnal Taxon Number 1d. gp. nov.

Diagnosis. Circular or moniliform columnals of distinctly heteromorphic stem; latus straight to convex and may be angulated outwards in longitudinal profile, sometimes with sculpture of columns of tubercles; circular crenularium peripheral with twenty-six to forty-four regularly disposed simple crenulae, circular areola smooth and planar to slightly concave, perilumen with circular outline and following pentaradiate outline of lumen on inner boundary, raised and planar with unusual sculpture, peripheral portion having crenula-like ridges and grooves (which do not coincide with crenulae of crenularium as there may be more or less in number) which gradually change adaxially into a vermiculate sculpture, sculpture continues to extremity of lumen where it is adjacent to lobes, but the raised sculpture may gradually loose relief and definition in the area adjacent to lumen angles, lumen central with straight sides, pentasteroidal to pentalobate in outline, branches or lobes differ in size.

Stratigraphical range of plesion. Arundian (Bundoran Shale Formation) to Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 1a gp. nov.

Plate 20, figs a, b; Plate 21, figs a, b; Plate 22, figs a-c; Plate 27, figs a, b; Plate 28, figs a, b; Figure 6.14.*a*

Holotype. Specimen TCD.35964, a pluricolumnal of ten ossicles, of which one end is broken, and which has had a *Crania* sp. brachiopod attached and an encrusting coral. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks after they dropped out of interbedded calcareous, muddy shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.35965, a single columnal from the type locality. Paratypes TCD.35966, a pluricolumnal of three ossicles, TCD.35967, a single columnal, and TCD.35968, a pluricolumnal of two ossicles, all taken from Bed BD:J8, a silty shale, near the top of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8141 5875. Paratype TCD.35969, a pluricolumnal of six ossicles, one end of which is broken away, from Bed BD:J12, a slightly silty calcareous shale, near the top of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8141 5875. Specimens vary in their preservation, some revealing only certain parts of the articular facet.

Diagnosis. Columnal Plesion A morphospecies with moniliform columnals, stem with noditaxis of four to eight columnals with nodals higher than internodals, nodals, priminternodals and secundinternodals may be cirriferous; latus moderately convex; central lumen pentalobate in outline with pointed to rounded angles, lobes differ in size.

Description. The columnals are circular in outline and have symplectial articulation. The peripheral crenularium is very narrow and has thirty-five to forty-four somewhat raised, regularly disposed simple crenulae with rounded apices and troughs. The areola is smooth and planar, and of a similar width to that of the crenularium. The perilumen is raised with a crenula-like sculpture peripherally that gradually changes so that the innermost section has a vermiculate sculpture. On paratype TCD.35966 sculpture definition is lost in the area adjacent to the lumen angles. The central lumen is pentalobate in outline with pointed to rounded angles, and the lobes are of different sizes. It has straight sides.

The latus is moderately convex and smooth, except where cirrus sockets occur, and on the holotype a row of tiny tubercles occur on some columnals at mid-height between the cirrus-related structures. The crenulate suture is coarse and square.

The longest pluricolumnals give a noditaxis of 212N, in which all columnals are non-cirriferous (paratype TCD.35969), to 21212N (holotype). On the holotype the columnals orders are differentiated from each other by their heights because some nodals, priminternodals and even secundinternodals bear cirrus sockets at columnal mid-height. Measurements, in mm, of the height of all columnals of the holotype and paratype TCD.35969 pluricolumnals and their inferred noditaxial orders are inserted in the following tables:

Holotype TCD.35964

KH	1.9	2.6	2.0	2.5	2.1	3.0	2.0	2.5	2.1
Order	2	1*	2	1*	2	N*	2*	1*	2*

Paratype TCD.35969

KH	2.3	2.0	2.7	2.0	2.4
Order	1	2	N	2	1

The holotype has one to five cirrus sockets or abortive cirri occurring on higher columnal orders. Some are apparently randomly disposed, but some columnals have up to five cirrus-related structures whose positions are consistent with pentaradiate symmetry. However, they are not always at angles of 72° from each other. Cirri from adjoining columnals are generally not exactly in line longitudinally, but are irregularly pentastichous. Cirral articula are generally not seen, but when they are present most appear to have a central circular canal. On paratype TCD.35965, however, cirral articula can clearly be seen. There are two narrow cirri of apparently constant diameter comprising two or three cirrals, and an enlarged non-circular cirrus socket unusually giving rise to two cirri. The cirral articula have a crenularium that covers about 50% of the facet with about eight high and deep, coarse crenulae. The inner part of the facet appears to comprise only a large, circular lumen, but this is unclear.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*PR*	*APR*	*LD*	*Ci*	*Ai*	*Pi*	*APi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35965	4.0	0.35	?	?	1.05	1.2	18	?	?	53	30	2.1	53	31	Bin: ?N
TCD.35964	4.8	0.5	0.3	0.98	1.28	1.25	21	13	41	53	26	1.9	40	36	Bin: IN2
TCD.35966	5.33	0.40	0.51	0.97	1.48	1.56	15	19	37	56	29	1.46	27	35	SEM: IN
TCD.35966	5.75	0.5	0.5	1.04	1.54	1.68	17	17	36	53	29	1.7	30	35	Bin: IN
TCD.35969	6.11	0.53	?	?	1.67	1.71	17	?	?	55	28	2.33	39	38	Bin: IN1
TCD.35968	6.25	0.5	0.42	1.25	1.67	1.92	16	13	40	53	31	1.8	29	about 41	Bin: IN1/2
TCD.35967	6.3	0.5	0.6	?	?	?	16	19	?	?	?	2.35	37	35	Bin: ?

Stereom. Paratype TCD.35966 shows that the stereom is regularly galleried. Its pore

diameters increase towards the lumen, with the largest pores appearing in the perilumen. The remainder of the articular facet has smaller pore diameters.

Remarks. The offset of cirri from the pentaradiate 72° positions probably occurs because the cirri are coinciding with the lobes of the lumen which, as explained, are unequal in size and are therefore themselves not exactly at 72° from each other.

The larger pore sizes in the perilumen would suggest that these were the sites where thicker and therefore stronger intercolumnal ligaments or through-going ligaments were attached during life. The remainder of the articular facet with smaller pores presumably housed only short, narrow intercolumnal ligaments that penetrated and held together only adjacent columnals (see Grimmer *et al.* 1985).

Paratype TCD.35966 was immersed in 40-45% hydrofluoric acid for five minutes, which revealed the stereom. The holotype and paratypes TCD.35965, TCD.35967, TCD.35968 and TCD.35969 received no such treatment.

Stratigraphical range. Arundian (Bundoran Shale Formation) to Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 1b gp. nov.

Plate 23, figs a, b; Plate 27, figs c, d; Figure 6.14.*b*

Holotype. Specimen TCD.35970, a pluricolumnal of four ossicles, with one end broken away so that the articular facet cannot be seen. Taken from Bed BD:J8, a silty shale near the top of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8141 5875.

Diagnosis. Columnal Plesion A morphospecies with cylindrical columnals, stem with noditaxis of at least two orders, nodals, priminternodals and secundinternodals may be cirriferous; latus straight, sometimes slightly angulated equatorially; lumen central, pentalobate in outline with truncated angles, lobes differ in size.

Description. The columnals are circular in outline with symplectial articulation. The peripheral crenularium is very narrow with twenty-eight very high, simple crenulae with squared apices and troughs. The areola is smooth and planar, and is of a similar width to

that of the crenularium. The perilumen has a crenula-like sculpture peripherally which changes to a vermiculate sculpture only in the small area directly adjacent to the angles of the lumen. The central lumen is pentalobate in outline with uneven sized lobes, and the angles are truncated. It has straight sides.

The latus is straight on most columnals, but cirriferous columnals may be symmetrically slightly angulated at columnal mid-height which can be seen in longitudinal profile. The crenulate suture is coarse and squared to slightly rounded.

Even from the longest pluricolumnal (the holotype), the noditaxis is unclear with three of the four columnals being cirriferous, but it is inferred that the highest cirriferous columnal is a nodal. The nodal has five small cirrus sockets or abortive cirri disposed in positions that are consistent with an uneven, but nevertheless, pentaradiate symmetry. On cirriferous internodals there are two or more cirrus-related projections, which are apparently disposed randomly. All projections, including cirrus sockets, are positioned at columnal mid-height.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*PR*	*APR*	*LD*	*Ci*	*Ai*	*Pi*	*APi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35970	4.50	0.50	0.45	0.53	0.98	1.54	22	20	24	44	34	1.95	43	28	Bin: ?

Remarks. The holotype was immersed in 40-45% hydrofluoric acid for five minutes and has suffered no cracking or breakages since.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 1c gp. nov.

Plate 24, figs a, b; Plate 27, figs e, f; Figure 6.14.*c*

Holotype. Specimen TCD.35971, a pluricolumnal of four ossicles with one end broken so that the articular facet is not seen at all. From Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Columnal Plesion A morphospecies, circular columnals of heteromorphic stem, noditaxis of at least two orders, nodals are cirriferous; latus angulated equatorially; lumen

central and pentasteroidal in outline with rounded angles, branches differ in size.

Description. The columnals are circular in outline with symplectial articulation. The crenularium is peripheral with twenty-eight high and deep, rounded, simple crenulae. The areola is smooth, planar and depressed, and it is wider than the crenularium. The perilumen has a crenula-like sculpture on its periphery changing into a vermiculate sculpture in the areas directly adjacent to the angles of the lumen. The lumen is central, pentasteroidal in outline with rounded angles, has uneven branches and has straight sides.

The entire latus is drawn into a symmetrical ridge at columnal mid-height which makes the columnals slightly angulated in longitudinal profile. There is no sculpture. The crenulate suture is not seen on the holotype.

The noditaxis is at least 212N with only the nodal being cirriferous. On the nodal of the holotype three small cirrus sockets or abortive cirri are disposed in positions, which are apparently consistent with an uneven pentaradiate symmetry. They are placed at columnal mid-height.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*PR*	*APR*	*LD*	*Ci*	*Ai*	*Pi*	*APi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35971	4.30	0.51	0.32	0.73	1.05	1.19	24	15	34	49	28	1.91	44	28	Bin: IN

Remarks. Because the heights of columnals in the holotype are similar, it is not easy to tell their orders apart unless they are cirrus-bearing.

The holotype was immersed in 20% by volume hydrogen peroxide until the liquid ceased effervescing. This removed a superficial, loose matrix.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 1d gp. nov.

Plate 25, figs a, b; Plate 26

Holotype. Specimen TCD.35972, a pluricolumnal of seven ossicles, of which the articular facet cannot be seen fully at either end, and which has a *Spirorbis ?pusillus* (Martin) worm attached to it. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks after they dropped out of interbedded calcareous, muddy shales and limestones of the Benbulben Shale Formation

(Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.35973, a pluricolumnal of two ossicles, paratype TCD.35974, a single columnal and paratype TCD.35975, a pluricolumnal of two ossicles, which is weathered quite badly, all are taken from the type locality

Diagnosis. Columnal Plesion A morphospecies with cylindrical to moniliform columnals, stem with noditaxis of four columnals with nodals higher than internodals, nodals may be cirriferous; latus with low, wide tubercles in columns with 50% offset at columnal mid-height; central lumen pentalobate in outline with rounded angles, lobes differ in size.

Description. The columnals are circular in outline and have symplectial articulation. The crenularium is very narrow and peripheral with twenty-six to about thirty-six moderately raised, simple, regularly disposed crenulae which have rounded apices and troughs. The culmina diminish height rapidly on both their inner and outer margins, but less so on the inner margin. Their sides are straight so that they are parallel. The areola is smooth and planar to slightly concave. It is of a similar width to that of the crenularium. The perilumen is raised to reach the level of articulation. It has a peripheral crenula-like sculpture that gradually changes to a vermiculate sculpture on the innermost section. The crenula-like ridges of the perilumen are often aligned with the culmina of the crenularium, but there are fewer in number so there may be one crenula-like ridge to two culmina. The central lumen is pentalobate in outline with rounded angles and lobes. The lobes on the holotype are slightly flattened so each appears as a mushroom-shape. They are of different sizes. The lumen has straight sides.

The latus is straight to weakly convex and with a distinct tuberculate sculpture. Low, but wide, tubercles occur in longitudinally orientated columns all around the circumference. The tubercle columns are aligned with culmina of the crenularium and are disposed in two columns, of two to four tubercles depending on the height of the columnal, which are offset by 50% at columnal mid-height. An uneven ridge may be created at columnal mid-height by the two columns of tubercles where they meet. The crenulate suture is coarse and squared, almost turret-like in some places.

The holotype pluricolumnal gives a noditaxis of 212N, the columnals orders being differentiated from each other by their heights. Measurements, in mm, of all columnals of

the holotype pluricolumnal and their inferred noditaxial orders are inserted in the following table:

Holotype TCD.35972

KH	1.8	2.3	2.0	3.0	2.0	2.3	1.9
Order	2	1	2	N	2	1	2

All columnals of the holotype are non-cirriferous. However, the highest columnal of paratype TCD.35975 bears three cirrus-related structures at columnal mid-height. The morphologies of the facets are unclear, but it can be seen that on the widest structure that there is a central, circular, very small lumen. Their positions are not consistent with a pentaradiate symmetry as none of the structures are aligned with the centre of the lobes or angles of the lumen on the articular facet.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*PR*	*APR*	*LD*	*Ci*	*Ai*	*Pi*	*APi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35975	3.7	0.3	0.4	0.66	1.06	0.98	16	22	36	57	26	2.1	59	26	Bin: ?N
TCD.35974	4.55	0.5	0.4	0.83	1.23	1.1	22	18	36	54	24	2.0	44	30	Bin: ?IN
TCD.35972	5.0	0.4	?	?	1.42	1.36	16	?	?	57	27	1.8	36	about 36	Bin: IN2
TCD.35973	5.1	0.5	0.54	0.9	1.44	1.22	20	21	35	56	24	2.2	43	33	Bin: ?IN1

Remarks. All the specimens were scrubbed with a toothbrush using a weak solution of household detergent. They were then immersed in 30% by volume hydrogen peroxide solution.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

Discussion. The vermiculate and crenula-like sculpture on the perilumen is present on opposing facets of all columnals (Figure 6.14.*a-c*). It is probable that ridges of the sculpture of one facet fitted into the troughs of an apposing facet, and vice versa.

Various morphological similarities and differences can be seen in these columnals. Similarities are that they all have a narrow peripheral crenularium, a smooth, planar areola, distinctive perilumen sculpture and a pentagonal symmetry to their lumen. The differences are in their lumen outline (variations from stellate to lobate and the shape of the angles), and latus outline and sculpture. From these data it may be inferred that: 1) all four columnal types belong to the same species or genus, each originating from a) different parts (proximal, medial or distal) of the same xenomorphic stem, or b) different

orders of a heteromorphic stem and, thus, be conspecific: or 2) the columnals belong to different or unrelated real crinoid species (or higher taxonomic group). The latter inference is more probable as Columnal Taxon Number 1a columnals are found in a wider stratigraphical range (Arundian to Holkerian). However, the sample size is too small to assertain this with any certainty. The described differences in morphologies are the reasons for four different variations being categorised as separate taxa that belong to one columnal plesion. Variations in the radii of the different facetal features within the plesion are likely to be ontogenetic (see Section 5.3.1).

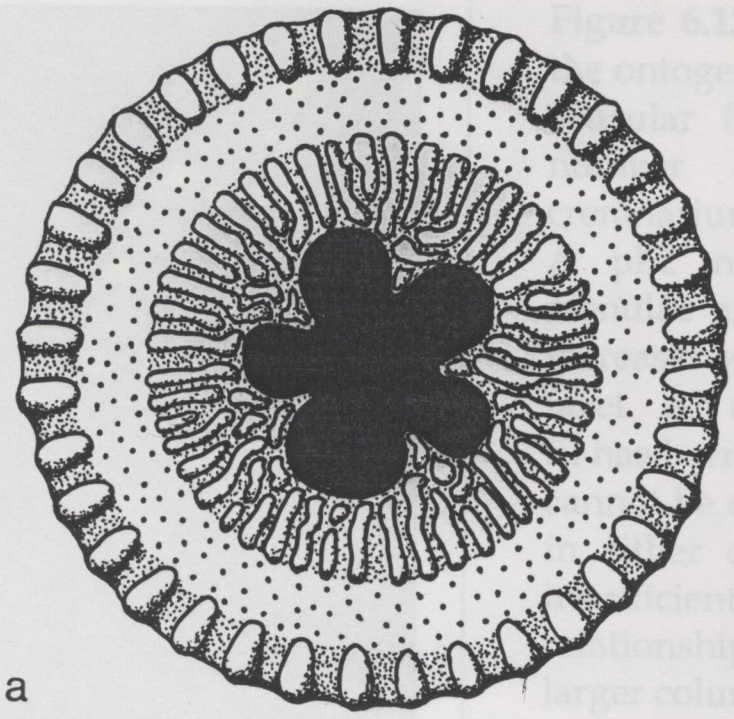
One of the most noticeable features of the lumen is the uneven sizes of the five lobes. Similar features are seen in Columnal Taxon Numbers 37a, 37b, 38 and 39 herein, as well as in some morphospecies of Moore and Jeffords (1968), e.g., *Cyclocharax fasciatus* (Pl. 23, fig. 7*b*), *Floricyclus granulosus* (Pl. 24, figs. 1, 2 and 3*a*) and *Cyclocion distinctus* (Pl. 24, figs. 15*a* and 16*a*; Pl. 25, figs. 1*a*, 2*a*, 3*a*, 4*a* and 5*a*). It may be that certain lobes carried specific extensions of the coelom or were aligned with certain features of the crown such as the anus or mouth.

Similar articular facets are seen on the columnals of the morphospecies *Fluctícharax undatus* Moore and Jeffords, 1968 (Osagian (Lower Mississippian), Kentucky) (Moore and Jeffords 1968, Plate 20, fig. 7*a*). Some of the columnals also have slightly outwardly angulated latera. The articular facets of columnals belonging to *Shroshaecrinus obliquistriatus* Simms, 1989 (Sinemurian (Lower Jurassic)) (Simms 1989*b*, Plate 14, fig. 19) also have similar sculpture to those in Columnal Plesion A herein.

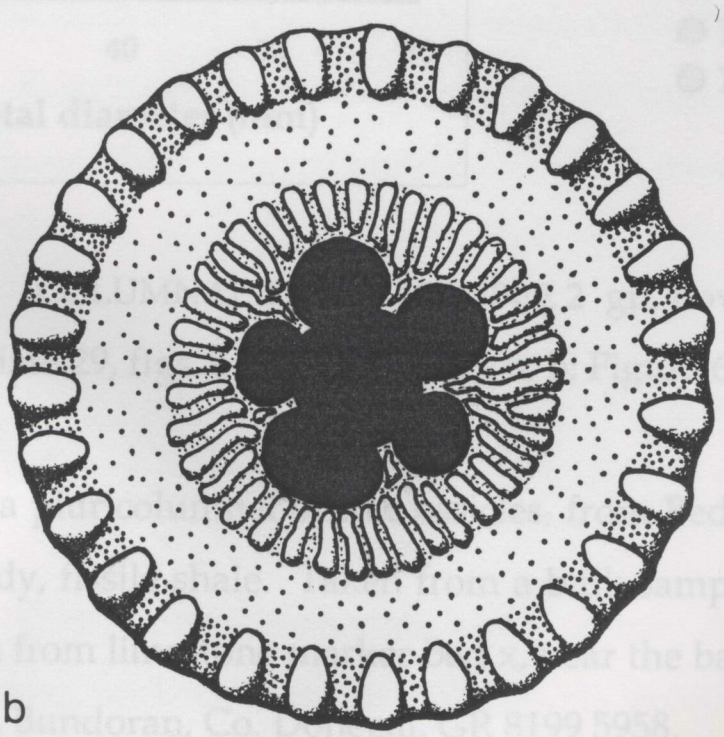
The number of crenulae on the crenularium in all members of Columnal Plesion A increases with the diameter of the articular facet (Figure 6.13). This is inferred to be ontogenetic.

Although often found in elliptical form (especially those collected from Bundoran), it is inferred that all columnals of the plesion were originally circular in outline, their present shape being a result of their being deformed by burial during diagenesis. The lumen shape, and relatively large size, rendered the columnals susceptible to deformation. Indeed, specimens with circular outlines (*i.e.* not deformed) are the ones that are most commonly found, especially those that were collected from Locality BB and this may be owing to some process occurring during diagenesis. Restoration to inferred original circular outline was achieved by using tools in Adobe Photoshop™ on an Apple Macintosh® computer to manipulate images (Plate 14, figs a-f), which were captured digitally from the scanning electron microscope (see Sections 3.3.3 and 3.4.2).

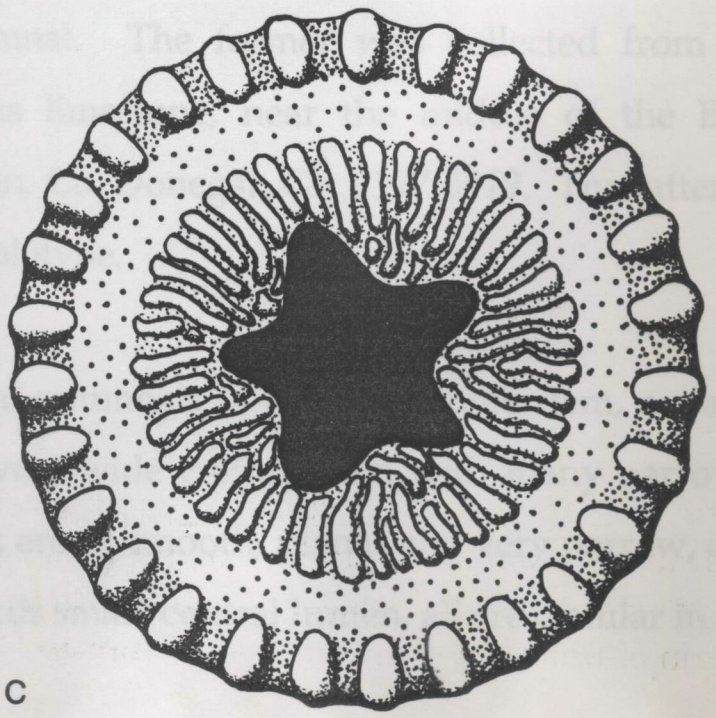
Figure 6.14. *a-c.* Idealised diagrams of articular facet architecture for members of Columnal Plesion A, Columnal Taxon Numbers 1a, 1b and 1c. Note subtle differences in lumen outline, number of crenulae and relative radii of facetal features. Average diameter of Columnal Taxon Number 1a = 5 mm, 1b = 4.5 mm and 1c = 4.3 mm.



a



b



c

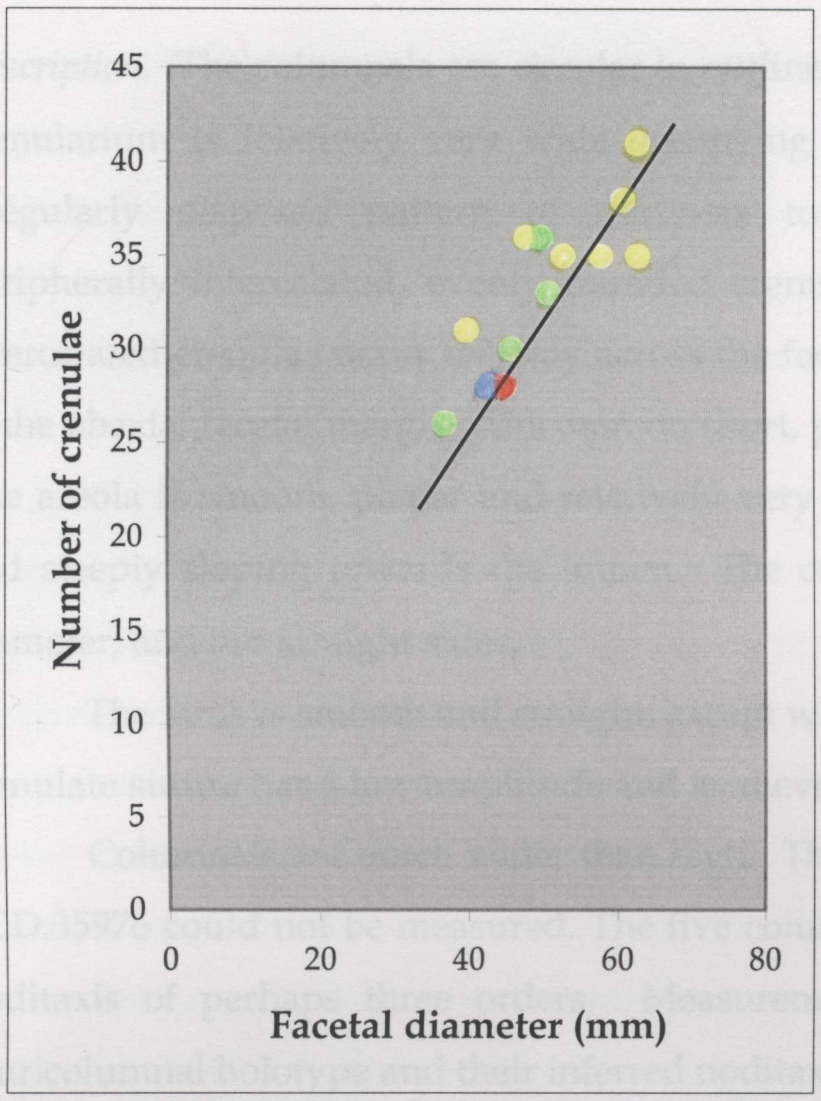


Figure 6.13. Scatter plot showing the ontogenic relationship between articular facet diameter and the number of crenulae of the crenularium in Columnal Plesion A pln. nov. The number of crenulae around the crenularium. increases with the diameter of the facet. An approximate line of best fit has been drawn on the graph. It cannot be extrapolated confidently in either direction since there is insufficient data to show what the relationship would be in smaller or larger columnals.

Key
- 1a
- 1b
- 1c
- 1d

COLUMNAL TAXON NUMBER 2 gp. nov.

Plate 29, figs a, b; Plate 30, figs a, b; Figure 6.15.*a*

Holotype. TCD.35978, a pluricolumnal of five ossicles, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Material. Paratypes TCD.35976, a pluricolumnal of ten ossicles, and TCD.35977, a single non-cirriferous columnal. The former was collected from the top of Bed BD:L1, a bioclastic argillaceous limestone, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8197 5919. The latter was collected in the same bulk sample as the holotype.

Diagnosis. Cylindrical columnals of heteromorphic stem, nodals higher than internodals; articular facet with very wide crenularium with many narrow, simple, bifurcating and intercalated crenulae, areola smooth, planar and very narrow, claustrum very narrow and sloping steeply towards small, central lumen, all are circular in outline.

Description. The columnals are circular in outline and have symplectial articulation. The crenularium is relatively very wide occupying 75% of the articular facet. It has an irregularly disposed pattern of thirty-six to forty-three simple, bifurcating and peripherally intercalated, evenly rounded crenulae. Bifurcations and terminations of intercalated crenulae occur halfway across the facet to give sixty to eighty-three crenulae at the abaxial facetal margin. Uncommon short, peripheral crenulae are also intercalated. The areola is smooth, planar and relatively very narrow. The claustrum is very narrow and steeply sloping towards the lumen. The central, circular lumen has a very small diameter, and has straight sides.

The latus is smooth and straight, except where cirrus-related structures occur. The crenulate suture has a low amplitude and is uneven.

Columnals are much wider than high. The ten component columnals of paratype TCD.35976 could not be measured. The five columnals of the holotype TCD.35978 give a noditaxis of perhaps three orders. Measurements, in mm, of all columnals of the pluricolumnal holotype and their inferred noditaxial orders (two possibilities) are inserted in the following table:

Holotype TCD.35978

KH	2.0	1.7	2.2	1.7	2.0
Order	1	2	N	2	1
Order	2	3	1	3	2

?Nodals are higher than ?priminternodals, and some are cirriferous (paratype TCD.35976). Large cirrus sockets occur at four points around a circumference, their positions being consistent with a pentaradiate symmetry. However, there is only one scar per columnal, and all are disposed at columnal mid-height. Nodicirral articula are circular in outline and overall concave. Simple crenulae occupy the crenularium, which covers at least 66% of the facet. The central part is obscured in all facets. They are disposed at columnal mid-height and are impressed onto the two adjacent ?priminternodals.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.35976	6.93	2.58	0.26	1.25	75	8	18	1.42	21	36	60	Bin: N
?TCD.35977	6.89	2.62	0.33	0.99	76	10	14	0.95	14	about 38	about 80	SEM: N
TCD.35977	7.43	2.80	0.29	1.25	75	8	17	0.8	11	40	76	Bin: IN
TCD.35978	7.85	2.97	0.41	1.08	76	10	14	2.17	28	43	83	Bin: N

Remarks. Pluricolumnals with the types of cirrus sockets described are likely to have originated from the distal end of a stem and may have been radicular acting as a root-like holdfast (Moore *et al.* 1968). However, if this were the case it would be expected that the cirri would be relatively larger and increasing their size distally. Even though it is not known which end is more distal, there still is not obvious increase in diameter. Non-cirriferous portions probably originated from more proximal stem sections.

Throughout ontogeny (the narrower columnals presumably were derived from younger individuals) the crenularium ratio increases only slightly, so that relatively it always covers about the same amount of the articular facet. However, the lumen ratios decrease and the areola ratios increase. The number of originating crenulae increases throughout ontogeny, rather than the crenulae widening, to fill the space created as the overall surface area of the crenularium grows. The number of bifurcations and peripheral intercalations increases at a greater rate also to accommodate growth.

Similar columnal articular facets with wide crenularia, small lumina and planar latera are seen in *Cyclocaudex plenus* Moore and Jeffords, 1968 ((Virgilian (Upper Pennsylvanian), Texas (Moore and Jeffords 1968, Plate 18, figs 1-5).

All the specimens were immersed in 40-45% hydrofluoric acid for five minutes, the stereom being revealed in paratype TCD.35977.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 3 gp. nov.

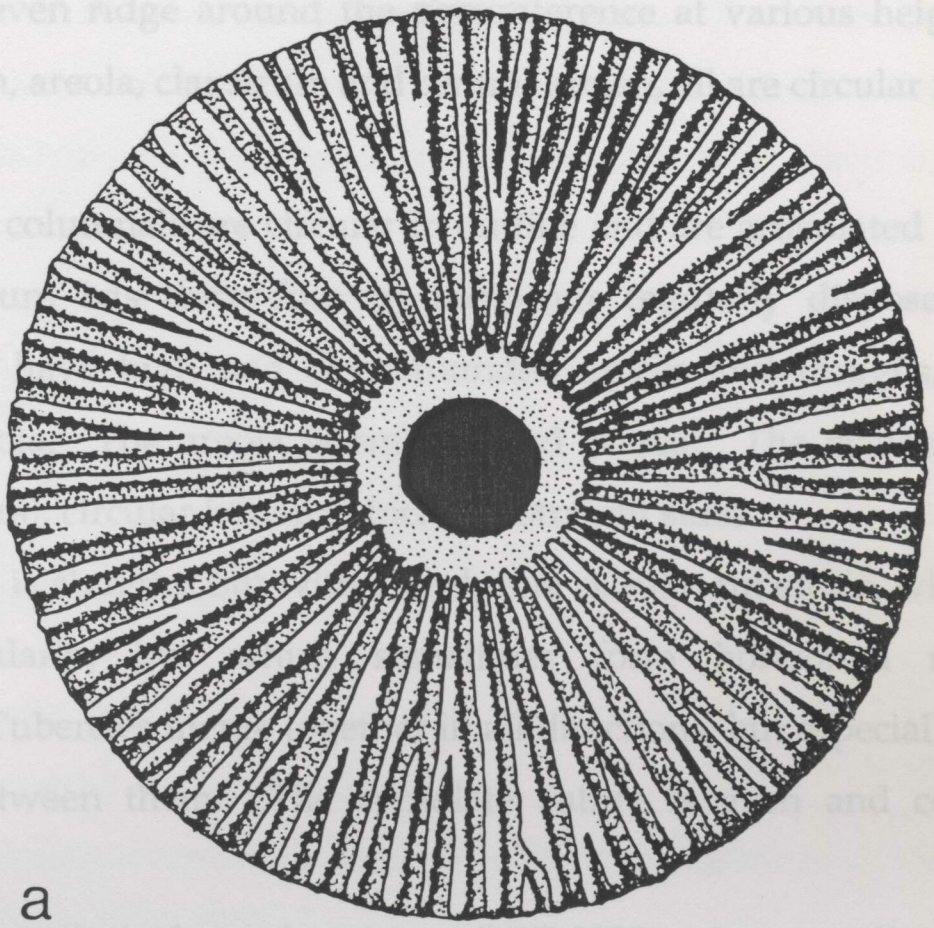
Plate 31, figs a, b; Figure 6.15.*b*

Holotype. Specimen TCD.35980, a single columnal, collected from the top of Bed BD:L1, a bioclastic argillaceous limestone, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8197 5919.

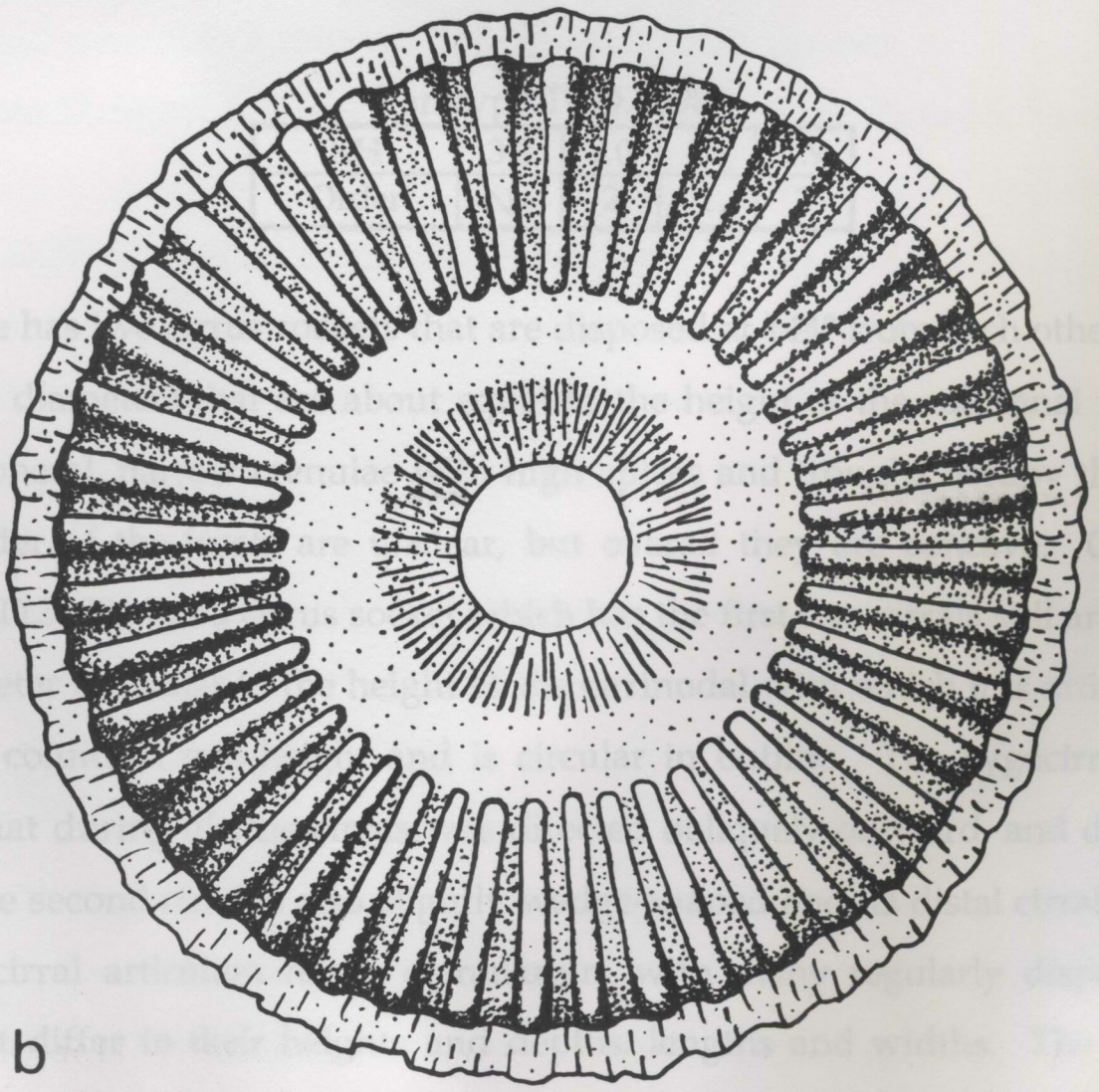
Material. Paratypes TCD.35979, a single columnal, TCD.35981, a pluricolumnal of four ossicles. Both are from the type locality.

Diagnosis. Cylindrical columnals of heteromorphic stem, nodals higher than internodals and may be cirriferous; latus with distinctive high tubercles, adjacent tubercles often

Figure 6.15. *a* and *b*. Idealised diagrams of articular facet architecture for Columnal Taxon Numbers 2 (fig. *a*) and 3 (fig. *b*). Average diameter of Columnal Taxon Number 2 = 7.0 mm and Columnal Taxon Number 3 = 4.0 mm.



a



b

merging forming small ridges between them, especially horizontally creating an intermittent, uneven ridge around the circumference at various heights; articular facet with crenularium, areola, claustrum and central lumen, all are circular in outline.

Description. The columnals are circular in outline and are articulated symplectially. The planar crenularium has thirty-four to forty-four regularly disposed simple, straight crenulae. They have high and deep rounded apices and troughs, and slope gently towards the areola. The areola is smooth and planar. The claustrum slopes steeply towards the central, circular lumen, which has straight sides.

The latus is straight, but with a sculpture of high tubercles, which are apparently disposed irregularly, but which sometimes form horizontal rows around the circumference. Tubercles merge together in all directions, but especially laterally, to form small ridges between them. The crenulate suture is even and coarse with a high amplitude.

The longest pluricolumnal, paratype TCD.35981, gives a noditaxis of at least 212N, with nodals being higher than internodals. Measurements, in mm, of all columnals of the paratype TCD.35981 pluricolumnal and their inferred noditaxial orders are inserted in the following table:

Paratype TCD.35981

KH	3.0	2.0	2.3	1.9
Order	N*	2	1	2

The holotype has two cirrus sockets that are disposed at 144° from each other. They both have similar diameters that are about equal to the height of the columnal itself. About twenty peripheral, narrow crenulae with high apices and troughs occupy the crenularia. The remainder of the facets are unclear, but overall they are concave. One nodal of paratype TCD.35981 has a cirrus socket which has the first two cirrals still articulated and whose diameter is similar to the height of the cirrinodal with which it is articulated. It is disposed at columnal mid-height and is circular in outline. The zygocirral is wedge-shaped so that during life the cirrus was directed obliquely outward, and downward or upward. The second cirral is also slightly wedge-shaped and its distal cirral articulum is seen. The cirral articulum has a crenularium with many regularly disposed, simple crenulae that differ in their heights and depths, lengths and widths. The crenularium covers relatively less of the cirrus facet in comparison to the columnal crenularium and its

articular facet. The remainder of the cirral articulum is overall concave, and the only other feature clearly seen is a smooth, circular areola. The remaining central portion of the cirral articulum is obscured by rock matrix or is broken away. The suture is crenulate and fairly regular between the zygocirral and the nodicirral articulum, and between the zygocirral and the second cirral.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35980	2.87	0.42	0.47	0.29	0.52	29	33	20	18	1.47	51	34	SEM: IN
TCD.35980	2.99	0.47	0.43	0.32	0.56	31	29	21	19	1.68	56	34	Bin: IN
TCD.35979	3.00	0.65	0.25	0.25	0.70	43	17	17	23	1.40	47	32	Bin: N
TCD.35981	5.00	1.00	0.65	0.35	1.00	40	26	14	20	3.0	60	about 41	Bin: N

Remarks. Unusually, the cirral articulum on paratype TCD.35981 has a large number of crenulae whose lengths and widths differ also.

Two specimens were immersed in 40-45% hydrofluoric acid, the holotype for three minutes and paratype TCD.35979 for six minutes.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 4 gp. nov.

Plate 32, figs a, b; Plate 33, figs a, b; Plate 34, figs a-c; Plate 35, figs a, b

Holotype. TCD.35982, a pluricolumnal of four ossicles, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Moniliform columnals of heteromorphic stem, nodals cirriferous and higher than internodals; articular facet with circular crenularium, areola and claustrum, and central lumen.

Description. The columnals are circular in outline. Articulation is symplectial. The crenularium of the articular facet has an irregular pattern of simple (forty-six crenulae in the most adaxial portion), bifurcating and small, peripherally intercalated crenulae (to give eighty-six touching the latus) that are high and deep and have rounded apices. The

areola is smooth and planar. The claustrum is in two sections, both of which are sloping towards lumen with the inner section sloping more steeply than the outer section. The lumen is central and apparently circular in outline with straight sides.

The latus is smooth and slightly convex, except where cirrus sockets occur. The crenulate suture is fine and uneven.

The holotype pluricolumnal gives an unclear noditaxis pattern with irregularly intercalated ?tertinternodals. Nodals are cirriferous and higher than internodals. Measurements, in mm, of all columnals of the holotype pluricolumnal and their inferred noditaxial orders are inserted in the following table:

Holotype TCD.35982

KH	2.1	1.8	2.0	1.7	2.5	1.7	1.5
Order	1*	2	1*	2	N*	2	3

Nodals bear from one to at least two cirrus sockets. Cirrus sockets occur at four points around a circumference, which are consistent with pentaradiate symmetry. Cirrus sockets are raised away from the surface of the latus and are positioned at columnal mid-height. They are circular in outline. The crenularium of the nodicirral articulum has simple, bifurcating and small, peripherally intercalated, high and deep, squared crenulae, which have an abrupt termination on their inner margin with the areola. The areola is much inflated with a rounded summit, and the lumen is small and circular. One cirriferous columnal has the zygocirral attached. The crenularium of the distal zygocirral articulum again has simple, bifurcating and small peripherally intercalated culmina, but these are longer than the crenulae of the nodicirral articula and graduate onto a planar, smooth areola. The central lumen is small and circular. The cirral narrows in diameter distally. The latus is smooth.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.35982	6.15	1.19	0.82	0.28	1.59	39	27	9	26	2.33	38	46	86	SEM: N

Stereom. The stereom is galleried. The meshwork becomes denser halfway across crenularium (Plate 33, fig. b).

Remarks. The holotype was immersed in 40-45% hydrofluoric acid for nine minutes and

the stereom was revealed.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 5 gp. nov.

Plate 36, figs a, b; Plate 37, figs a, b; Plate 38, figs a, b; Plate 39, figs a, b

Holotype. TCD.35983, a pluricolumnal of eight ossicles, from Bed BD:J8, a silty shale, near the top of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8141 5875.

Material. Paratype TCD.35984 from the type locality is a pluricolumnal of six ossicles of which the terminal columnals at both ends are broken so that the articular facet cannot be seen at all on one of the ossicles and is half visible on the other. Paratype TCD.35985, a pluricolumnal of four ossicles, collected from the top of Bed BD:L1, a bioclastic argillaceous limestone, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8197 5919.

Diagnosis. Basaltiform with rounded corners to subrounded columnals, stem heteromorphic, nodals higher than internodals and commonly cirriferous; latus with distinctive high tubercles, adjacent tubercles uncommonly merging laterally to form small, uneven ridges; pentagonal crenularium coincident with outline of columnal and with simple crenulae extending normally from long sides, areola pentagonal, central, ?circular lumen.

Description. The symplectially articulating columnals of the holotype and paratype TCD.35984 are pentagonal in outline with rounded corners. Paratype TCD.35985 has columnals that are slightly more rounded, but nevertheless still pentagonal in outline. In all specimens, the crenularium of the articular facet is pentagonal with the corners coinciding with those of column. Crenulae extend further inwards onto the areola towards the centre of each long side. Seven to ten simple culmina extend normally from the long sides to the edge of the areola. The corner of the facet is occupied by either one small, peripheral culmen, or a 'V' is formed by two culmina from adjacent long sides, with

a peripheral crenella disposed in the extremity of the corner. On the opposing facet crenellae occupy the positions of the culmina, and vice versa. The areola is pentagonal in outline with slightly concave long sides, and again coinciding with the pentagonal outline of the columnal. It is smooth and planar. The lumen is central and ?circular in outline.

The latus is straight, but with a sculpture of high tubercles, some of which merge with adjacent tubercles to form small ridges between them that are randomly orientated. However, on paratype TCD.35984 the tubercles are slightly more spinose and do not merge at all. The crenulate suture is coarse and evenly rounded.

The largest pluricolumnal (the holotype) gives a noditaxis of 3231323N, and paratypes TCD.35984 and TCD.35985 give at least 212N. Measurements, in mm, of all columnals of the holotype and paratype pluricolumnals and their inferred noditaxial orders are inserted in the following tables:

Holotype TCD.35983

KH	1.6	0.9	1.2	0.8	1.3	0.8	1.2	0.8
Order	N*	3	2	3	1	3	2	3

Paratype TCD.35984

KH	1.2	1.0	1.7	1.0	1.3	1.0
Order	1	2	N*	2	1	2

Paratype TCD.35985

KH	1.4	1.0	1.3	1.0
Order	1	2	1	2

The nodals, which are higher than internodals, bear one cirrus socket and may also bear one narrow abortive cirrus. Both are close to columnal mid-height, so that the extremities of the nodicirral articula are touching the suture on one side. They are both disposed half-way along long sides on the latus so that their positions are consistent with a pentaradiate symmetry. On the holotype a nodicirral articulum is observed. It is circular in outline and has a crenularium which slopes towards the areola and which has sixteen regularly disposed crenulae. The areola is smooth and planar. The lumen constitutes two small pores that overlap each other slightly giving a dilobate outline. It has its long axis orientated longitudinally relative to the pluricolumnals long axis. Both of the pores are eccentrically disposed relative to the outline of the nodicirral articulum. However, one of the pores is at columnal mid-height. Internodals are apparently non-cirriferous.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35983	3.65	0.50	0.87	0.90	27	48	25	1.53	42	8 per long side	SEM: N
TCD.35983	3.76	0.57	0.78	1.06	30	42	28	1.60	43	8 per long side	Bin: N
TCD.35984	4.2	0.60	?	?	29	?	?	1.2	29	8 per long side	Bin: IN1
TCD.35985	4.9	0.88	?	?	36	?	?	1.4	29	10 per long side	Bin: IN

Remarks. Latera of Columnal Taxon Number 5 have a sculpture, which is similar to that of Columnal Taxon Number 3. When looking at Columnal Taxon Number 5 in facetal view it appears there is an epifacet surrounding the facet. However, this is only a ridge formed by the tuberculate sculpture, which is seen in profile. Considering this similarity, it could be inferred that the crinoids from which they originated were closely related. Indeed, if xenomorphy is to be considered, these two columnal types could even have been conspecific, each type originating from different portions of the same crinoid stem. However, since the columnal outlines and the facetal morphologies of the two morphotypes are so different they are unlikely to be even congeneric.

Some similar tuberculate sculpture has been reported for some Lower Jurassic crinoids, for example, *Isocrinus tuberculatus* (Miller, 1821) (see Simms 1989*b*, Plate 7, figs 17, 20).

Moore *et al*. (1968, p. 11) mentioned that the pores of cirrals may be transversely dumbbell-shaped (=dilobate herein) or that the pores may even separate to form two circular pores. The nodicirral articulum on the holotype has a dilobate pore which, it is inferred, would have had such cirrals attached to it.

Paratype TCD.35984 was immersed in 40-45% hydrofluoric acid for five minutes and paratype TCD.35985 for four minutes.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 6 gp. nov.

Plate 40, fig. a

Holotype. TCD.35986, a pluricolumnal of ?four ossicles, from Bed BD:E5, interbedded calcareous, muddy shale and encrinitic packstone, near the base of the Bundoran Shale Formation (Arundian) at Bundoran, Co. Donegal, GR 8181 5963.

Diagnosis. Moniliform columnals of apparently homeomorphic stem; crenulate suture very squared resembling turrets; articular facet with narrow crenularium, steeply sloping claustrum and central lumen, all are circular in outline.

Description. The columnals are circular in outline. Articulation is symplectial. The crenularium is narrow and terminates abruptly. The forty-eight simple crenulae are equal in size, regularly disposed and have squared apices and troughs. The claustrum is smooth and slopes very steeply towards the central, circular lumen.

The latus is smooth and slightly convex. The crenulate suture cannot be seen.

There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*CLR*	*LD*	*Ci*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35986	3.86	0.61	0.74	1.16	32	38	30	1.36	35	48	Bin
TCD.35986	3.88	0.58	0.75	1.22	30	39	31	?	?	48	SEM

Remarks. See Columnal Taxon Number 7.

The holotype was immersed in 40-45% hydrofluoric acid for three minutes.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 7 gp. nov.

Plate 40, fig. b

Holotype. A single columnal, specimen TCD.35987, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Moniliform columnals; articular facet with crenularium, convex claustrum, and central lumen, all are circular in outline.

Description. The columnal is circular in outline and has symplectial articulation. The crenularium has forty-five straight and rounded crenulae, which are usually simple, but

there are also a few short ones that are intercalated peripherally, and some that bifurcate once to produce a total of forty-six crenulae peripherally. Some are wider than others. The claustrum has a gentle slope peripherally then curves down to slope steeply towards the central, circular lumen. Overall, it is convex.

The latus is smooth and slightly convex. There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*CLR*	*LD*	*Ci*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching claustrum*	*No. crenulae touching latus*	*Extras*
TCD.35987	3.86	0.56	1.02	0.7	29	53	18	1.86	48	45	46	SEM: IN

Remarks. Observed on the crenularium of the holotype is a depression that can also be seen in lateral view. This suggests that when the columnal was articulated the adjacent columnal was cirriferous and the cirral articulum was wide so that it impressed onto this columnal.

This morphospecies differs from Columnal Taxon Number 6 in the slope of the claustrum where Columnal Taxon Number 6 has an abrupt straight descent to the lumen and Taxon number 7 has a claustrum that is initially convex and then slopes steeply.

The holotype was immersed in 40-45% hydrofluoric acid for three minutes revealing the stereom. It has since cracked into two pieces, but has been glued back together using acetone-diluted Paraloid 72 glue crystals.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 8 gp. nov.

Plate 41, figs a-c

Holotype. Specimen number TCD.35988, a pluricolumnal of five ossicles, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Moniliform columnals of distinctly heteromorphic stem, noditaxis of at least three orders, higher orders being higher and wider; distinct lateral sculpture with low

tubercles being regularly disposed, one fitting in each 'groove' of regular crenulate suture, one tubercle directly above it which joins by an oblique ridge to tubercle above which is offset by 50%, this lays below a tubercle which fits into 'ridge' of opposite suture; articular facet with at least crenularium, areola and claustrum, all appear circular in outline.

Description. The columnals articulate symplectially and are circular in outline. The crenularium has fifty-three regularly disposed simple crenulae with rounded apices and troughs. The areola is smooth and planar. The claustrum is smooth and sloping slightly towards the centre of the facet.

The latus is convex with convexity increasing in higher orders of the noditaxis. Symplectial articulation gives a regular, coarse, crenulate suture. The lateral sculpture is especially distinct on nodals. It comprises regularly disposed low tubercles, the first row of which fall into the area created by the 'groove' of the suture below it at the bottom of the columnal. A second row of tubercles lies directly above each of these tubercles, each being directly in line with a tubercle from the first row below it. Each is joined by a low, oblique ridge to a tubercle of another row above. This third row of tubercles is offset from the second row below it by 50%. A fourth row of tubercles lies above this row, each tubercle disposed directly above one of those of the third row. Each fits into the space created by the 'ridge' of the suture above it.

The longest pluricolumnal (the holotype) has a noditaxis of 212N with (presumably) nodals being higher and wider than internodals. Measurements, in mm, of all columnals of the holotype pluricolumnal and their inferred noditaxial orders are inserted in the following table:

Holotype TCD.35988

KH	1.2	1.0	1.7	1.0	1.3
Order	1	2	N	2	1

All columnals are non-cirriferous.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35988	4.90	0.61	0.47	?	?	25	19	?	?	1.24	25	53	Bin: IN1
TCD.35988	4.93	0.76	?	?	?	31	?	?	?	1.24	25	53	SEM: IN1

Remarks. The holotype was immersed in 40-45% hydrofluoric acid for four minutes

revealing the stereom.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 9 gp. nov.

Plate 42, figs a-c; Plate 43, figs a, b

Holotype. TCD.35989, a pluricolumnal of eleven ossicles, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Material. Two paratypes, both pluricolumnals, specimen TCD.35990 with eight ossicles which have slipped from their original articulated positions, and specimen TCD.35991 with seven ossicles which is too deformed to make any measurements. Both were extracted from the same bulk sample as the holotype.

Diagnosis. Cylindrical columnals of heteromorphic stem, nodals higher than internodals and bearing cirrus-related structures; articular facet with wide crenularium, planar areola, steeply sloping claustrum and central lumen, all are circular in outline.

Description. The columnals are circular in outline and have symplectial articulation. The crenularium is wide with an irregular pattern of about fifty to fifty-eight simple, bifurcating and peripherally intercalated raised crenulae with round apices and troughs. Intercalations and bifurcations occur at any point across the crenularium to give about one-hundred to one-hundred-and-two crenulae terminating adjacent to the latus. The areola is planar and appears to be pitted. The claustrum is steeply sloping towards a central, circular lumen.

The latus is straight and smooth, except where cirrus-related structures occur. The crenulate suture is fairly even and coarse with a high amplitude.

The long pluricolumnals has a noditaxis of 2221222N (paratype TCD.35990) to 3231323N (holotype) with nodals being higher than internodals. Measurements, in mm, of all columnals of the holotype and paratype TCD.35990 pluricolumnals and their

inferred noditaxial orders are inserted in the following tables:

Holotype TCD.35989

KH	1.6	1.5	1.8	1.3	1.7	1.3	2.3	1.4	1.5	1.4	1.8
Order	2	3	1*	3	2	3	N*	3	2	3	1

Paratype TCD.35990

KH	1.4	2.3	1.7	1.7	1.7	1.9	1.7	1.7
Order	?	N*	2	2	2	1*	2	2

Cirrus-related structures may occur on both nodals and priminternodals. All other internodals appear to be non-cirriferous. One priminternodal on paratype TCD.35990 has one circular cirrus socket with a central pore, but the remainder of this articular facet is unclear. One nodal has only a small pseudocirrus scar. The holotype has one circular cirrus socket, on a nodal, and one abortive cirrus or pseudocirrus scar, on a priminternodal, which are disposed at positions that are consistent with pentaradiate symmetry. The cirrus socket is not located at columnal mid-height so that its extremity on one side crosses the suture between, and impresses onto, the adjacent columnal. It measures 2.2 mm in diameter and protrudes away from the latus at one side so that it is directed obliquely either upward or downward. The nodicirral articulum comprises a circular crenularium, which is sloping inwards and has about twenty small crenulae, an areola, which is smooth and sloping gently inwards and a tiny, central, circular lumen. Overall, the nodicirral articulum is bowl shaped.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.35990	6.57	1.57	0.29	?	?	48	9	?	?	?	?	58	102	SEM: IN
TCD.35989	6.58	1.40	0.75	?	?	42	23	?	?	?	?	about 50	about 100	SEM: IN2
TCD.35989	7.0	1.58	0.58	0.64	1.4	45	17	18	20	1.6	23	about 50	about 100	Bin: IN2
TCD.35990	7.2	1.8	0.3	0.75	1.5	50	8	21	21	1.4	19	58	102	Bin: IN

Stereom. The stereom is regularly galleried as seen on paratype TCD.35990.

Remarks. On the crenularium of paratype TCD.35990 it is difficult to count the number of crenulae touching the latus as some of them bifurcate right at its edge. However, it is observed that on the holotype and paratype TCD.35989, which are columnals of almost the same articular facet diameter, the number of crenulae is similar. The areola ratio on

the holotype is twice that of the paratype.

The noditaxis of the holotype (3231323N) is a simple Type III pattern of Webster (1974). The paratype TCD.35990 (2221222N) could be a more complex Type II pattern, which Webster (1974) does not mention. The most complex pattern mentioned there is 22122N. The difference between the patterns of the holotype and paratype means that there may be slight differences in the way some columnals grow within higher level plesions as well as species. The columnal that measures 1.4 mm high is curious. It may be a tertinternodal, belonging to the next noditaxis that may have three orders of internodals.

The holotype and paratype TCD.35991 were immersed for five minutes, and the paratype TCD.35989 for nine minutes, in 40-45% hydrofluoric acid.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 10 gp. nov.

Plate 44, figs a, b; Plate 45, figs a-c

Holotype. TCD.35992, a pluricolumnal of seven ossicles, from Section BD:G, a silty shale, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8176 5901.

Diagnosis. Cylindrical columnals of heteromorphic stem, nodals higher than internodals and with or without abortive cirri; latus with many small randomly disposed low tubercles; articular facet with circular crenularium, areola and claustrum, and central, rounded pentagonal lumen.

Description. The symplectially articulating columnals are circular in outline. The crenularium has thirty-seven high and deep, rounded crenulae which may be simple, bifurcating or peripherally intercalated to give fifty-five crenulae touching the latus. Bifurcations occur approximately half-way across the crenularium, and short intercalated crenulae also terminate here. The areola is smooth and planar. The claustrum is gently sloping towards a central lumen whose outline is pentagonal with rounded corners and with very shallow depressions along the long sides.

The latus is straight with many small, low, randomly disposed tubercles. The crenulate suture is fine and fairly regular with a high amplitude.

The longest pluricolumnal (the holotype) suggests a noditaxis of 212N with nodals being higher than internodals. Measurements, in mm, of all columnals of the holotype pluricolumnal and their inferred noditaxial orders are inserted in the following table:

Holotype TCD.35992

KH	1.6	2.0	1.7	2.1	1.7	1.9	1.7
Order	2	1	2	N*	2	1	2

Nodals may have abortive cirri which occur at columnal mid-height. They are disposed around the circumference in positions that correspond to pentaradiate symmetry and are circular in their outlines.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.35992	3.48	0.59	0.37	0.42	0.70	33.85	21.42	24.35	20.19	1.38	39.65	37	55	SEM: IN2
TCD.35992	3.65	0.69	0.33	0.45	0.72	37.81	17.81	24.66	19.73	1.58	43.29	37	55	Bin: IN2

Stereom. The stereom is galleried as seen on the holotype.

Remarks. The holotype was immersed in 40-45% hydrofluoric acid for six minutes and the stereom was revealed.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 11 gp. nov.

Plate 46, figs a, b

Holotype. TCD.35993, a pluricolumnal of three ossicles, one of which has slipped slightly, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Cylindrical columnals of heteromorphic stem, columnals all of different heights; crenularium wider on one side with crenulae which have bulbous inner terminations, claustrum smooth and in three parts, outer claustrum sloping gently adaxially, medial claustrum sloping at a greater angle adaxially, inner claustrum inclined upwards adaxially, with a very narrow termination sloping down towards central lumen with straight sides, all are circular in outline and central relative to the inner boundary of the crenularium.

Description. The columnals are circular in outline. Articulation is symplectial. The crenularium is wider on one side than the other, but it maintains a circular inner boundary. It has flattened crenulae that have bulbous inner terminations. They are initially simple and fifty-five in number adaxially, but may bifurcate, or be peripherally intercalated, with bifurcations and intercalated crenulae occurring in outer half of the crenularium to give eighty-six crenulae terminating at the latus. The claustrum is smooth and has three distinct divisions. The outer claustrum inclines gently downwards and adaxially. The medial claustrum is inclined downwards at a greater angle. The inner claustrum is inclined adaxially upwards. Along its inner margin it has a very narrow portion that slopes towards the lumen. The lumen is circular in outline. The claustra and lumen are positioned centrally relative to the inner boundary of the crenularium.

The latus is smooth and straight. The crenulate suture has flattened apices and troughs and is of high amplitude.

The noditaxis is unknown, but the stem is heteromorphic as the three columnals of the longest pluricolumnal (the holotype) are of different heights. Measurements, in mm, of all columnals of the holotype pluricolumnal and their inferred noditaxial orders (two possibilities) are inserted in the following table:

Holotype TCD.35993

KH	1.8	2.0	1.8
Order	2	1	2
Order	3	2	3

There is no evidence of any cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*OCLR*	*MCLR*	*ICLR*	*LD*	*Ci*	*OCLi*	*MCLi*	*ICLi*	*Li*	*KH*	*KHi*	*No. crenulae touching OCL*	*No. crenulae touching latus*	*Extras*
TCD.35993	5.68	1.07	0.74	0.63	?	?	38	26	22	?	?	1.59	28	55	86	SEM: IN
TCD.35993	5.87	1.13	0.75	0.55	0.16	0.69	39	26	19	5	12	1.8	31	55	86	Bin: IN

Remarks. Inside of the crenularium this columnal has many portions sloping in various directions and at different corners so that it is difficult to place a name on each. All have been attributed as various portions of the claustrum.

Bulbous inner terminations seen in this columnal morphospecies are similar to the beaded ones of *Mooreanteris waylandensis* Miller, 1968 (Virgilian (Upper Pennsylvanian), Texas) (Moore and Jeffords 1968, Plate 18, fig. 8*a*).

The holotype was immersed in 40-45% hydrofluoric acid for five minutes.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 12 gp. nov.

Plate 5, fig. a; Plate 28, figs c, d; Plate 47, figs a, b

Holotype. Two specimens; TCD.35994, a pluricolumnal of twenty-nine ossicles, both end columnals being broken so that an articular facet cannot be seen. Taken from a loosely coiled stem section of over 510 mm in length; TCD.35995, a pluricolumnal of thirty-two ossicles, both ends of which are broken so that an articular facet cannot be seen. Taken from the same stem as specimen TCD.35994, but from the other end. Collected from top of Bed BD:K5, a shale parting between a sandy limestone and an argillaceous limestone, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8180 5895.

Diagnosis. Circular columnals of distinctly heteromorphic stem, nodals higher and wider than internodals; latus of nodals and priminternodals strongly angulated in longitudinal profile, sloping asymmetrically so that the apex is not at columnal mid-height and is almost at one edge of the columnal, secundinternodals moniliform, articular facet unknown.

Description. The symplectially articulating columnals are circular in outline. The articular facet is not seen except on specimen TCD.35995 where what appears to be a narrow, circular, crenulated perilumen can be seen, but this is inconclusive.

The entire latera of the nodals and priminternodals are asymmetrically, strongly angulated so that in longitudinal profile it can be seen that the equatorial apex is not at columnal mid-height. The asymmetry is always in the same direction. Internodals have a slightly convex, but rounded rather than angulated latus. The apex of the ridge is irregularly pitted. Nodals have a greater diameter than internodals. The maximum columnal diameter (nodals) is about 7.5 mm and the minimum (IN2) is 7 mm. The columnals are overall slightly narrower and lower in TCD.35994 than in TCD.35995. The crenulate suture is open with a very regular, moderate amplitude.

The pluricolumnals show a noditaxis of 212N where nodals are higher and wider than internodals. Secundinternodals are much lower than nodals and priminternodals. All columnals are non-cirriferous.

Columnal heights, in mm, in specimen TCD.35995.

Noditaxis number	*N*	*IN2*	*IN1*	*IN2*
1	-	-	-	0.5
2	1.2	0.5	1.0	0.5
3	1.2	0.5	1.1	0.4
4	1.3	0.4	1.0	0.4
5	1.2	0.3	0.8	0.5
6	1.2	0.5	1.0	0.5
7	1.2	0.5	1.2	0.5

Remarks. It is not known whether the off-centre apex of the angulated latus is towards the proximal or distal end of the crinoid stem, but it is always offset in the same direction.

In addition to the 510 mm of stem section that was preserved, the impression (external mould) left on the bedding surface on which the stem was found gives a total length of stem of 910 mm. It does not taper at all and there is no evidence of the crown or any cirrus-related structures so it is inferred that the stem during life was even longer. Although the columnals are lower and slightly narrower at one end of the stem, since the calyx and no cirri or attachment structure was found it cannot be determined which end of the stem is proximal and which is distal.

The lateral stem morphology of this columnal type is not unlike that of the columnal species *Acanthocrinus kersivienensis* described by Le Menn (1985, p. 42, Plate 5, Figs 1-4, 6) with its strongly angulated asymmetry. The articular facets of *A. kersivienensis* and those of the current specimens cannot be compared since in the latter they cannot be

seen. The attitude of the *A. kersivienensis* stem is generally found to be coiled, as are the other stems of members of the family Rhodocrinitidae Roemer, 1855 and the current specimen *in situ*. The other new species of the genus described by Le Menn (1985) was *A. faouensis*. The morphologies of *A. kersivienensis* and the specimens herein do not compare well with *A. faouensis*. Since the genus *Acanthocrinus* only appears in the Devonian then the stem described herein is unlikely to belong to this genus. Descriptions and figures in the literature of other members of the Rhodocrinitidae are vague so stem morphology cannot be readily compared with the current material to establish its origin. However, the proximal part of the stem of the Tournaisian *Rhodocrinites verisimilis* (Grenfell, 1876) figured in Ausich and Sevastopulo (in press, Plate 1, Figs 1-8) is similar to the present columnal types so there could be some phylogenetic connection between the two stems. The lateral appearance of this stem is similar to that of 'Pluricolumnal of circular section' from the Caradoc of Co. Tyrone in Donovan (1989*a*, Plate10, fig. 8). In that specimen the columnals, like the ones herein, . have angulated latera, different widths and different heights

The holotype specimens were immersed in 40-45% hydrofluoric acid for five minutes. This removed some of the matrix, but a lot still remains.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 13 gp. nov.

Plate 48, fig. a

Holotype. Specimen TCD.35996, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Small (about 2.5 mm diameter) moniliform columnals, high compared to width; latus with distinct sculpture of randomly disposed, different sized, long, tapering protuberances; articular facet with crenularium, areola and central lumen, all are circular in outline.

Description. The columnal is circular in outline and high in comparison to its width. Articulation is symplectial. The crenularium has twenty-six simple, high and deep crenulae and bifurcating crenulae with lower amplitudes. The areola is smooth and planar. The central lumen is obscured.

The latus is slightly convex with a distinct sculpture of long, tapering protuberances with rounded terminations, which are projecting normally from the latus. They differ in size and are randomly disposed.

There are no cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35996	2500	310	620	640	25	50	26	1970	79	26	SEM

Stereom. The stereom is regularly galleried. The crenularium has small pores and bars, and the size of both increases adaxially. This may have been for attachment of thicker and stronger intercolumnal ligaments.

Remarks. The holotype was immersed in hydrofluoric acid of concentration 3.6% for one week. During the process it cracked due to a volume reduction on its alteration from calcite to calcium fluoride making it fragile. As a consequence, since its examination in the SEM, small fragments have broken off. Therefore, the scanning electron micrograph shows more detail of the articular facet than can now be observed on the specimen itself. However, where sections have broken away a clear view of the stereom is revealed.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 14 gp. nov.

Plate 48, fig. b

Holotype. Specimen TCD.35997, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Cylindrical columnals; latus drawn out into symmetrical, equatorial ridge which covers central 33% of latus and is rounded in longitudinal profile, ridge surface is uneven; articular facet with crenularium, outer claustrum, inner claustrum and central lumen, all are circular in outline.

Description. The columnal is circular in outline with symplectial articulation. The crenularium has forty-two simple, regularly disposed, shallow, rounded crenulae. The outer claustrum is smooth and steeply sloping down, at more than 45°, towards the centre of the columnal. The inner claustrum is a narrow, thin horizontal 'ledge' after a vertical drop from the inner extremity of the outer claustrum. The lumen is central and circular in outline.

The latus has a ridge disposed at columnal mid-height which covers the central 33% of the lateral surface. It is narrow and rounded in longitudinal profile with an uneven, equatorially running apical surface. The latus above and below the ridge is straight and smooth.

There is no evidence of any cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35997	5.85	1.01	0.64	0.34	1.87	35	22	12	32	1.49	25	42	SEM

Remarks. The holotype was immersed in 3.6% hydrofluoric acid for one week. It has a few cracks following a volume reduction on its alteration from calcite to calcium fluoride.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 15 gp. nov.

Plate 49, fig. a

Holotype. Specimen TCD.35998, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Small (about 2.5 mm diameter) cylindrical columnals, very high in comparison to width, some columnals with cirripores; articular facet with circular crenularium, areola and concave claustrum, and central ?pentagonal lumen.

Description. The columnal is circular in outline and high in comparison to its width. Articulation is symplectial. The crenularium has thirty-one simple, somewhat bulbous crenulae that are evenly disposed. The areola has an uneven surface, but is planar. The claustrum is smooth with a concave surface, which is sloping towards the lumen. The lumen is central and appears to be pentagonal in outline.

The latus is straight and smooth.

The holotype has a single small cirripore at columnal mid-height.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35998	1580	180	180	250	370	23	22	31	23	1300	83	31	SEM

Remarks. It is not known whether the holotype is a nodal although the presence of a cirripore indicates it is.

The holotype suffered cracking following immersion in 3.6% hydrofluoric acid for one week and its alteration from calcite to calcium fluoride, and subsequently some fragments have broken off the articular facet.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 16 gp. nov.

Plate 50, fig. a

Holotype. Specimen TCD.35999, a pluricolumnal of three ossicles, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Diagnosis. Very small (less than 1 mm diameter), strongly moniliform columnals of heteromorphic stem; latus strongly convex with rounded or flattened sides, on either side

of suture of adjacent columnals an sculpture follows line of suture so that it appears there is a gap between columnals in articulated specimens, sculpture carries extensions of crenulae and covers about 40% of lateral surface in total; articular facet comprises crenularium with simple bulbous crenulae, areola and central lumen, all are circular in outline.

Description. The symplectially articulating columnals are circular in outline with an overall bulbous shape. The crenularium is peripheral with sixteen bulbous, simple crenulae whose lateral extremities continue out onto the latus so that their edges are seen in lateral view. The areola is smooth and planar. The lumen is central and circular in outline.

The latus is strongly convex with a rounded, or sometimes flattened, equatorially running apex. Longitudinally directed ridges and grooves, which are extensions of the crenulae from the crenularium, extend out onto latus and cover about 20% of the lateral surface at both ends of the columnals. The crenulate suture is regular, fairly coarse and squared.

The noditaxis is unknown, but from the holotype pluricolumnal there are at least two columnal orders each having different heights. There are no cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KD*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.35999	688	?	?	?	?	?	?	?	934	?	16	SEM: ?IN

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 17 gp. nov.

Plate 50, fig. b

Holotype. Specimen TCD.53000, a pluricolumnal of two ossicles, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Diagnosis. Very small (less than 1 mm diameter) circular columnals of heteromorphic

stem, columnals very high compared to width and barrel shaped, nodals higher than internodals and cirrus-bearing; latus with striations around whole circumference running longitudinally, wide, low, equatorial flange with gently sloping surfaces; articular facet with crenularium, areola and central lumen, all are circular in outline.

Description. The columnals are circular in outline and articulation is symplectial. The crenularium has sixteen simple crenulae, which have squared apices and troughs. They are irregular in their widths, yet are fairly evenly disposed. The areola is smooth and planar. The lumen is central and circular in outline.

The latus has longitudinally oriented striations running around the entire circumference that are fairly evenly spaced, each aligned with the culmina of the crenularium. At columnal mid-height a wide, but low, flange is disposed with its two surfaces gently sloping away from the latus. On the nodal the total diameter of the flange is 276 μm and on the internodal is 340 μm. Overall, the latus is very slightly convex, except where the flange is disposed. The crenulate suture is turret-like.

The noditaxis includes at least two orders in the holotype. The (probable) cirrinodal has three circular cirrus sockets, two disposed on one side of the equatorial flange and one on the other. One of the scars has a diameter of 347 μm, and the other two are of similar dimensions. All have their peripheral extremities in line with the flange so they take the place of it when the two coincide. They are disposed in positions that are consistent with pentaradiate symmetry, but no two cirrus sockets are aligned in the same pentaradiate position. From one cirrus socket it is observed that the nodicirral articulum comprises a circular crenularium with six bulbous crenulae, which covers 66% of the facet, and a central, circular lumen with straight sides.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53000	700	100	150	200	29	43	29	1000	143	16	Bin: IN

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 18 gp. nov.

Plate 49, fig. b

Holotype. Specimen TCD.53001, a single columnal, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Diagnosis. Very small (about 2 mm diameter) moniliform columnals; articular facet with only small, central, circular lumen and concave areola that extends to periphery and is terminated by a narrow articular rim, synostosial articulation.

Description. The columnal is circular in outline and articulation is synostosial. The articular facet has a peripheral articular rim with an uneven apex, but it has no crenulae as such. The areola is concave with a steeper incline peripherally, becoming more horizontal towards the lumen. The central lumen is small and circular in outline.

The latus is smooth, and convex to slightly angulated at columnal mid-height.

There is no evidence of any cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*AR*	*LD*	*Ai*	*Li*	*KH*	*KHi*	*Extras*
TCD.53001	2073	833	407	80	20	600	29	SEM: ?IN

Stratigraphical range. Arundian (Bundoran Shale Formation).

Remarks. This columnal is the only circular, synostosially articulating columnal in the present study. It is rare to find such columnals amongst Carboniferous genera (Donovan 1990).

COLUMNAL TAXON NUMBER 19 gp. nov.

Plate 51, fig. a

Holotype. Specimen TCD.53002, a single columnal, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Diagnosis. Very small (about 1 mm diameter) cylindrical columnals, much wider than high; latus with equatorial flange with sloping surfaces so that it is narrowest at its periphery; articular facet with crenularium, areola and very small central lumen, all are circular in outline.

Description. The symplectially articulating columnal is circular in outline. The crenularium is peripheral with twenty-four high and deep wedge-shaped, simple crenulae, which have rounded apices and troughs. The areola is smooth and planar until it nears its periphery where it curves upwards and therefore makes the entire facet appear slightly concave. The lumen is central, circular and very small occupying less than 5% of the articular facet.

The latus has a flange at columnal mid-height whose surfaces are sloping away from the latus. It has an average height of 233 μm. Overall, the latus is straight, except where the flange is disposed.

There are no cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53002	1216	145	435	56	24	72	5	510	42	24	SEM: ?IN

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 20 gp. nov.

Plate 51, fig. b

Holotype. Specimen TCD.53003, two columnals which were originally articulated, which have now slipped, but are still joined together. Collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Diagnosis. Very small (less than 1 mm diameter) rounded pentagonal columnals of distinctly heteromorphic stem, nodals higher and wider than internodals and with an epifacet; latus of nodals straight with rounded extremities, but on internodals seen as zigzag ridge; all columnals with rounded pentagonal crenularium, corners coincident

with those of columnal, three to four crenulae per long side and orientated normally to it, perilumen circular, inflated on one or both facets and carrying extensions of crenulae, lumen central and circular in outline.

Description. The columnals are pentagonal in outline with rounded corners and are united by symplectial articulation. The larger columnal has a diameter of 722 µm and is presumably a nudinodal. It has a crenularium which is rounded pentagonal in outline and whose corners coincide with those of the columnal. The inside boundary is circular, following the outline of the perilumen. It has low, regularly disposed, simple crenulae that are positioned normally to the long sides of the latus. On the facet opposing the smaller columnal there are two culmina on each of the long sides and one in each corner with crenellae in-between, and on the facet apposing the smaller columnal the positions of crenellae and culmina are reversed. On both facets the crenularium does not reach the latus. Instead it is surrounded by an epifacet, which is smooth and rounded and extending to a latus that has smooth, straight sides. The perilumen is circular in outline, smooth and inflated on both facets so that it resembles half a donut. It holds extensions of the crenulae from the crenularium, but these are very low and only extend half-way across its surface. The lumen is small, central and circular in outline.

The smaller columnal, an internodal of 705 µm diameter, has a similar articular facet morphology to that of the nodal. However, the crenularium reaches the latus as there is no epifacet. Crenulae extend normally from the long sides. On the facet that is apposing the nodal the crenularium has crenulae occupying positions that interlock with crenulae on the nodal with which it is articulated. On its opposing facet the positions of the culmina and crenellae are reversed. The articulating facet appears to be flat overall, whereas the opposing facet is overall convex, the perilumen again resembling a donut. Both carry low extensions of the crenulae. Only the lumen on the opposing facet can be seen and it is central and circular in outline.

The latus of the internodal is zigzagged where 50% offset culmina from opposing sides of the columnal are joined by oblique ridges. The columnal is slightly convex in longitudinal profile.

The noditaxis is at least 1N with nodals being distinctly higher and wider than internodals. There is no evidence of any cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*PR*	*LD*	*Ci*	*Pi*	*Li*	*KH*	*KD*	*KHi*	*No. crenulae*	*Extras*
TCD.53003: small columnal	705	114	164	150	32	46	21	?	705	?	3-4 per long side	SEM: ?IN
TCD.53003: large columnal	722	126	160	150	35	44	21	?	980	?	3-4 per long side	SEM: ?N

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 21 gp. nov.

Plate 52, fig. a

Holotype. Specimen TCD.53004, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (less than 1 mm diameter) cylindrical columnals, as high as wide; articular facet with very narrow, peripheral crenularium, smooth, planar, areola and small, slightly eccentric lumen, all are circular in outline.

Description. The columnal is circular in outline, is as high as wide and has symplectial articulation. The crenularium is peripheral with twenty-one regularly disposed small, simple, bulbous crenulae. The areola is smooth and planar. The lumen is small, circular in outline and slightly eccentric.

The latus is smooth and straight with no cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53004	816	88	268	104	22	66	13	800	98	21	SEM: ?IN

Stereom. The stereom is galleried. The holotype shows that the crenularium and outer part of the areola have pores of smaller diameter and bars, which are narrower than those of the inner part of the areola. The stereom increases in its pore diameter half-way across the areola. There are some larger pores in this inner portion of the areola that were probably for through-going ligaments during life. However, there appears to be no

structured pattern to their positioning and they are more likely to have housed wider, and therefore stronger, intercolumnal ligaments. Some sample measurements are included in the following table:

Stereom microstructure morphometrics, measurements in microns.

Specimen TCD.53004	*Bar widths*	*Pore diameters*	*Large pore diameters*
Crenularium and outer portion of areola	3.56	3.60	-
	5.23	4.17	-
	5.81		-
Inner portion of areola	4.97	5.41	14.16
	5.08	6.69	16.90
	8.80		30.50
	8.93		

Remarks. The holotype suffered a large crack, which is seen on the latus, following immersion for one week in 3.6% hydrofluoric acid and its alteration from calcite to calcium fluoride.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 22 gp. nov.

Plate 53, figs a, b

Holotype. Specimen TCD.53005, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (less than 1 mm diameter) circular columnals which are barrel shaped, nodals with a very high columnal height index and cirriferous; latus symmetrically slightly angulated longitudinally; articular facet with crenularium, areola and central lumen, all are circular in outline.

Description. The columnal is circular in outline and is much higher than it is wide. Articulation is symplectial. The crenularium has fourteen regularly disposed wedge-shaped, simple crenulae. The areola is smooth and very slightly sloping down towards a central, circular lumen that has straight sides.

The latus is smooth and very gently sloping away in both directions from mid-

height of the columnal so that it is symmetrically slightly angulated in longitudinal profile.

The holotype, which is probably a nodal, has a single circular cirrus socket at columnal mid-height which has a greater relief at one side. The nodicirral articulum has a raised, narrow crenularium with nine bulbous crenulae, a smooth, planar areola, and a small, central, circular lumen. In relation to the diameter of the articular facet that of the socket diameter is fairly large at about 300 μm.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53005	580	107	128	110	37	44	19	950	164	14	SEM: N

Stereom. The holotype shows that the stereom is regularly galleried. The areola has larger pore sizes than the crenularium, and they are especially larger towards the lumen. Presumably the larger pore sizes near the axial canal are for the accommodation of wider, stronger intercolumnal ligaments or through-going ligaments.

Stereom microstructure dimensions in microns.

Specimen TCD.53005	*Bar widths*	*Pore diameters*
Crenularium	2.94 4.12 4.99	5.70 6.24
Areola	4.26 4.70 6.09	5.96 6.40

Remarks. The holotype suffered only small cracks following immersion in 3.6% hydrofluoric acid for one week and its alteration from calcite to calcium fluoride.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 23 gp. nov.

Plate 54, figs a, b

Holotype. Specimen TCD.53006, a single columnal from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale

Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (less than 1 mm diameter) circular columnals with a high columnal height index; latus with equatorial ridge which is almost semi-circular in longitudinal section and covering central 33% of lateral surface; articular facet unknown except that a circular crenularium is present.

Description. The columnal is circular in outline and is much higher than it is wide. Articulation is symplectial. The articular facet is unclear. The crenularium appears to have a constant radius with about eighteen regularly disposed simple crenulae, and is covering about 40% of the articular facet.

The latus is smooth and has a wide, bulbous, semi-circular ridge (flange in the measurement table below) covering the central 33% of the latus longitudinally. The edges of the ridge slope to meet the lateral surface at around 45°. The remaining lateral surface outside of the ridge is straight.

There are no cirrus related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*KD*	*CR*	*Ci*	*FLR*	*FLi*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53006	710	1050	120	34	170	32	960	135	about 18	SEM: ?IN

Remarks. Although the articular facet is not really known from this specimen, the lateral ridge is characteristic enough to distinguish the taxon.

An equatorial flange of a similar relative height and width, but with a squared lateral apex, appears on the columnal morphospecies *Malovicrinus* cf. *implicatus* Stukalina, 1970 (Caradoc (Ordovician)) (Donovan 1986*a*, Plate 6, fig. 10).

The specimen was immersed in 3.6% hydrofluoric acid for one week, and has suffered a large crack down one lateral side following a volume reduction during its alteration from calcite to calcium fluoride.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 24 gp. nov.

Plate 52, fig. b

Holotype. Specimen TCD.53007, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (about 500 μm diameter) cylindrical columnals with very high columnal height index; latus with tuberculate sculpture all around circumference, tubercles low and extending longitudinally with two or three tubercles per column, eleven to twelve columns, which are offset by 50% at columnal mid-height, each column coincides with culmen on articular facet; articular facet with crenularium, areola and central lumen, all are circular in outline.

Description. The columnal is circular in outline and very high in comparison to its width. The crenularium has eleven to twelve broad, wedge-shaped, simple crenulae, which are high and deep and have rounded apices and troughs. The areola is smooth and planar. The lumen is central and circular in outline.

The latus is straight with a sculpture of low, but wide, tubercles extending in longitudinally orientated columns around the entire circumference. There are eleven or twelve columns comprising two or three tubercles each on each half of the columnal, and these are offset by 50% at columnal mid-height. The columns coincide with culmina of the articular facets. Articulation is symplectial.

There is no evidence of any cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53007	500	100	100	100	40	40	20	800	160	11-12	Bin: ?IN

Remarks. Owing to the very high columnal height index of over 160 and the 50% offset of the longitudinally extending tubercle columns half-way down the latus, this could in fact be two columnals that are still articulated and very tightly sutured, the suture not being visible. However, a similar 50% offset of vertical ridges is seen in *Schyschcatocrinus* sp. B of Gluchowski (1993, p. 58, Fig. 10, F).

Following immersion in 3.6% hydrofluoric acid for one week the holotype has acquired many cracks owing to a volume reduction following its alteration from calcite to calcium fluoride.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 25 gp. nov.

Plate 55, figs a, b

Holotype. Specimen TCD.53008, a pluricolumnal of two ossicles, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (about 1 mm diameter) cylindrical columnals of heteromorphic stem, higher ordered columnals being greater in height than lower orders, all columnals are higher than wide, some are cirriferous; articular facet comprises only circular crenularium and large, central, circular lumen.

Description. The columnals are circular in outline and higher than they are wide. The articular facet has only a crenularium, which has thirteen regularly disposed, simple, high crenulae with rounded apices and troughs, and a large, central, circular lumen with straight sides.

The latus is straight and smooth, except for where cirrus sockets are disposed. Articulation is symplectial, but the crenulate suture cannot be seen.

The noditaxis is unknown, but the stem is heteromorphic with at least two orders, both of which are cirriferous. The different orders have different heights, but are of the same diameter. There are two circular cirrus sockets of about 350 µm diameter, and both have very high relief. The cirrus facet of the larger columnal has a very large, central, circular lumen with straight sides, and is surrounded by a narrow lip with no evidence of any crenulae on its surface. The smaller cirrus facet is obstructed so that no morphological features be can seen, but it can be seen that it is circular in outline. This probably represents a node-like abortive cirrus.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*LD*	*Ci*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53008	980	220	540	45	55	1013	103	13	SEM: ?IN1

Remarks. It is inferred that the holotype probably represents two columnals that are very tightly sutured the suture, therefore, not being seen. If the specimen were to be treated as one columnal only, the columnal height index would be very high at over 277. If it were treated as two columnals, there would be a larger columnal of 1706 μm high (the broken end of the specimen), which is of a higher order, and a smaller columnal being a cirriferous internodal of 1013 μm high. The cirrus sockets would be at columnal mid-height. For these reasons, and for purposes of description, the specimen has been taken to be two articulated columnals.

The holotype was immersed in 3.6% hydrofluoric acid for one week and sustained many cracks owing to volume reduction caused by its alteration from calcite to calcium fluoride. The fragment that has broken off the larger columnal did so before examination under the SEM.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 26 gp. nov.

Plate 56, fig. a

Holotype. Specimen TCD.53009, a pluricolumnal of sixteen ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Circular columnals of distinctly heteromorphic stem, higher orders are greater in height, nodals and priminternodals may be cirriferous; latus straight and smooth; circular crenularium with many simple crenulae, some bifurcate or are peripherally intercalated, areola circular, smooth and planar, circular claustrum slopes gently towards lumen, lumen central and circular in outline.

Description. The columnals are circular in outline and all orders are wider than high. The crenularium is peripheral, covering only 15% of the articular facet, with many regularly disposed crenulae. Most are simple, but there are some peripherally intercalated and

bifurcating crenulae. They have high and deep apices and troughs, which are slightly rounded, but the sides are quite steep so that they are almost parallel. There are about eighty-one crenulae touching the areola and about one-hundred touching the latus. The areola is smooth and planar with a rapid inner termination with the claustrum. The claustrum slopes down gently from the areola, but its width cannot be deciphered. The lumen appears to be circular in outline.

The latus is straight to slightly convex and is smooth, except where cirrus-related structures are deposited. Articulation is symplectial. The crenulate suture is irregular zigzagged with a low amplitude.

The noditaxis from the holotype is 434243414342434N, which is a complete noditaxis of five orders. The higher the columnal order the greater the height of the columnal. The following are measurements, in mm, of all columnals of the pluricolumnal holotype and their inferred noditaxial orders;

KH	0.8	1.0	0.8	1.3	0.7	1.2	0.7	1.6	0.7	1.2	0.7	1.3	0.8	1.1	0.8	2.0
Order	4	3	4	2	4	3	4	1*	4	3	4	2	4	3	4	N*

Three cirrus sockets occur on the holotype, one on the priminternodal and two on the nodal. They are all disposed at columnal mid-height and are positioned at 72° from each other, so, are consistent with a pentaradiate symmetry. The two on the nodal are wider and protrude further from the latus. However, the details of the articular facets cannot be seen in any detail.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CL*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.53009	6.37	0.5	0.65	?	?	16	20	?	?	0.8	13	about 81	about 100	Bin: IN4

Remarks. The stereom changes density across the different morphological features of the articular facet.

The holotype was scrubbed using a toothbrush in water only.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 27 gp. nov.

Plate 57, fig. a

Holotype. Specimen TCD.53010, a single columnal, which fragmented into at least five pieces during collection from the bedding plane upon which it was found. It has been glued back together quite successfully using acetone-diluted Paraloid 72 glue crystals. One articular facet is fully visible. It was collected from the upper surface of Bed BD:K5, a shale parting between a sandy limestone and an argillaceous limestone, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8180 5895.

Diagnosis. Very wide (sometimes over 20 mm diameter) cylindrical columnals; peripheral, outer crenularium planar with many simple, bifurcating and intercalated narrow crenulae, crenulae originating on narrow, steeply sloping inner crenularium, central lumen relatively very wide, all are circular in outline.

Description. The columnal is circular in outline with a very low columnal height index. Articulation is symplectial. The crenularium is in two sections. The outer crenularium is peripheral and horizontal with many narrow crenulae, which are simple, bifurcating or peripherally intercalated. Intercalated crenulae are mostly small and disposed only on the extreme periphery. Bifurcations occur at any point across the crenularium, but there are some crenulae which bifurcate twice, once near the inner/outer crenularium boundary and once on the very periphery of the outer crenularium. There are one-hundred-and-ninety-two crenulae touching the latus. The inner crenularium is very narrow and sloping steeply at about 45° towards the lumen. The origins of the crenulae of the outer crenularium appear on the surface of the inner crenularium and there are one-hundred-and-thirty-six in number. They do not bifurcate here at all and therefore appear wider than on the outer crenularium. All the crenulae have rounded apices and troughs. The lumen is central and circular in outline with straight sides. It is relatively extremely wide occupying over half of the articular facet.

The latus has straight sides and no sculpture.

There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*OCR*	*ICR*	*LD*	*OCi*	*ICi*	*Li*	*KH*	*KHi*	*No. crenulae originating on inner crenularium*	*No. crenulae touching latus*	*Extras*
TCD.53010	20.8	3.3	1.0	12.2	32	10	59	2.2	11	136	192	Bin: IN

Remarks. There are a substantial amount of crenulae touching the latus as compared with the number of them originating on the inner crenularium. This suggests that rather than the crenulae simply getting wider, bifurcations and intercalations of new crenulae occurred in an attempt to accommodate growth.

This type of columnal has a very wide lumen and thus was susceptible to deformation during burial if it was deposited on its side in the sediment. However, if the articular facet was positioned horizontally in the bed of deposition the columnal would more likely be preserved intact, such as the holotype herein.

The articular facets of the morphospecies *Graphosterigma grammoides* Moore and Jeffords, 1968 (Osagian (Lower Mississippian), Indiana) (Moore and Jeffords 1968, Plate 14, figs 2*c*, 3*b*), and *Cyphostelechus claudus* Moore and Jeffords, 1968 (Desmoinesian (Middle Pennsylvanian), Texas) (Moore and Jeffords 1968, Plate 14, fig. 4*a*) are similar to those of Columnal Taxon Number 27 herein; a very wide lumen and an outer and inner crenularium, the latter of which carries extensions of the crenulae from the outer crenulariularium down its slope. The latus of the latter is gently convex. However, that of the former has an equatorial flange.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 28 gp. nov.

Plate 57, figs c, d; Plate 58, figs a, b; Plate 59, figs a, b; Figure 6.16

Holotype. Specimen TCD.53011, a pluricolumnal of thirteen ossicles. The facet of the first columnal is seen in its entirety. The twelfth and thirteenth columnals are mostly broken away so that it is the articular facet of the eleventh columnal that is partly seen. Collected from the top of Bed BD:L1, a bioclastic argillaceous limestone, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8197 5919.

Material. Paratype TCD.53012, a pluricolumnal of six ossicles, with only one half of one articular facet being visible. Collected in a bulk sample from between 0.30 and 0.50 m down from the top of Bed BD:A23, a calcareous muddy shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8191 5965. Paratype TCD.53013a and b, a pluricolumnal of about eleven ossicles, has been sectioned along a plane, which approximates to a medial longitudinal section to give part and counterpart. Some of the central part of the pluricolumnal was lost during sectioning. The articular facet is not seen in any detail on any part. Collected in a bulk sample from Bed BD:B28, interbedded thin, argillaceous limestones and dark grey, calcareous fissile shales, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8191 5959.

Diagnosis. Very wide (up to 27 mm diameter) cylindrical columnals of heteromorphic stem which may become very long (almost 2 m), nodals higher and extending further adaxially than internodals and with or without cirrus related structures, very low columnal height index; very wide outer crenularium with extremely fine crenulae which may be simple, bifurcating or intercalated, inner crenularium very narrow, sloping gently towards lumen and carrying origins of crenulae of outer crenularium, lumen with straight sides, often eccentric, all are circular in outline.

Description. The columnals are circular in outline and their heights are less than 10% of their diameters. Articulation is symplectial. The crenularium is in two parts. The outer crenularium is very wide occupying well over 50% of the articular facet and is planar. It has extremely fine, shallow, rounded crenulae that, in the case of paratype TCD.53012, may not be even in their diameters, rather appearing 'boudinage-like' along their entire lengths. Simple, straight crenulae alternate irregularly with bifurcating and peripherally intercalated crenulae so that about two-hundred-and-forty-eight crenulae reach the latus. Crenulae may bifurcate up to four times. Bifurcations and intercalations occur at various distances across the outer crenularium, but as seen in paratype TCD.53012, they appear to occur at regular intervals giving the impression of a series of concentric rings. Traversing from the outside in, crenulae become overall slightly wider in each ring. The inner crenularium slopes gently towards the lumen at less than 45°, and to a much lesser degree in the holotype. It holds the origins of the crenulae of the outer crenularium (fifty-six to about one-hundred-and-two in number) and, thus, they are at their widest here. The

	Number of ossicles in pluricolumnals	Length of pluricolumnals (mm)	Mean height of ossicles in pluricolumnals (mm)
Distal end	38	58	1.53
	37	60	1.62
	68	117	1.72
	34	60	1.76
	31	56	1.81
	missing section	-	-
	64	80	1.25
	43	82	1.91
	7	13	1.86
	19	37	1.95
	16	30	1.88
	17	31	1.82
	16	30	1.88
	38	75	1.97
	25	51	2.04
	Ossicles unclear	34	-
	Ossicles unclear	110	-
	30	70	2.33
	9	22	2.44
	12	25	2.08
	Ossicles unclear	68	-
Proximal end	19	49	2.58
	2	5	2.5
	No measurement for 131 mm and to top of stem		
	Total number of ossicles	**Total length of stem with identifiable ossicles (mm)**	**Mean ossicle height (mm)**
	525	951	1.81

Figure 6.16. Columnal data for stem in field of 1.89 m length composed of Columnal Taxon Number 28.

lumen is circular in outline with straight sides. In the holotype it is central, but in paratypes TCD.53012 and TCD.53013a and b it is eccentric in its position.

The latus is straight with a rough surface. The crenulate suture is uneven and very fine with a low amplitude. A straight very low, narrow ridge may follow the line of the suture.

The noditaxis is 212N to 3231323N with columnal heights increasing in higher orders. Nodals are not seen to be wider in lateral view, but the medial axial longitudinal section of paratype TCD.53013a and b reveals that they extend adaxially further into the axial canal and, thus, make the lumen diameter narrower. All nodals on the type material show that cirrus sockets are disposed at columnal mid-height, and can be very wide (on the holotype it measures about 6 mm in diameter) impressing onto several adjacent columnals. They are circular in their outlines and are overall concave and cone-shaped. On the holotype some of the crenularium can be seen on the nodicirral articulum and on a very small portion of the broken zygocirral, which is still articulated. It reveals that there are many fine crenulae, at least peripherally, and it appears that the lumen is represented by a small central pore.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*OCR*	*ICR*	*LD*	*OCi*	*ICi*	*Li*	*KH*	*KHi*	*No. crenulae originating on inner crenularium*	*No. crenulae touching latus*	*Extras*
TCD.53011	15.5	5.9	0.5	2.9	75	6	19	6.0	4	56	about 248	Bin: IN3
TCD.53013 a and b	22.6	?	?	?	?	?	?	17.5	8	unclear	unclear	Bin: IN2
TCD.53012	27.0	9.3	0.9	6.5	69	7	24	2.0	7	about 102	unclear	Bin: IN3

Remarks. Part of two stems, 1.60 m and 1.89 m in length, which are composed of this type of columnal, have been found in the Bundoran Shale Formation at Bundoran, G819 595 (Mannifield and Sevastopulo 1998) (data on longer stem collected in field see Figure 6.16). Neither of the stems taper measuring 11 mm and 13 mm in diameter respectively. From observations of the longer stem in the field it is known that cirrus sockets, such as those seen on the holotype and paratypes, were host to radicular cirri at the distal end of the stem, and acted as a root-like holdfast. Cirri extend at right angles from the stem at positions that are consistent with pentaradiate symmetry, but there are no more than two cirri on each nodal. The longest cirrus (which is incomplete) measures 140 mm and comprises many cirrals of 8 mm diameter, which widen rapidly in close proximity to the

stem. In the most distal 100 mm of the stem (which continued for another 95 mm at least as is shown by the presence of an external mould of the stem) similar cirri or the large cirrus sockets to which they were attached are disposed. Moving proximally, for the next 135 mm of the stem only pseudocirrus scars are observed on nodals and a central pore is not always present. Their diameters decrease down to 1 mm.

The articular facet feature termed 'inner crenularium' herein is synonymous with the feature termed 'claustrum' in Mannifield and Sevastopulo (1998).

The apparent concentric rings, which are made by the bifurcating and intercalating crenulae, most likely show stages of growth, their inner boundaries depicting the onset of growth spurts. To cover the increasing surface area created as a result of growth of the crenularium bifurcation and intercalation is necessary, rather than the crenulae simply increasing in width.

The holotype was immersed in 40-45% hydrofluoric acid for three minutes.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 29 gp. nov.

Plate 60, figs a, b

Holotype. Specimen TCD.53014, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Material. Paratype TCD.53015, a single columnal, collected in the same bulk sample as the holotype from the type locality.

Diagnosis. Very small (about 1 mm diameter) basaltiform columnals; latus with small, irregularly disposed tubercles; crenularium pentagonal, corners coincident with those of columnal, three to five crenulae extend normally from each long side, areola smooth, planar and coincidentally pentagonal, central, circular lumen.

Description. The columnals are pentagonal in outline with rounded corners and articulate

symplectially. The crenularium is pentagonal in outline and its corners coincide with those of the columnal. On one articular facet of the holotype three culmina are regularly disposed per long side with two smaller ones occupying the corners. The most central culmina are slightly wider and longer than those on the outside of them, extending slightly further adaxially. Crenulae are high and deep with rounded apices and troughs and are somewhat bulbous. Crenellae and culmina of one facet are disposed in reversed positions on the opposing facet. The areola is smooth, planar and pentagonal in outline, its corners again coinciding with those of the columnal outline. The central lumen is circular in outline and has straight sides.

The latus is straight, but with an uneven surface with some very small, irregularly disposed tubercles.

There are no cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53014	796	106	192	201	27	48	25	?	?	4-5 per long side	SEM: ?IN
TCD.53015	1039	153	233	268	30	45	26	?	?	4-5 per long side	SEM: ?IN

Stereom. Paratype TCD.53015 shows that the stereom galleried. There is an increase in dimensions of pore size and bar size from the crenularium towards the areola.

Remarks. Both the holotype and paratype TCD.53015 were immersed in 3.6% hydrofluoric acid for one week. No damage or cracking occurred in either specimen on their alteration from calcite to calcium fluoride.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 30 gp. nov.

Plate 61, figs a, b; Plate 62, fig. a

Holotype. Specimen TCD.53016, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Material. Paratype TCD.53017, a single columnal, which shows less detail than the holotype. Collected from the type locality in the same bulk sample as the holotype.

Diagnosis. Very small (about 1 mm diameter) rounded pentagonal columnals; latus with equatorial angulated ridge; crenularium coincidentally pentagonal with four to five high and deep crenulae projecting normally from each long side, steep drop to coincidentally pentagonal areola, lumen central and circular in outline.

Description. The columnals are pentagonal in outline with rounded corners and long sides, and are much higher than they are wide. Articulation is symplectial. The crenularium is pentagonal in outline, its corners coinciding with those of the columnal. Its long sides are straight and its corners are sharp. The crenulae have squared apices and troughs and a very high amplitude so that where they terminate abruptly by the areola there is a very steep drop. On one articular facet two or three long culmina project normally from each of the long sides, with two smaller ones (almost half the length of those disposed centrally) in the corners. However, in one corner it appears that the culmen is just initiating bifurcation. On the opposing articular facet the positions of the culmina and crenellae are reversed so that crenellae occupy the corners. The areola is smooth and planar with a pentagonal outline, but following the outline of the lumen on its inner margin. The lumen is circular in outline and central with straight sides.

A ridge is disposed at columnal mid-height so that the latus is considerably angulated, but symmetrical, in longitudinal profile. The ridge has an uneven apex.

There are no cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53016	906	153	206	188	34	46	21	?	?	4-5 per long side	SEM: ?IN
TCD.53017	1202	282	227	185	47	38	15	?	?	4-5 per long side	SEM: ?IN

Stereom. The holotype shows that the stereom is regularly galleried. The dimensions of the pores and bars remain fairly constant across the crenularium and the outer part of the areola. However, the innermost third of the areola has some larger pore sizes and bar sizes, maybe for attachment of wide and strong intercolumnal ligaments. There appear to be four very large pores near the inner extremity of the areola. They hold positions that are consistent with a pentaradiate symmetry, each coinciding with corners of the

columnal. The large pores of the innermost areola may have been where wider through-going ligaments were situated. However, this may be an artefact of preservation or preparation techniques.

Stereom microstructure dimensions in microns.

Specimen TCD.53016	*Bar widths*	*Pore diameters*
Crenularium	3.10	9.32
	4.70	10.10
	4.75	-
Areola	6.52	8.68
	6.85	11.50

Remarks. The culmen in one of the corners that bifurcates is probably an indication of growth. As the overall area of a pentagonal articular facet increases the crenulae must accommodate for that growth by multiplying with bifurcations or intercalations only at the corners.

The holotype and paratype TCD.53017 were immersed in 3.6% hydrofluoric acid for one week and sustained no damage or cracking on their alteration from calcite to calcium fluoride.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 31 gp. nov.

Plate 62, fig. b

Holotype. Specimen TCD.53018, a single columnal, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (< 1 mm diameter) pentagonal columnals with sharp corners; rounded, symmetrical, wide equatorial ridge covers central 33% of convex latus; crenularium pentagonal with three to four crenulae per long side, areola pentagonal, lumen central and circular in outline, all pentagonal features coincidental with columnal outline.

Description. The columnal is pentagonal in outline with fairly sharp corners and straight sides. Articulation is symplectial. The crenularium is pentagonal in outline, its corners coinciding with those of the columnal. Crenulae are high and deep with slightly flattened apices and troughs. On one facet two or three simple culmina project normally from each long side with either two small bifurcating culmina or one large culmen occupying the corners. On the opposing articular facet the positions of the culmina and crenellae are reversed. The areola is pentagonal in outline, smooth and very slightly concave. Its corners are coincidental with those of the columnal. The lumen is central, circular in outline and has straight sides.

The latus is overall slightly convex, but it has a narrow rounded ridge at columnal mid-height. The ridge covers only the central 33% of the lateral surface, the remainder of the latus being smooth. The ridge has an uneven surface and is bulbous in each of its five corners.

There are no cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53018	841	79	236	212	19	56	25	290	34	3-4 per long side	SEM: ?IN

Remarks. The holotype was immersed in 3.6% hydrofluoric acid for one week and suffered no cracking or damage through volume reduction on its alteration from calcite to calcium fluoride.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 32 gp. nov.

Plate 63, figs a, b

Holotype. Specimen TCD.53019, a pluricolumnal of three ossicles, one of the end columnals having a section broken away. From Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (< 1 mm diameter) circular columnals of heteromorphic stem, nodals higher than internodals and cirriferous; latus straight to concave; articular facet with crenularium, areola and small, central lumen, all are circular in outline.

Description. The columnals are circular in outline, and are as high as they are wide. Articulation is symplectial. The crenularium has fifteen simple crenulae, which are high and deep with rounded apices and troughs. They are regularly disposed and all of a similar size. The areola is smooth and planar. The central lumen is very small and circular in outline.

The latera of the internodals are concave with the top and bottom edges flaring-out. The latus of the nodal appears to be more straight. There is no sculpture. The crenulate suture is round to angular with a high amplitude.

The holotype has a noditaxis of at least 1N. The nodal is higher than the internodals. It has two large cirrus sockets which are disposed at columnal mid-height, and each has a diameter of about 50% of the columnal height. The details of the nodicirral articulum are unclear, but it can be seen that it is circular in outline, has raised edges with large crenulae, a small central lumen and that, overall, it is concave.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53019	713	151	183	46	42	51	2	583	82	15	SEM: at least IN1

Remarks. The holotype was immersed in 3.6% hydrofluoric acid for one week where it suffered a great amount of cracking following a volume reduction as it was altered from calcite to calcium fluoride. Some fragments were broken away but, have been fixed back onto the specimen using acetone-diluted Paraloid 72 glue crystals.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 33 gp. nov.

Plate 64, figs a, b

Holotype. Specimen TCD.53020, a single columnal, of which both articular facets are very clearly seen. From Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone

marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (about 1 mm diameter), wedge-shaped, circular columnals of heteromorphic stem, nodals cirriferous; latus smooth and concave; articular facet with very wide crenularium and small, central lumen, both are circular in outline.

Description. The columnal is circular in outline, as high as it is wide and slightly wedge-shaped. Articulation is symplectial. The crenularium is very wide, covering over 80% of the articular facet. On it are few triangular-shaped, elongate crenulae with rounded apices and troughs that are simple, bifurcating or peripherally intercalated. About nine crenulae originate adjacent to the lumen and about nineteen terminate at the latus. The lumen is central, circular in outline and very small.

The latus is concave and smooth, except where a cirrus socket is disposed.

A (probable) cirrinodal has a cirrus socket, which is located above or below columnal mid-height. A section is missing as the socket would have been imposed onto the adjacent columnal when the columnal was still articulated. Taking into account the wedge-shape of the columnal, on the latus the cirrus socket is positioned mid-way between the highest and lowest sides. The cirrus socket is almost as wide as the columnal articular facet. It has a high relief, especially towards the columnal mid-line. It is directed obliquely outwards, and either upwards or downwards while maintaining a circular outline. The nodicirral articulum is unclear in its morphology, but it can be seen that it is overall slightly concave and that there are about thirteen apparently simple crenulae disposed on the crenularium.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*LD*	*Ci*	*Li*	*KHx*	*KHy*	*mean KHi*	*No. crenulae touching lumen*	*No. crenulae touching latus*	*Extras*
TCD.53020	1200	505	130	84	11	850	1000	77	about 9	about 19	Bin: N
TCD.53020	1070	461	148	86	14	-	-	-	about 9	about 19	SEM: N

Stereom. The stereom is galleried. It appears that the pore diameters are fairly constant over the entire articular facet. However, the bar widths seem to become narrower towards the centre of the facet, thus, overall increasing the number of pores. Presumably this created more sites for more intercolumnal ligaments to be attached.

Remarks. The stem is most likely to be heteromorphic since the holotype is a cirrinodal. However, the holotype is the only columnal, so it is not possible to determine a noditaxis pattern.

The holotype suffered a few large cracks and a volume reduction following immersion in 3.6% hydrofluoric acid for one week when it was altered from calcite to calcium fluoride, but it has been repaired using acetone-dissolved Paraloid 72 glue crystals.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 34 gp. nov.

Plate 65, fig. a

Holotype. Specimen TCD.53021, a single columnal, of which one articular facet is clearly seen and the other end of the columnal is broken away. From Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (about 1 mm diameter) cylindrical columnals; crenularium with bulbous crenulae, areola concave, raised perilumen and narrow, central lumen, all are circular in outline.

Description. The columnal is circular in outline with a very distinct articular facet, and articulation is by symplexy. The crenularium has about ten very high and deep, bulbous, simple crenulae which slope adaxially into the areola at more than 45°. Their sides are almost parallel. The areola is a smooth, slightly concave channel between the raised crenularium and perilumen. The perilumen is a raised narrow rim with no sculpture. It is not as high as the crenulae of the crenularium. Transitions between these features are gradational. The lumen is central and circular in outline.

The latus is smooth and straight.

There are no cirrus-related structures.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*PR*	*LD*	*Ci*	*Ai*	*Pi*	*Li*	*No. crenulae*	*Extras*
TCD.53021	1289	167	224	62	385	26	35	10	30	10	SEM: ?IN

Remarks. Following its immersion in 3.6% hydrofluoric acid for one week the holotype suffered severe cracking. However, breakage only occurred after the specimen had been removed from the SEM. stub to which it was attached.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 35 gp. nov.

Plate 65, fig. b; Plate 66, figs a, b

Holotype. Specimen TCD.53022, a pluricolumnal of four ossicles, which has been deformed so that it is ellipsoidal transversely. Taken from Bed BD:E5, a dark grey, slightly silty, calcareous crinoidal shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8181 5963.

Material. Three paratypes, all pluricolumnals, specimen TCD.53023 comprising six ossicles, and specimens TCD.53024 and TCD.53025 both comprising two ossicles. All are well preserved, but also deformed transversely into an ellipse, and were taken from the type locality.

Diagnosis. Circular columnals of apparently homeomorphic stem; latus slightly convex, sometimes with low, equatorial ridge, sculpture of very small, randomly disposed tubercles; crenularium in two parts, outer crenularium planar with many simple, bifurcating and intercalated crenulae, inner crenularium gently sloping towards centre with origins of crenulae, both are circular in outline, central part of articular facet unknown.

Description. The columnals are circular in outline. Articulation is symplectial. The crenularium is in two parts, the outer one being planar and relatively wide, occupying about 50% of the articular facet, and the inner one being narrow and gently sloping

towards the centre of the columnal. Both are traversed by many high and deep, rounded crenulae. About thirty-seven crenulae originate on the inner crenularium and are simple here. Bifurcation is only observed on the outer crenularium along with intercalated and simple crenulae. The bifurcations and intercalations occur at various points across the outer crenularium, but bifurcations only occur once. About one-hundred-and-four to one-hundred-and-twenty-four crenulae terminate at the latus. The lumen is apparently central, but its outline cannot be seen on any specimen.

The latus is slightly convex on the holotype and on paratypes TCD.53024 and TCD.53025, but on paratype TCD.53023 a very small ridge is seen at columnal mid-height. However, this has an uneven surface and does not form an angulated longitudinal profile. The lateral surface of all columnals has a sculpture of very small, randomly disposed, low tubercles. The crenulate suture is fairly even and very fine with high and deep rounded apices and troughs, the sides of each 'wave' becoming straight so that they are parallel.

The columnals appear to be of uniform height within each pluricolumnal showing no differentiation. There is no evidence of any cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*OCR*	*ICR*	*LD*	*OCi*	*ICi*	*Li*	*KH*	*KHi*	*No. crenulae originating on inner crenularium*	*No. crenulae touching latus*	*Extras*
TCD.53024	6.1	1.6	?	?	52	?	?	2.7	44	about 36	about 124	Bin
TCD.53025	6.3	1.9	?	?	60	?	?	2.5	40	about 36	about 107	Bin
TCD.53022	6.5	2.1	?	?	65	?	?	3.3	51	about 38	about 104	Bin
TCD.53023	7.8	2.6	0.9	?	67	23	?	2.2	28	about 36	about 116	Bin

Stereom. The stereom is galleried (Plate 66, fig. b).

Remarks. It is inferred that the columnals were originally circular and were deformed into their present transverse outline during diagenesis.

It is suggested that the stem to which this type of columnal belonged was homeomorphic.

The holotype and the three paratypes were immersed in 40-45% hydrofluoric acid for nine-and-a-half minutes.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL TAXON NUMBER 36 gp. nov.

Plate 57, fig. b

Holotype. Specimen TCD.53026, a single, delicate columnal of which some is broken away and missing. From the Benbulben Shale Formation (Holkerian), taken from Locality CP3a, 3 m up from the base of the high cliff, which is made of an extensive black shale, on the west side of the bay in Carrickphatrick, Co. Sligo, GR 4366 3522. No further specimens have been collected for description.

Diagnosis. Moniliform columnals; latus smooth; narrow, circular, peripheral crenularium with very high and deep, rounded crenulae, areola circular at outer periphery, very wide, smooth and planar except at peripheries where it slopes gently upwards, vertical drop to tetragonal claustrum with rounded corners and slight incurves along long sides, lumen tetralobate with rounded corners, lobes coincident with corners of claustrum.

Description. The columnal is circular in outline. Articulation is symplectial. The crenularium is very narrow and peripheral with about seventy simple crenulae. The crenulae have rounded apices and troughs and are very high and deep so that the sides of the crenulae are parallel. Some are wider than others. The areola is very wide occupying over half of the articular facet. It is planar centrally, but slopes upwards at both its inner and outer edges where it meets the claustrum and the crenularium. The claustrum follows a vertical drop down from the edge of the areola. It is tetragonal in outline with rounded corners and incurves along the long sides. The lumen is tetralobate in outline with rounded corners and wide rounded lobes. The lobe extremities are coincident with the corners of the claustrum.

The latus is smooth and convex.

There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53026	7.3	0.4	2.2	0.5	1.1	11	60	14	15	1.2	16	about 70	Bin: ?IN

Remarks. Unusually, the lumen of this columnal type has tetrameral symmetry. This is not observed in any other columnals in the present study of Carboniferous material, and it deviates away from the pentaradiate echinoderm symmetry. The columnal

morphospecies *Tetragonocyclicus bifurcatus* Donovan 1989 (Ordovician) (Donovan 1989*a*, Text-fig. 34, D) also has a circular (-to highly rounded) outline with a tetragonal lumen.

The holotype was deemed too delicate to be put into the SEM.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL PLESION B pln. nov.

Type species. Columnal Taxon Number 37a gp. nov.

Other species. Columnal Taxon Number 37b gp. nov.; Columnal Taxon Number 38 gp. nov.; Columnal Taxon Number 39 gp. nov.

Diagnosis. Circular columnals of heteromorphic stem, nodals higher than internodals, nodals cirriferous or noncirriferous; latus straight to weakly convex, smooth or with sculpture of very small, low relief pimples around circumference on central 33% of latus; narrow, peripheral, circular crenularium with fifty-three to seventy-three simple crenulae, areola planar except at peripheries where it slopes gently upwards towards crenularium and/or perilumen (if present), inner boundary follows outline of perilumen, perilumen pentagonal to pentalobate in outline and coincidental with lumen seen as narrow, slightly raised or planar area surrounding lumen with sculpture of short crenula-like structures which may be inverted, if perilumen is not present a similar sculpture occupies the areola, lumen pentalobate with flattened lobe extremities and sharp to truncate angles, lobes are of different sizes.

Stratigraphical range of plesion. Arundian (Bundoran Shale Formation) to Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 37a gp. nov.

Plate 67, figs a, b

Holotype. Specimen TCD.53027, a pluricolumnal of four ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on

sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.53028, a single columnal, collected in the same sample as the holotype. Paratype TCD.53029, a single columnal, was collected from the top of Bed BD:L1, a bioclastic argillaceous limestone, near the middle of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8197 5919.

Diagnosis. Columnal Plesion B morphospecies with circular columnals of heteromorphic stem, nodals higher than internodals; latus slightly convex; narrow, peripheral, circular crenularium, with simple crenulae, areola circular and planar except at peripheries where it slopes gently upwards towards crenularium and perilumen, perilumen pentalobate in outline following outline of lumen, seen as narrow, raised boundary with sculpture of very short crenula-like structures, lumen pentalobate with blunt lobe extremities and pointed angles, lobes differ in their sizes.

Description. The columnals are circular in outline and are symplectially articulated. The peripheral crenularium is narrow with fifty-three to about sixty short, simple, regularly disposed crenulae that have high and deep, somewhat bulbous apices and troughs. The areola is smooth and planar, except at its inner and outer extremities, where it slopes up slightly towards the perilumen and crenularium respectively. Its inner outline follows that of the perilumen. The perilumen is pentalobate in outline and is seen as a slightly raised, narrow boundary following the outline of the lumen. It has an sculpture of short crenula-like structures, which can be seen on most specimens. The lumen is pentalobate in outline with fairly sharp angles and wide lobes with flattened extremities. The lobes are of slightly different sizes. Longitudinally, the lumen is concave.

The latus is smooth and weakly convex. The crenulate suture is regular and low with rounded apices and troughs.

The longest pluricolumnals give a noditaxis of 212N or 3231323N with the higher orders being greater in height. Measurements, in mm, of all columnals of the holotype pluricolumnal and their inferred noditaxial orders are inserted in the following table:

Holotype TCD.53027

KH	0.6	1.3	0.7	1.6
Order	2	1	2	N
Order	3	2	3	1

All columnals are non-cirriferous.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*PR*	*APR*	*LD*	*Ci*	*Ai*	*Pi*	*APi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53029	6.20	0.58	?	?	1.42	2.13	19	?	?	46	34	2.05	33	about 60	SEM: ?
TCD.53029	6.35	0.64	?	?	1.54	1.99	20	?	?	49	31	2.44	38	about 60	Bin: ?
TCD.53027	6.6	0.4	1.7	0.2	1.9	2.0	12	52	6	58	30	0.6	9	53	Bin: ?IN2
TCD.53028	8.5	0.6	1.7	0.2	1.9	3.5	14	40	5	45	41	2.3	27	58(57)	Bin: ?

Stratigraphical range. Arundian (Bundoran Shale Formation) to Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 37b gp. nov.

Plate 68, fig. a

Holotype. Specimen TCD.53030, a very well preserved pluricolumnal comprising two ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.53031, a pluricolumnal of three ossicles collected in the same bulk sample as the holotype.

Diagnosis. Columnal Plesion B morphospecies with circular columnals of heteromorphic stem, different orders with different heights; latus with sculpture of very small, low relief pimples around circumference; narrow, peripheral, circular crenularium with simple crenulae, areola circular, planar except at outer periphery where it slopes gently upwards, perilumen pentagonal in outline with rounded angles, angles coincidental with lumen lobes and planar with sculpture of short crenula-like structures, lumen pentalobate with flattened lobes and round to truncate angles, lobes differ in size.

Description. The columnals are circular in outline, and articulation is symplectial. The crenularium is narrow and peripheral with seventy-three simple, regularly disposed crenulae, which have high and deep rounded apices and troughs and parallel sides. The areola is smooth and planar, except at its periphery where it slopes upwards slightly to meet the crenularium. Its inner boundary follows that of the perilumen, which is rounded pentagonal in outline, its corners coinciding with the lobes of the lumen, and it is level with the plane of the areola. It has a sculpture of inverted short crenula-like structures, their long axes being radial. The lumen is pentalobate in outline with wide lobes, which differ slightly in their sizes. The lobes have slightly flattened extremities and three of the angles are rounded and two are truncate. The lumen is concave longitudinally.

The latus is straight with a sculpture of very small, low relief pimples, which run around the whole circumference. They only appear to cover the central 33% of the latus. The crenulate suture is regular, low and rounded to angular.

The noditaxis has at least two orders with the higher order being greater in height, but it is not known what orders they are. Measurements, in mm, of all columnals of paratype TCD.53031 pluricolumnal and their inferred noditaxial orders (six possibilities) are inserted in the following table:

Paratype TCD.53031

KH	2.8	0.8	1.4
Order	N	2	1
Order	N	3	2
Order	N	4	3
Order	1	3	2
Order	1	4	3

The facetal morphometrics remain the same on the two columnal orders visible in specimen TCD.53030. There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*PR*	*LD*	*Ci*	*Ai*	*Pi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53031	4.6	0.35	?	?	1.78	15	?	?	39	2.8	61	40	Bin: ?N
TCD.53030	10.5	0.9	1.4	0.95	4.0	17	27	18	38	2.0	19	73	Bin: at least IN2

Remarks. The paratype TCD.53031 is inferred to be an immature specimen of the columnal morphospecies. With growth the number of crenulae on the crenularium increases, while the proportion of the facet that the lumen and crenularium occupy remain constant.

The holotype was immersed in 40-45% hydrofluoric acid for three minutes. Following this the specimen was immaculately clean for examination. Paratype TCD.53031 was scrubbed using a toothbrush in a weak solution of household detergent and then immersed in 30% by volume hydrogen peroxide for five minutes.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 38 gp. nov.

Plate 57, figs e, f; Plate 68, fig. b; Plate 69, figs a, b; Figures 6.17-6.22

Holotype. Specimen TCD.53032, a very well preserved pluricolumnal of two ossicles, with a crack extending from one pentalobe of the lumen to the latus. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.35954, a pluricolumnal of one-hundred-and-twelve ossicles along which there are several sites of disarticulation. It has been successfully glued back together exactly as it was found using epoxy resin. The terminal columnal at the proximal end reveals the articular facet. Collected in the summer of 1999 by Stuart Bennett from a calcareous, muddy shale at the type locality. Paratypes TCD.53033, a pluricolumnal of four ossicles and TCD.53034, a pluricolumnal of six ossicles and paratype TCD.53035, a single columnal which is broken so that a longitudinal section can be seen. All these paratypes were taken from the same bulk sample as the holotype.

Diagnosis. Columnal Plesion B morphospecies with circular or unevenly rounded pentagonal columnals, heteromorphic stem with noditaxis of up to six orders, height increasing with order, nodals to tertinternodals may be cirriferous; latus smooth; circular crenularium slightly wider on one radius, crenulae mainly simple, few bifurcating and intercalated crenulae, circular areola slightly eccentric, at level of articulation, sculpture of fine tubercles and apposing pits, slightly eccentric lumen pentalobate with rounded to flattened lobes and rounded to truncate angles, lobes differ in size.

Description. The columnals are essentially circular in outline with symplectial articulation.

However, a rounded pentagonal, or uneven, appearance is produced by the disposition of cirrus-related structures in columnals where they occur. The crenularium is slightly wider on one radius so that the areola and lumen are positioned eccentrically, although the lumen is positioned centrally relative to the areola. The crenularium has thirty-nine to sixty-two crenulae originating at the areola and thirty-nine to about ninety-two terminating at the latus. They are simple, bifurcating or peripherally intercalated, the latter often being quite long and almost reaching the inner boundary of the crenularium, especially on smaller the specimen TCD.53034. Some seem to have just finished bifurcating as they are almost the full radius of the crenularium, but, in pairs, are bending towards each other at the inner end. Some crenulae impose further into the areola than others. The culmina are fairly regularly disposed with moderately high and deep rounded apices and troughs. They have steeply inclined, but not parallel, sides. Some are wider than others. The areola is circular in outline and at the level of articulation. Its inner boundary follows that of the lumen. It has a sculpture of many small, irregularly disposed tubercles that may be inverted to receive tubercles of the apposing facet. The lumen is pentalobate in outline with rounded to slightly flattened lobes and the angles are rounded to truncate. The lobes differ in their sizes. Longitudinally, the lumen is straight as seen in the longitudinal section of specimen TCD.53035.

The latus is straight to slightly convex and smooth, except where cirrus-related structures occur. The crenulate suture is uneven with high and deep apices and troughs that are rounded.

The noditaxis of this stem type can be deciphered from the paratype TCD.35954. The higher the order and the more distal the noditaxis the greater the height of the columnal (Figures 6.17-6.19). However, the latter theory does not appear to apply to nodals whose trend is to decrease overall in height distally (Figures 6.17-6.19). There are no other differences in lateral or articular facetal morphology between orders and the stem does not taper, at least not along the length of this paratype portion. The noditaxes patterns for the paratype TCD.35954 are as follows:

Noditaxis number	*Noditaxis*	*Additional comments*
1	2434N	five orders, incomplete due to missing portion
2	32314342434N	five orders, but lacking four IN4's
3	434243414342434N	five orders, complete
4	32341434234N	five orders, but lacking four IN4's
5	434243414342434N	five orders, complete
6	4342434143424345N	six orders, but only one IN5
7	434243414342434N	five orders, complete
8	434243414535425453	six orders, but only four IN5's, also incomplete due to missing portion

This is a Type IV to Type V noditaxis pattern of Webster (1974) and is very regular (see Figure 6.16). Measurements, in mm, of all columnals of paratypes TCD.53033 and TCD.53034 pluricolumnals and their inferred noditaxial orders are inserted in the following tables:

Paratype TCD.53033

KH	1.8	2.7	2.0	2.3
Order	2	N*	2	1

Paratype TCD.53034

KH	1.3	1.0	3.0	0.8	1.3	0.7
Order	1	2	N*	2	1	2

Cirrus-related structures do not occur on the holotype. However, all the paratypes do have such structures. Paratype TCD.53033 has four abortive cirri, three being aligned with lobes of the lumen, consistent with pentaradiate symmetry, and one being aligned with neither lobes or angles of the lumen. Paratype TCD.53034 has three abortive cirri disposed on the nodal at positions consistent with pentaradiate symmetry. There is also a single cirrus socket, which is not aligned with lobes or angles of the lumen. It is orientated normal to the latus and is raised away from it. The articular facet has a diameter of 1.4 mm and is circular in outline with eighteen simple crenulae on the crenularium, which are of unknown length. The remainder of the facet is unclear. Paratype TCD.53035 has a single cirrus socket with probably just a single zygocirral still articulated. The diameter of the zygocirral articular facet is about 1 mm at its distal end. It tapers gradually to this point. All that can be seen of the morphology is that the crenularium covers about 66% of the facet and this surrounds a central circular ?lumen which is straight down. Paratype TCD.35954 has cirrus-related structures disposed on all nodals, priminternodals, most secundinternodals and uncommonly on tertinternodals (Figures 6.20). The details of these are given fully in Figure 6.21. From this figure it can

be seen that cirrus-related structures, most of which appear to be abortive cirri, are disposed along position 3 on the diagram with their numbers decreasing at either side of this along positions 4 and 2 with even fewer in positions 5 and 1. Where cirrals occur they are directed obliquely outwards and generally upwards (Figure 6.22). Their articular facets are similar to those on the holotype. Where cirrus sockets have a large diameter the columnal increases in height directly both above and below. In addition, some of the larger cirrus sockets have wrinkles around their bases. At the distal end of the paratype stem section a fossula is present. However, it does not appear that it was connected to a cirrus as there is no evidence of a socket, although there is an uneven and irregular depression around the opening. The fossula opening disturbs the heights of the columnals below and above. In the vicinity immediately surrounding the opening the columnal below increases in height as the one above decreases.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.53034	6.46	1.53	0.76	1.88	47	24	29	1.3	20	39	39	Bin: IN1
TCD.53033	9.5	1.25	1.88	3.24	26	40	34	1.8	19	59	59	Bin: IN2
TCD.53032	10.6	1.5	2.11	3.38	28	40	32	2.0	21	70	70	Bin: ?IN
TCD.53035	about 11.5	about 1.9	?	?	about 33	?	?	1.8	about 16	?	?	Bin: IN
TCD.35954	13.8	2.23	2.2	4.94	32	32	36	2.5	18	62	about 92	Bin: IN3

Noditaxial indices for specimen TCD.35954. # indicates that the measurement was gained by averaging when columnals were missing.

Noditaxis	*NHy*	*NTHy*	*INHy*	*Ni*	*INi*
1	3.0	?	?	?	?
2	3.6	#31.0	#27.4	#11.61	#88.39
3	3.0	32.4	29.4	9.26	89.68
4	3.2	#31.0	#27.8	#10.32	#89.68
5	3.0	35.2	32.2	8.52	91.48
6	3.1	38.1	35.0	8.14	91.86
7	3.0	35.3	32.3	8.50	91.50
8	#3.1	#47.6	#44.5	#6.51	#93.49

Remarks. Paratype TCD.35954 has a total length of 230 mm. It has eight noditaxes, *1* and *8* being incomplete by loss during taphonomy, and seven or eight columnals were lost from the distal end during collection (see Plate 69, figs a, b). It was extracted from a steep outcrop just above the sheep tracks. It was deposited horizontally in the shale horizon.

The changing width of the areola apparently is not influenced by the positioning of the cirri and the lumen lobes.

A finely tuberculate sculpture on the areola of *Cyclocaudex typicus* Moore and

Noditaxis portion *1*	*2*	*3*	*4*
N=3.0	N=3.6	N=3.0	N=3.2
IN1=x	IN1=2.6	IN1=2.9	IN1=2.6
IN2=2.5	IN2=(2.3 to 2.6)=2.45	IN2=(2.5 to 2.6)=2.55	IN2=(2.5 to 2.6)=2.55
IN3=2.0	IN3=(1.9 to 2.1)=1.95	IN3=(2.0 to 2.1)=2.08	IN3=(1.9 to 2.0)=1.98
IN4=(1.5 to 1.7)=1.6	IN4=(1.5 to 1.6)=1.525	IN4=(1.6 to 1.7)=1.64	IN4=(1.5 to 1.6)=1.53

5	*6*	*7*	*8* (distal)
N=3.0	N=3.1	N=3.0	N=x
IN1=2.7	IN1=2.9	IN1=2.8	IN1=3.0
IN2=2.7	IN2=2.8	IN2=(2.7 to 2.9)=2.8	IN2=(2.6 to 2.9)=2.75
IN3=(1.9 to 2.1)=2.03	IN3=(2.2 to 2.3)=2.28	IN3=(2.1 to 2.3)=2.23	IN3=(2.3 to 2.5)=2.38
IN4=(1.5 to 1.7)=1.6	IN4=(1.6 to 1.8)=1.73	IN4=(1.4 to 1.8)=1.64	IN4=(1.7 to 1.9)=1.8
	IN5=1.4		IN5=(1.3 to 1.4)=1.38

a.

b.

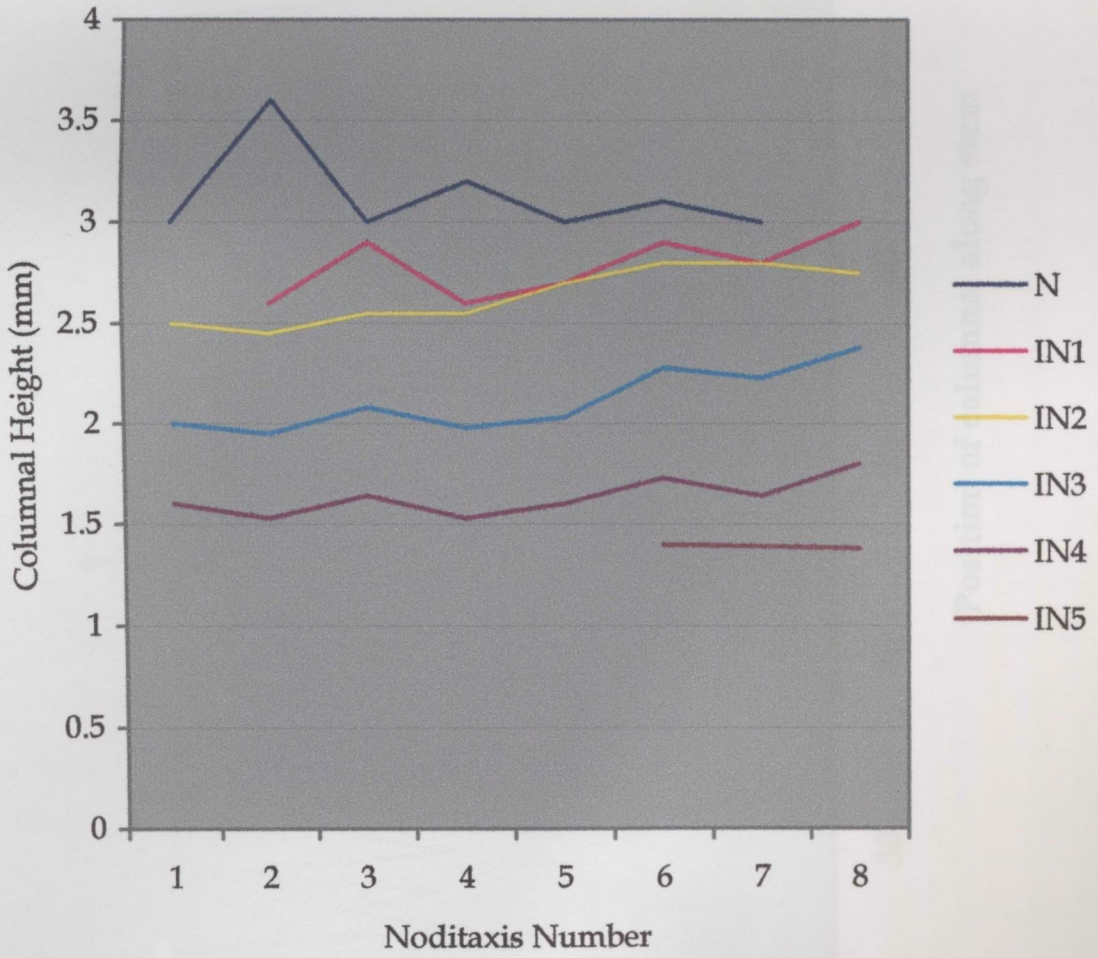


Figure 6.17. *a* and *b*. *a*. Table showing mean columnal heights (in millimetres) of orders within each of the eight noditaxes of specimen TCD.35954. Those numbers in brackets show the range of heights of that columnal order within that particular noditaxis. x=columnal(s) not present due to incomplete noditaxis or missing portion. Noditaxis portion *1* is the most proximal pluricolumnal section. *b*. Data from table displayed in a graph. Notice that there is an overall trend for the mean height of each of the columnal orders to increase in height a) distally along the stem, and b) as the order becomes higher. An exception to this is the nodal heights whose heights appear to decrease distally.

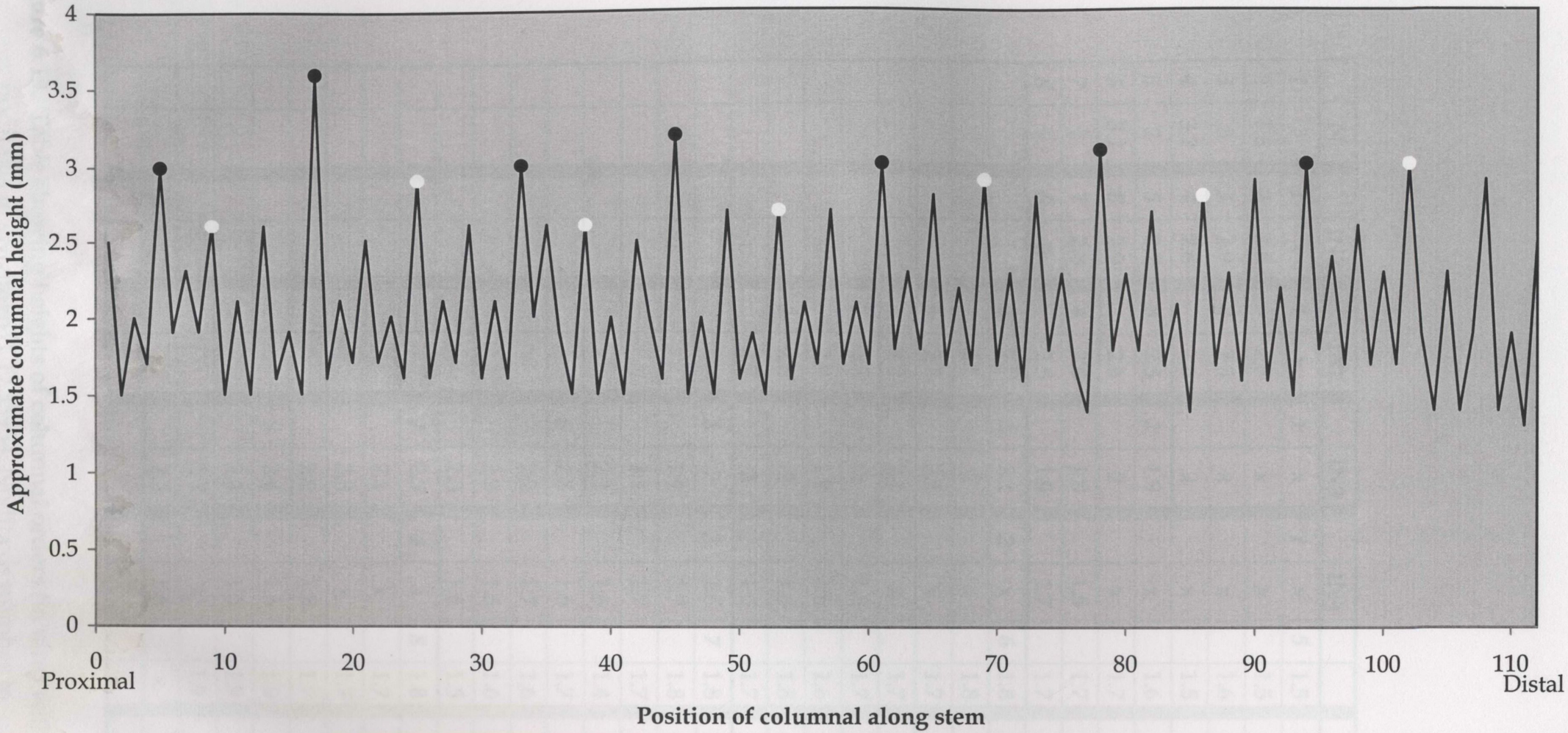


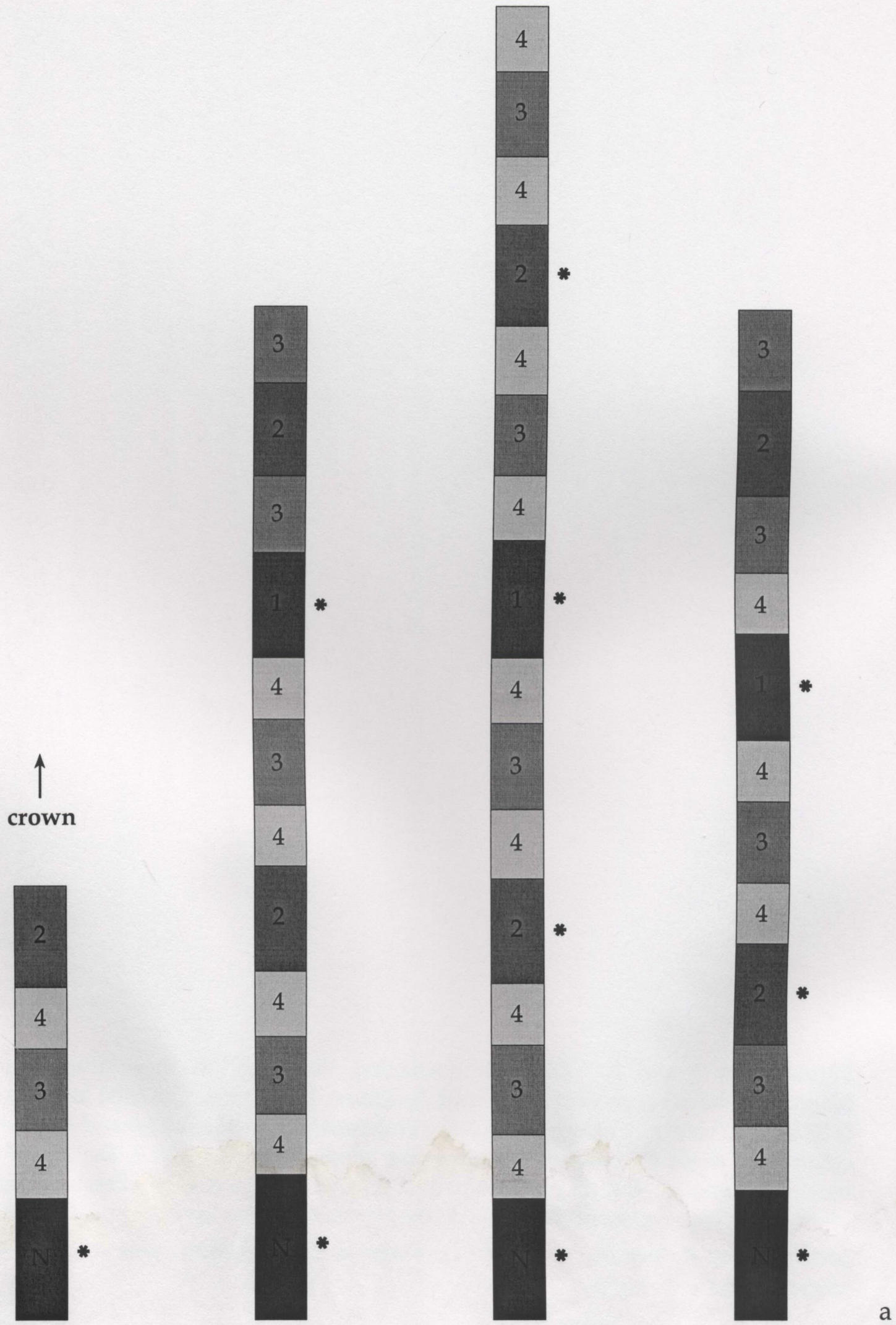
Figure 6.18. Graph showing change in columnal height along stem portion, specimen TCD.35954. Black dots indicate nodals, white dots indicate priminternodals (graphical method after Simms 1989).

	N		IN1		IN2		IN3		IN4				IN5
1	3	***1***	x	***1***	x	***1***	x	***1***	x	***5***	1.5	***6***	x
2	3.6	***2***	2.6		2.5		x		x		1.5		x
3	3	***3***	2.9	***2***	2.3		x		x		1.6		x
4	3.2	***4***	2.6		2.6		2		x		1.5		x
5	3	***5***	2.7	***3***	2.5	***2***	1.9		x		1.6		x
6	3.1	***6***	2.9		2.6		2		x		1.7		x
7	3	***7***	2.8	***4***	2.6		1.9		1.5		1.7		x
8	x	***8***	3		2.5		1.9		1.7		1.7		x
				5	2.7	***3***	2.1	***2***	x	***6***	1.8		x
					2.7		2		x		1.8		x
				6	2.8		2.1		x		1.7		x
					2.8		2.1		x		1.7		x
				7	2.7	***4***	2		1.5		1.7		x
					2.9		1.9		1.5		1.6		x
				8	2.6		2		1.6		1.8		x
					2.9		2		1.5		1.7		1.4
						5	2	***3***	1.6	***7***	1.8	***7***	x
							1.9		1.7		1.8	***8***	x
							2.1		1.7		1.7		x
							2.1		1.6		1.4		x
						6	2.3		1.6		1.7		x
							2.2		1.7		1.6		x
							2.3		1.6		1.6		x
							2.3		1.6		1.5		x
						7	2.3	***4***	x	***8***	1.8		x
							2.1		x		1.7		x
							2.3		x		1.7		1.4
							2.2		1.5		1.7		1.4
						8	2.4		1.5		1.9		x
							2.3		1.5		1.9		1.4
							2.3		x		1.9		1.3
							2.5		1.6		x		x
													x

Figure 6.19. Table showing heights of columnal orders (in mm) within each noditaxis in specimenTCD.35954. Noditaxis number in bold-italics. Measurements in plain text.

Figure 6.20. *a* and *b*. Diagram displaying the variation in noditaxis pattern for a heteromorphic stem section taken from specimen TCD.35954. The total length of the section is 23.04 cm (vertically exaggerated here) and there are one-hundred-and-twelve component columnals. Eight portions of noditaxes are labelled here as *1* to *8*, the top of *1* being the most proximal portion of the section and the base of *8* the most distal. In each noditaxis N=nodal, 1=priminternodal, 2=secundinternodal etc., with lower orders getting progressively lighter in colour on the diagram. * indicates those columnals possessing cirrus-related structures.

1 *2* *3* *4*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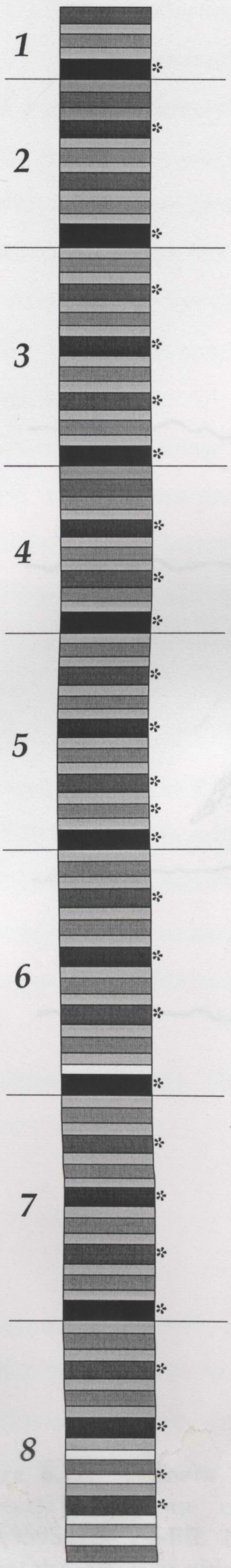
4 3 4 2 * 4 3 4 1 * 4 3 4 2 * 4 3 4 N *
4 3 4 2 * 4 3 4 1 * 4 5 3 * 5 4 2 * 5 4 5 3
b

Figure 6.21. Diagram showing entire section of specimen TCD.35954 (see text and previous diagram for information on specimen and colour coding for columnal noditaxis orders). * indicates columnals with cirrus-related structures that are explained in the adjacent table. Numbers in italic type down left-hand side of stem section represent noditaxis number. Numbers in plain type across top of table each represent five points around a circumference where cirrus-related structures may be disposed. Each is aligned with one of the five lobes of the lumen so are positioned at approximately 72° from each other. Position 3 is used as a reference point since this is the position in which most cirrus-related structures are disposed. The specimen is rotated in a clockwise direction through 360° intercepting positions 3, 4, 5, 1 and 2 in turn. Measurements in the table represent the approximate diameter of cirrus sockets, even when zygocirrals are articulated, and the base of abortive cirri. Diagram is approximately to scale.



← clockwise

5	4	3	2	1
	2.5 mm - zygocirral	1.3 mm - cirrus socket	low, rounded	
	5.0 mm - zygocirral			
	abortive cirrus		4.0 mm - zygocirral + 1 cirral	
		2.2 mm - zygocirral + 1 or 2 cirrals		
abortive cirrus	2.5 mm - zygocirral + 1 or 2 cirrals	0.8 and 1.3 mm - two cirrus sockets, each with 1 or 2 cirrals		abortive cirrus
	abortive cirrus	abortive cirrus		
	abortive cirrus	3.8 mm - zygocirral		
abortive cirrus	3.5 mm - zygocirral	2.0 mm - zygocirral		
		abortive cirrus		
	abortive cirrus			abortive cirrus
	abortive cirrus	abortive cirrus		
		abortive cirrus	abortive cirrus	
	2.5 mm - zygocirral	abortive cirrus		
		2.0 mm - abortive cirrus		
	low, rounded	abortive cirrus	abortive cirrus	
		1.8 mm - zygocirral + ?1 cirral		
	low, rounded	1.8 mm - zygocirral		
abortive cirrus	cirripore	3.0 mm - zygocirral + ?1 cirral		
abortive cirrus	cirripore	3.5 mm - zygocirral + ?1 cirral		low, rounded
	3.5 mm - zygocirral + ?1 cirral	1.2 mm - ?zygocirral	low, rounded tubercle with central	
	2.5 mm - zygocirral + ?1 cirral	2.5 mm - zygocirral + ?1 cirral	abortive cirrus	
abortive cirrus		2.5 mm - zygocirral + ?1 cirral	2.5 mm - abortive cirrus	
low, rounded tubercle	low, rounded tubercle	2.0 mm - abortive cirrus	2.0 mm - abortive cirrus	
		3.0 mm - zygocirral + 1 or 2 cirrals		
	low, rounded tubercle	3.0 mm - zygocirral + ?1 cirral		
			fossula opening, not aligned with cirri	
low, rounded tubercle	low, rounded tubercle	2.0 mm - abortive cirrus	low, rounded tubercle with central	abortive cirrus

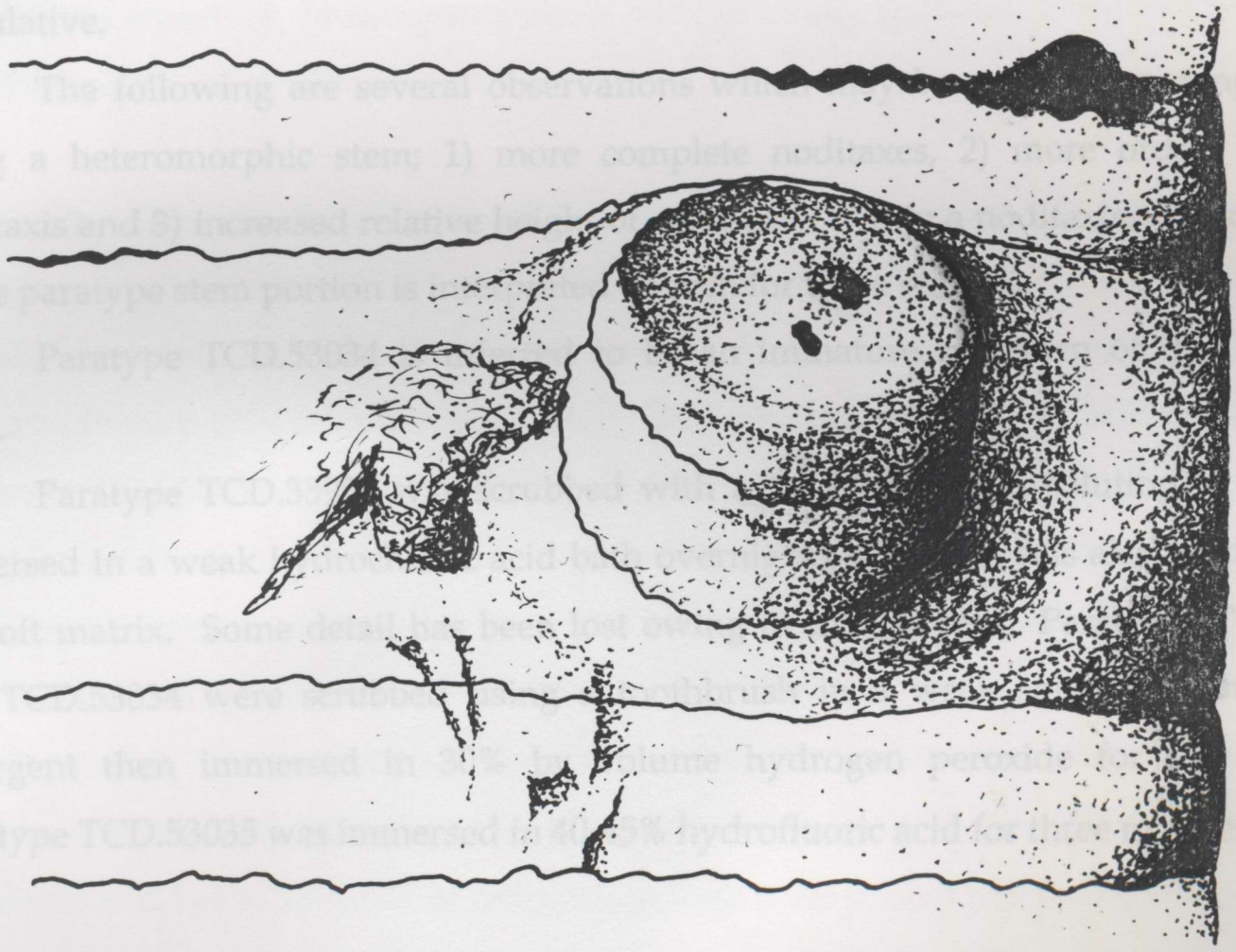


Figure 6.22. Camera lucida drawing of a cirrus socket, of 4.0 mm diameter, with zygocirral and one cirral still articulated on a columnal of specimen number TCD.35954/38.V4-BB. Note how socket is circular, but the two cirrals are wedge-shaped so that the cirri was able to have direction, upwards in this case, when fully articulated.

Jeffords, 1968 (Virgilian (Upper Pennsylvanian), Texas) (Moore and Jeffords 1968, Plate 17, fig. 4*a*) is similar to that seen on Columnal Taxon Number 38 herein.

The concentration of cirri along one side of the stem could suggest that the crinoid had a reclined lifestyle similar to the extant isocrinids *Cenocrinus asterius* (Linné) and *Endoxocrinus parrae* Gervais. Macurda and Meyer (1974) describe how these two species anchor to the substrate using four or five groups of cirri, with terminal claws, which continue along the stem, mainly along one side, until it bends and becomes upright. Cirri are also situated on the upright part of the stem and no other method of attachment is used. Until a longer portion of the stem described is found this conjecture is merely speculative.

The following are several observations which may be expected moving distally along a heteromorphic stem; 1) more complete noditaxes, 2) more orders within a noditaxis and 3) increased relative height of columnals within a noditaxis. The distal end of the paratype stem portion is interpreted as such for these reasons.

Paratype TCD.53034 is inferred to be an immature specimen of this columnal Type.

Paratype TCD.35954 was scrubbed with a toothbrush in a solution of Jif® then immersed in a weak hydrochloric acid bath overnight. A needle was also used to rid of the soft matrix. Some detail has been lost owing to this process. Paratypes TCD.53033 and TCD.53034 were scrubbed using a toothbrush in a weak solution of household detergent then immersed in 30% by volume hydrogen peroxide for five minutes. Paratype TCD.53035 was immersed in 40-45% hydrofluoric acid for three minutes.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 39 gp. nov.

Plate 70, figs a, b

Holotype. Specimen TCD.53037, a very well preserved pluricolumnal of three ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.53038, a pluricolumnal of five ossicles. Paratypes TCD.53039 and TCD.53040, single columnals. All were collected in the same bulk sample as the holotype.

Diagnosis. Columnal Plesion B morphospecies with circular or unevenly rounded pentagonal columnals of heteromorphic stem, nodals higher than internodals and cirriferous; latus smooth and straight, may have upflaring extremities; circular crenularium slightly wider on one side, many simple, bifurcating and peripherally intercalating crenulae which are horizontal with abrupt inner terminations, areola eccentric, much depressed below level of articulation, circular and planar, fine tubercles to vermiculate sculpture, lumen pentalobate with generally flattened lobes and truncate or rounded angles, lobes differ in size.

Description. The columnals are circular in outline or may be unevenly pentagonal where cirrus-related structures occur on the latus. They are symplectially articulating. The crenularium occupies about 30% of the articular facet. Crenulae are simple, bifurcating and peripherally intercalated. Essentially they are regularly disposed, but as seen on specimen TCD.53038 especially, their widths may change so that in certain areas the crenulae look 'fatter'. There are fifty-two to fifty-six crenulae originating adjacent to the areola and fifty-nine to sixty-five touching the latus. Crenulae are medium heights and depths with evenly rounded apices and troughs. However, they have steep sides that are almost parallel. Their relief is constant across the crenularium, until they reach the inner boundary where they terminate abruptly with a very steep slope. The areola is planar and depressed below the level of articulation with a very steep peripheral slope upwards to the crenularium. Its entire surface is covered with a finely tuberculate to vermiculate sculpture. Its inner boundary follows the outline of the lumen. The lumen is pentalobate in outline with rounded to slightly flattened lobes and rounded to truncate angles. The lobes are of different sizes. Laterally the lumen is straight.

The latus is straight, but the top and bottom edges flare out slightly adjacent to the suture on specimen TCD.53038. The crenulate suture is a regular zigzag which is rounded and with a low amplitude.

The smallest columnal of the holotype (whose morphometrics are displayed in the table below), which is positioned at one end of the pluricolumnal, is 0.6 mm high, the central one is higher and the highest is positioned at the other end. The highest columnal is wedge-shaped. The central columnal becomes lower from above and below to about

half of its original height at one position, but it is not known why this occurs. This represents an incomplete noditaxis as a lower columnal should ideally be situated between the ?nodal and the adjacent internodal (of 1.4 mm high). The columnals are of different heights, but in a regular pattern, in paratype TCD.53038 giving a probable noditaxis of 212N with nodals being higher than internodals and cirriferous. However, a priminternodal bears cirrus-related structures also. Measurements, in mm, of all columnals of the holotype and paratype TCD.53038 pluricolumnals and their inferred noditaxial orders are inserted in the following tables:

Holotype TCD.53037

KH	0.6	1.4	2.9
Order	?	?	?N*

Paratype TCD.53038

KH	1.7	2.7	1.7	2.3	1.7
Order	2	N*	2	1*	2

On the holotype the highest columnal has cirrus-related structures disposed at five positions which are fairly equally spaced around the circumference, each aligned with a lobe of the lumen and positioned at columnal mid-height. All the structures are of different diameters. A large cirrus socket occupies one, three have a zygocirral perhaps with one further cirral and one has a large abortive cirrus. Each is disposed at columnal mid-height. Those sockets with cirrals attached have them directed obliquely outwards, either upwards or downwards. The morphology of the cirrus socket cannot be fully seen, but a crenularium with about twenty-four simple crenulae occupies 66% of a concave facet. One cirral articular facet has a similar morphology, but is narrower and therefore has fewer crenulae. The nodal and priminternodal on paratype TCD.53038 each have five cirrus-related structures, three abortive cirri and two cirrus sockets, which are each aligned with the lobes of the lumen. Those of the priminternodal are all positioned at columnal mid-height, but those of the nodal are all close to columnal mid-height. The morphologies of the cirrus socket articular facets are unclear. A curious large tubercle appears between the cirrus-related structures close to columnal mid-height on the opposite side. It resembles one of the larger abortive cirri, but whether it is one or not is questionable. Paratype TCD.53039 has a single abortive cirrus and two cirrus sockets occupying three successive pentaradiate positions and all positioned at columnal mid-height. The sockets both measure about 2.5 mm across their articular facets and are

overall concave. On one about seventeen crenulae of the crenularium can just about be deciphered and some are seen on the other also, but the remainder of articular facets are unclear. Paratype TCD.53040 has a single cirrus socket at columnal mid-height which is aligned with a lobe of the lumen. It measures about 1 mm in diameter across its distal articular facet. However, details of the facet cannot be clearly seen, although it appears that the lumen may be dilobate in outline.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.53038	5.85	0.78	1.27	1.76	27	43	30	1.7	29	46	47	Bin: IN2
TCD.53037	8.6	1.73	1.32	2.5	40	31	29	0.8	9	52	65	Bin: ?IN3
TCD.53040	9.06	1.60	1.49	2.88	35	33	32	2.3	25	52	54	Bin: ?N
TCD.53039	10.33	1.78	1.65	3.48	34	32	34	3.0	29	56	59	Bin: ?N

Remarks. Twenty-four crenulae on the crenularium of a cirrus socket on the holotype is a lot compared with other cirrus sockets belonging to other types of stem.

This morphospecies is very similar to *Cyclopentagonopa granulosa* Moore, 1939 (p. 190, Plate 1, Figures 1*a*, *b*) from the Sam Creek Limestone Member of the Savanna Formation, (Desmoinesian; Pennsylvanian) Oklahoma.

All three paratypes were immersed in 40-45% hydrofluoric acid for three minutes to remove occluding matrix.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

Discussion. Some of the morphospecies belonging to Plesion B herein have similar characters to some morphospecies belonging to the morphogenus *Floricyclus* of Moore and Jeffords (1968). Specimen TCD.53030 resembles *F. hebes* in its articular facet, but the latus of *F. hebes* has no sculpture. Specimens TCD.53027 and TCD.53028 resemble *F. pulcher* in both their articular facet and latus morphologies. *F. hebes* was described from the Mingus Shale, Texas and *F. pulcher* from the Cabaniss Formation, Kansas. Both are Desmoinesian (Middle Pennsylvanian) in age. However, all more closely resemble variations of articular facets belonging to *Floricyclicus granulosus* Moore and Jeffords, 1968 (Virgilian (Upper Pennsylvanian), Texas) (Moore and Jeffords 1968, Plate 26, figs 9-13).

COLUMNAL TAXON NUMBER 40 gp. nov.

Plate 71, fig. a

Holotype. Specimen TCD.53041, a pluricolumnal of five ossicles with a fragment missing from one end. However, this fragmentation means that a longitudinal section can be seen. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Cylindrical columnals of heteromorphic stem, nodals higher than internodals and cirriferous; latus smooth and straight; crenularium with many simple, bifurcating and peripherally intercalated crenulae, lumen very small, both are circular.

Description. The columnals are circular in outline, have a low columnal height index and are symplectially articulating. The articular facet is simple with only a lumen and a crenularium, both of which occupy about 50% of the facet. The crenularium has many fine crenulae which are narrow and fairly shallow and with slightly rounded apices and troughs. Seventy-one crenulae originate next to the lumen. These are simple, peripherally intercalated (which may be long or short), or bifurcating once or twice so that about one-hundred-and-thirteen crenulae terminate at the latus. The lumen is longitudinally concave.

The latus is straight with no sculpture. The crenulate suture is coarse, high and deep with some flattened apices and troughs and almost turreted in some places.

The noditaxis from the holotype is at least 212N with nodals being higher than internodals. Measurements, in mm, of all columnals of the holotype pluricolumnal and their inferred noditaxial orders are inserted in the following table:

Holotype TCD.53041

KH	1.7	1.9	1.7	2.0	1.7
Order	2	1	2	N*	2

The nodal of the holotype has one abortive cirrus, which is deposited close to columnal mid-height. A nodose cirrus-related structure occurs between the nodal and final

secundinternodal. This is probably the outer impression of a fossula.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*LD*	*Ci*	*Li*	*KH*	*KHi*	*No. crenulae touching lumen*	*No. crenulae touching latus*	*Extras*
TCD.53041	11.15	2.9	5.35	52	48	1.7	15	71	about 113	Bin: IN2

Remarks. The articular facet of *Lomalegnum hormidium* Moore and Jeffords, 1968 (Osagian (Lower Mississippian), Iowa) (Moore and Jeffords 1968, Plate 13, fig. 2*a*) is similar in size and .

The holotype was scrubbed using a toothbrush in a weak solution of household detergent. It was then immersed for five minutes in 30% by volume hydrogen peroxide.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 41 gp. nov.

See Columnal Plesion D.

COLUMNAL PLESION C pln. nov.

Type species. Columnal Taxon Number 42a gp. nov.

Other species. Columnal Taxon Number 42b gp. nov.

Diagnosis. Moniliform columnals, distinctly heteromorphic stem; latus distinctly convex, smooth, large cirrus sockets impress onto adjacent columnals or cause heightening of columnal and lowering of adjacent columnals; circular crenularium with mostly simple, but also peripherally intercalated and bifurcating, culmina may be curiously incomplete or trifurcating, areola with sculpture or convex claustrum, lumen generally rounded pentagonal, all are positioned centrally.

Stratigraphical range of plesion. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 42a gp. nov.

Plate 72, figs a, b; Plate 73, figs a, b; Plate 74, figs a, b; Plate 75, figs a, b

Holotype. Specimen TCD.53043, a pluricolumnal of ten ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.53044, a pluricolumnal of twelve ossicles, taken from the same bulk sample as the holotype.

Diagnosis. Columnal Plesion C morphospecies, noditaxis of three orders, nodals commonly cirriferous; large cirrus sockets impress onto adjacent columnals; incomplete culmina appose grooves on bifurcating culmina, lumen rounded pentagonal in outline, central with straight sides.

Description. The columnals are circular in outline with symplectial articulation. The circular crenularium occupies just over a third of the total articular facet diameter. It has twenty-six to about fifty-five crenulae touching the areola and about forty-two to about fifty-nine touching the latus. They are mainly simple and vary in their widths. Bifurcating and peripherally intercalated crenulae also occur. On the measured facet of the holotype incomplete culmina are intercalated between each entire culmen. These incomplete culmina are narrower than the entire culmina. A small peripheral culmen is followed, moving adaxially, by a space and then a further portion of culmen, which reaches in as far as the entire culmina. This inner culmen may have a separated node at its outer extremity. The inner culmina are all about the same length, as are the peripheral culmina, and they are lower in height than the wider culmina. Only a single peripherally bifurcation occurs on one culmen. On the opposing facet bifurcating culmina with elongate, irregular apical grooves mark where the incomplete culmina would have been positioned when articulated with an apposing columnal. On paratype TCD.53044 similar incomplete culmina are seen on one facet, but they are less complete and are more irregular and fewer. Overall, the crenulae are very high and deep with rounded apices and troughs. Their sides are very steep so that they are almost parallel. They slope

gradually downwards in towards the areola. The areola has a circular outer boundary, but its inner boundary follows that of the lumen. It is planar with a coarse sculpture of ?vermiculae. The lumen has a rounded pentagonal outline that can be clearly seen on the holotype. It has straight sides.

The latus is convex and smooth, except when cirriferous. The crenulate suture is coarse with a high amplitude, but is irregular. Depressions can be seen in the apices and troughs where the grooves of crenulae occur.

The pluricolumnals are distinctly heteromorphic. From the two specimens the noditaxis is clearly a 212N arrangement. Some nodals are cirriferous and they are distinctly higher and more convex than the internodals, which are less in height. Measurements, in mm, of all columnals of the two pluricolumnal specimens and their inferred noditaxial orders are inserted in the following tables:

Holotype TCD.53043

KH	1.6	0.8	1.2	0.8	1.5	0.8	1.2	0.9	1.8	0.9
Order	N*	2	1	2	N	2	1	2	N*	2

Paratype TCD.53044

KH	1.7	1.0	1.3	0.8	1.9	0.9	1.3	0.8	1.5	0.8	1.2	1.7
Order	N*	2	1	2	N	2	1	2	N*	2	1	N*

Cirrus sockets occur on several of the nodals, but not all. The holotype has two sockets on the terminal nodal. They are positioned at about 144° from each other so show evidence of pentaradiate symmetry. One socket measures 2.2 mm in diameter and is overall slightly concave. The crenularium occupies about 40% of the articular facet diameter. It has twenty-two irregularly disposed crenulae, which are mostly simple. A smooth, gently concave areola reaches down to a small, centrally disposed, circular lumen. The facet is higher than the nodal on which it is disposed and is positioned close to columnal mid-height, so that it is impressed onto the adjacent columnal. The facet is directed obliquely outwards and either upwards or downwards. The second facet on this nodal has a diameter which is just less than the height of the columnal and is again disposed close to columnal mid-height. It still has a zygocirral articulated whose crenularium can be seen to have both simple and peripherally intercalated crenulae. However, the remaining facet morphology is unclear. It is distinctly cuneate with the highest side positioned laterally rather than upwards or downwards. The cirrus socket itself also protrudes outwards more on one side than the other, this side coinciding with the highest side of the

zygocirral. The single cirrus socket on the other cirrinodal has a diameter of 2.2 mm and has a similar articular facet morphology to that of the other sockets on this pluricolumnal. It is aligned with neither of them, but is positioned at 72° from one of them. Paratype TCD.53044 has a single cirrus socket on three of its nodals, none of which are aligned, but all of which are disposed at positions that are consistent with pentaradiate symmetry. All are similar to those of the holotype. The one belonging to one terminal nodal, however, is very clear and the stereom can be seen. It measures 1.5 mm in diameter, is slightly concave and has small amount of relief away from the columnal latus. The crenularium radii measure about 0.2 mm across. It has about twenty-one probably simple crenulae that have high and deep rounded apices and troughs, much like those of the columnal articular facet itself. The areola is gently concave and surrounds a central, small, apparently dilobate lumen. One of the lobes is slightly larger and is positioned centric to the facet.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.53044	3.70	0.73	0.76	0.73	39	41	20	1.7	46	26	about 42	Bin: N
TCD.53043	4.35	0.83	0.82	1.05	38	38	24	1.6	37	about 55	about 59	Bin: N

Stereom. The stereom shows galleried microstructure. On a cirrus socket of paratype TCD.53044 the stereom has large pore sizes on the innermost part of the areola, but they are smaller on the remainder of the areola and on the crenularium.

Remarks. Nodal indices could not be calculated because it is not known which end of the pluricolumnals are proximal.

As far as is known the curious intercalation of culmina has not previously been mentioned in the literature.

The specimens were immersed in 40-45% hydrofluoric acid for six minutes, which cleared most of the occluding matrix and revealed some of the stereom. The remaining loosened matrix was removed using a needle followed by a light scrub using a toothbrush in water.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 42b gp. nov.

Plate 76, figs a, b

Holotype. Specimen TCD.53045, a pluricolumnal of fourteen ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Columnal Plesion C morphospecies, noditaxis of three orders, nodals may be cirriferous; large cirrus sockets cause columnals to increase height and adjacent columnals to become lower; crenularium with curious trifurcating crenulae on internodals adjacent to cirriferous nodals, claustrum circular, lumen ?rounded pentagonal in outline, central.

Description. The columnals are circular in outline and have symplectial articulation. The crenularium is circular in outline. It has thirty-seven mainly simple crenulae on one articular facet, which are of distinctly varying widths. The crenulae are high and deep with rounded apices and troughs, and the sides are vertical so that they are parallel. On the opposing facet of the pluricolumnal almost fully grown peripherally intercalated culmina appear also. Two very wide culmina trifurcate (Plate 76, fig. b). In the first the trifurcation occurs from a common point along the culmen about a third of the way in across the crenularium. The centre and left forks are about of equal size and have only a small angle separating them, the central one being directed straight out towards the latus. The left fork is slightly wider than the other two and a larger angle separates it from the central fork. To the left of this culmen an unevenly trifurcating culmen occurs. It bifurcates heterotomously initially, the wider fork directed straight out to the latus. The narrower fork is at an angle to the first and bifurcates isotomously. The right fork of the central culmen joins laterally with the left fork of a wide, isotomously bifurcating culmen disposed to its right. The left fork of the central culmen joins with the right fork of the unevenly trifurcating culmen to its left. This rapid forking occurs due to the flaring out and sinking of the crenularial area of the articular facet in an attempt to accommodate the adjacent cirrinodal (not present in this pluricolumnal). The circular claustrum slopes down to the lumen and is convex. The lumen outline is unclear, but it is probably rounded pentagonal.

The latus is convex and smooth. The crenulate suture is open with a low amplitude, although this may be due to pressure solution.

From the long pluricolumnal it can be seen that the stem is distinctly heteromorphic. The noditaxis is 212N, but one secundinternodal is not developed adjacent to the large cirrinodal. Higher ordered columnals are greater in height and are laterally more convex. Measurements, in mm, of all columnals of the holotype pluricolumnal and their inferred noditaxial orders are inserted in the following table:

Holotype TCD.53045

KH	0.5	1.0	0.6	1.4	0.5	1.0	0.6	1.5	1.0	0.4	1.1	0.5	1.0	0.5
Order	2	1	2	N	2	1	2	N*	1	2	N	2	1	2

A single cirrus socket occurs on the highest nodal of the holotype. It measures 2 mm in diameter, is circular in outline and is disposed close to columnal mid-height. It is directed obliquely outwards and either upwards or downwards. The crenularium is wider on one side than the other, the narrower side coinciding with the highest side of the socket. It occupies just under half the diameter of the articular facet. There are sixteen simple crenulae, most of which are wide, probably about to bifurcate, and one very narrow, probably recently disposed one. The areola is gently concave downwards towards the lumen. The lumen outline is unclear, but it is positioned centric to the facet itself. Overall the facet is concave, the concavity increasing towards the highest end of the facet. The articular facet is wider than the height of the columnal itself so the columnal has become higher almost equally both up and down. To accommodate this the adjacent secundinternodals have become lower, but only on the side adjacent to the nodal.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*CLR*	*LD*	*Ci*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53045	4.40	0.75	0.88	1.15	34	40	26	0.5	11	37	Bin: IN2

Stereom. The stereom has a galleried microstructure as can be seen in the articular facet of the holotype. The pore sizes are smaller in the crenularium than those in the claustrum.

Remarks. Since it is not known which end of the pluricolumnal is proximal nodal indices could not be calculated.

The curious trifurcation as described above, as far as is known, has not previously been mentioned in the description of crinoid columnals.

The holotype was immersed in 40-45% hydrofluoric acid for six minutes, which cleared the occluding matrix and revealed some of the stereom. Any remaining loosened matrix was removed with a light brush using a toothbrush and water. Some of the detail of the articular facet was lost when Blu-Tack®, which was used to mount the specimen for examination, was being removed.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

Discussion. Stems of the columnal morphospecies *Preptopremnum rugosum* Moore and Jeffords, 1968 (Virgilian (Upper Pennsylvanian), Texas) (Moore and Jeffords 1968, Plate 27, figs 1-9) have columnals with convex latera, nodicirral articula, and are obviously heteromorphic. With these morphological features they are similar to members of Columnal Plesion C morphospecies herein. Other similar morphospecies illustrated by previous authors include *Heterostelechus jeffordsi* Miller, 1968 (Moore and Jeffords 1968, Plate 28, figs 2-6) and *Heterostelechus keithi* Miller, 1968 (Moore and Jeffords 1968, Plate 28, figs 8-10) (both Virgilian (Upper Pennsylvanian), Texas). Also the latera (but not the articular facets as they are slightly pentagonal in outline) are similar to those in pluricolumnals of *Blothronagma cinctutum* Moore and Jeffords, 1968 (Atokan (Middle Pennsylvanian), Oklahoma) (Moore and Jeffords 1968, Plate 16, fig. 12*a*).

COLUMNAL TAXON NUMBER 43 gp. nov.

Plate 77, fig. a

Holotype. Specimen TCD.53046, a single, well preserved nodose columnal. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Moniliform columnals of heteromorphic stem, nodals cirriferous; latus convex with random, finely tuberculate sculpture; crenularium wide with many simple, bifurcating and peripherally intercalated rounded crenulae, steeply sloping narrow

claustrum, lumen central, all are circular in outline.

Description. The columnals are circular in outline and have symplectial articulation. The crenularium is wide occupying 64% of the articular facet. It has many fine crenulae that are simple, bifurcating or peripherally intercalated. The latter extend into the crenularium by different amounts. About seventy-five crenulae are touching the claustrum and about two-hundred terminate at the latus. The crenulae are fairly shallow and have rounded apices and troughs. The narrow claustrum slopes steeply at more than 45° downwards towards the lumen. The lumen is central and circular in outline and is longitudinally straight. The articular facet has two lateral concavities where cirrus sockets are situated on the latus.

The latus is evenly convex. It has a sculpture of fine, low tubercles that are randomly orientated. Some tubercles are elongate. Articulation is symplectial.

The noditaxis is unknown. Two large cirrus sockets are disposed at 144° from each other. They therefore show evidence of pentaradiate symmetry and their presence suggests that this is a nodal. The sockets are strongly concave, but because the columnal is very low this is only seen on the columnal articular facet. Their diameters are 6.5 mm and 7.0 mm. When the columnal was articulated the cirrus sockets would have been impressed over several columnal latera. The entire morphology of the nodicirral articula cannot be deciphered. However, it is observed that the lumen is disposed slightly close to columnal mid-height. The crenularium would appear to have many crenulae as compared with other sockets of other columnal morphotypes.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*CL*	*LD*	*Ci*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching claustrum*	*No. crenulae touching latus*	*Extras*
TCD.53046	11.86	3.78	0.75	2.8	64	13	24	1.7	14	about 75	about 200	Bin: N

Remarks. This nodal is probably part of the distal portion of a stem as the diameter of the cirrus socket is very large in comparison with the diameter of the columnal itself.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 44 gp. nov.

Plate 77, fig. b

Holotype. Specimen TCD.53047, a pluricolumnal of ten ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.53048, a single columnal, taken from the same bulk sample as the holotype.

Diagnosis. Circular columnals of heteromorphic stem, nodals higher than internodals and sometimes with cirrus-related structures; latus straight and smooth; crenularium narrow with many mostly simple crenulae, outer claustrum sloping gently inwards, slightly concave, inner claustrum sloping steeply inwards, lumen central, all are circular in outline.

Description. The columnals are circular in outline and are wider than high. The crenularium covers about 20% of the total articular surface. It has regularly disposed mostly simple crenulae (the holotype), but also has peripherally intercalated and bifurcating crenulae on larger specimens (the paratype). They are sixty-four to seventy-four in number. They are of medium height and depth and their apices and troughs are rounded. The outer claustrum is sloping down gently towards the centre of the columnal and is slightly concave also. The inner claustrum slopes very steeply down towards the centre of the columnal, but its radius cannot be seen on any specimen. The boundary between the outer and inner claustrum is rounded. The lumen appears to be circular in outline, but its diameter cannot be determined from any specimen.

The latus is straight and smooth. Articulation is symplectial. The crenulate suture is irregular zigzagged with slightly flattened to rounded apices and troughs and a low amplitude.

The inferred noditaxis from the holotype is a Type II pattern, $N1_{1\text{-}3}$. The nodals are higher than the internodals, nodals measuring 2.4 to 2.5 mm in height and priminternodals ranging from 1.8 to 2.0 mm. However, there are no lateral differences.

Internodals are not as distinct in the holotype specimen. Measurements, in mm, of all columnals of the pluricolumnal holotype and their inferred noditaxial orders are inserted in the following table:

HolotypeTCD.53047

KH	1.9	2.0	1.8	2.4	1.9	2.0	2.0	2.5	1.8	2.0
Order	1	1	1	N	1	1	1	N*	1	1

A single very small cirrus-related structure occurs on the second inferred nodal. It appears as a blocked cirripore or may be an abortive cirrus, but it has no articular facet to suggest it was ever truly cirrus-bearing.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*OCLR*	*ICLR*	*LD*	*Ci*	*OCLi*	*ICLi*	*Li*	*KH*	*KHi*	*No. crenulae touching lumen*	*No. crenulae touching latus*	*Extras*
TCD.53048	6.65	0.7	0.7	?	?	21	21	?	?	1.9	29	64	64	Bin: IN
TCD.53047	9.60	1.0	0.9	?	?	21	19	?	?	1.7	18	?	74	Bin: ?

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 45 gp. nov.

Plate 78, fig. a; Plate 79, figs a, b

Holotype. Specimen TCD.53049, a pluricolumnal of two ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Rounded basaltiform columnals of heteromorphic stem, higher ordered columnals greater in height, non-cirriferous; latus straight, smooth; articular facet with coincidentally pentagonal crenularium, simple crenulae extend normally from long sides, areola coincidentally pentagonal outline, remainder of facet unknown.

Description. The columnals are rounded pentagonal in outline and are symplectially

articulating. The crenularium outline follows that of the columnal. Its inner boundary is coincidentally pentagonal, but each of the long sides is convex so that mid-way along each side the crenulae extend further into the areola than do those at the corners. It occupies just over 20% of the articular facet diameter. There are eleven to thirteen crenulae per long side, in total fifty-eight touching the areola and sixty touching the latus. The crenulae are high and deep with rounded apices and troughs. Their sides are very steep so that they are almost parallel. Culmina in the corners are narrower than those along the long side. They have attained their full lengths in three corners of the facet, but in the extremities of the other two corners, extending directly inwards, short peripheral culmina are disposed. The morphology of the remaining articular facet inside the crenularium cannot be clearly seen. However, the area directly inside the crenularium appears to be planar, so this is probably the areola.

The latus is straight and is lacking sculpture. The crenulate suture is coarse, of short wavelength and high amplitude and has rounded apices and troughs.

The noditaxis is not known since the pluricolumnal is not long enough. However, the stem is heteromorphic with at least two orders, the columnals measuring 1.7 and 2.0 mm high. Neither of the columnals is cirriferous.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.53049	6.22	0.71	?	?	23	?	?	1.7	27	11-13 per long side	58	60	Bin: IN

Stereom. The stereom microstructure is galleried (Plate 79, figs a, b). On comparing the stereom areola to the crenularium, the bars are thicker and pores larger in the former.

Remarks. Columnals of the morphospecies *Pentaridica rothi* Moore and Jeffords, 1968 (Virgilian (Upper Pennsylvanian), Texas) (Moore and Jeffords 1968, Plate 9, figs 12,13) have the same rounded pentagonal outline, and a similar arrangement of corner crenulae.

The holotype was immersed in 40-45% hydrofluoric acid for four minutes.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 46a gp. nov.

Plate 80, figs a, b; Plate 81, figs a, b

Holotype. Specimen TCD.53050, a pluricolumnal of only two ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Moniliform columnals of heteromorphic stem, higher ordered columnals have greater height; latus smooth, moderately convex; articular facet with crenularium which has only simple crenulae, areola narrow, smooth, planar, claustrum slopes moderately down towards lumen, lumen, all are circular in outline and positioned centrally.

Description. The columnals are circular in outline and articulate symplectially. The crenularium is circular with forty-two simple crenulae. They are regularly disposed and their thicknesses vary only slightly. The crenulae are moderately high and deep with almost flattened apices and troughs. The areola is narrow, occupying only 13% of the total facet diameter. The claustrum slopes at about 45° down towards the lumen. The lumen is circular in outline.

The latus is moderately convex and smooth. The crenulate suture is coarse and even with a moderate amplitude and with rounded apices and toughs.

The stem is heteromorphic with higher ordered columnals being greater in height, the two columnals measuring 2.0 and 2.3 mm high. There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53050	4.15	0.73	0.27	0.80	0.55	35	13	39	13	2.0	48	42	Bin

Stereom. The stereom has galleried microstructure. Pore sizes are larger and bars are thicker in the claustrum than they are in the areola and crenularium. There are several much larger pores that can clearly be seen positioned all around the claustrum. These may be an artefact of preservation or part of the original microstructure.

Remarks. The holotype was immersed in 40-45% hydrofluoric acid for six minutes

revealing the stereom.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 46b gp. nov.
Plate 78, fig. b

Holotype. Specimen TCD.53051, a pluricolumnal of six ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Moniliform columnals of heteromorphic stem, higher ordered columnals are greater in height; latus moderately convex, smooth; articular facet with crenularium, crenulae simple, bifurcating or peripherally intercalated, areola narrow, claustrum slopes gently downwards to lumen, all are positioned centrally and are circular in outline.

Description. The columnals are circular in outline and have symplectial articulation. The crenularium is circular in outline. The crenulae are simple, bifurcating or peripherally intercalated. There are thirty touching the areola and forty-seven touching the latus. Culmina thicken towards the latus where they are about to bifurcate. They have high and deep rounded apices and troughs and their sides are sloping at about 60°. The areola occupies only about 11% of the total articular facet. It is smooth and planar. The circular claustrum slopes at a very shallow angle, probably about 30°, down towards the lumen. The lumen is central and circular in outline.

The latus is moderately convex and smooth. The crenulate suture cannot be deciphered.

The stem is heteromorphic with higher ordered columnals being greater in their heights. The noditaxis could be 1N or 212N. Concavity does not alter between orders. Measurements, in mm, of all columnals of the holotype pluricolumnal are inserted in the following table:

Holotype TCD.53051

KH	2.3	1.7	2.4	1.8	2.2	1.8
Order	N	1	N	1	N	1
Order	1	2	N	2	1	2

There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.53051	3.80	0.86	0.20	0.57	0.55	45	11	30	14	2.2	58	30	47	Bin

Remarks. Although the morphologies of Columnal Taxon Numbers 46a and 46b are similar, the bifurcating crenulae of the latter shows that growth of the crenularium was achieved by different means. In addition, the second group has a more heteromorphic stem.

The holotype was immersed in 40-45% hydrofluoric acid for six minutes.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 47 gp. nov.

Plate 56, fig. b

Holotype. Specimen TCD.53052, a pluricolumnal of six ossicles, which has been eroded along one side so no longer has a true circular outline. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.53253, a pluricolumnal of three ossicles, taken from the same bulk sample as the holotype.

Diagnosis. Cylindrical columnals of heteromorphic stem, nodals being higher than internodals and sometimes cirriferous; latus smooth and straight to slightly convex; very wide crenularium with simple, bifurcating and peripherally intercalated crenulae, very small central lumen, both are circular in outline.

Description. The columnals are circular in outline and are higher than they are wide. Articulation is symplectial. The articular facet is simple with only a crenularium and lumen. The crenularium is very wide occupying over 85% of the articular facet. Many crenulae are regularly disposed comprising simple, peripherally intercalated and bifurcating and types with bifurcations occurring once or twice across the crenularium. About twenty-four to thirty crenulae originate next to the lumen and about forty-six to about ninety terminate at the latus. The crenulae are high and deep with flattened apices and troughs, and have very steep sides so that they are parallel. The central, circular lumen is very small with longitudinally straight sides.

The latus is smooth and straight, except for higher orders that become slightly convex in their outlines. The columnals articulate by symplexy. The regular crenulate suture is open with a low amplitude and rounded apices and troughs.

The noditaxis is ?1NN to 1N from the paratype and holotype. Nodals are higher than internodals and may be cirriferous. Measurements, in mm, of all columnals of the holotype and paratype pluricolumnals and their inferred noditaxial orders are inserted in the following tables:

Holotype TCD.53052

KH	1.4	1.7	1.4	1.6	1.4	1.7
Order	1	N*	1	N	1	N

Paratype TCD.53253

KH	1.2	1.5	1.6
Order	?1	?N	N*

On the holotype the edge of a cirrus socket is imposed on the first priminternodal implying that the adjacent columnal was cirriferous and therefore likely to be a nodal. The second nodal has a single circular cirrus socket of 3.4 mm diameter which is disposed at columnal mid-height. Overall it is slightly concave with about forty simple crenulae on a circular crenularium whose total diameter is 1.0 mm. There is a small central lumen, but the remainder of the articular facet cannot be deciphered. It is directed outwards normal to the latus. On the paratype a single socket on the nodal measures 2.6 mm diameter and, from what can be seen of it, has a similar articular facet morphology to that of the cirrus socket on the holotype. It is directed obliquely outwards from the latus and faces either upwards or downwards. On both specimens the height of the nodal increases in the area immediately surrounding the cirrus socket.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*LD*	*Ci*	*Li*	*KH*	*KHi*	*No. crenulae touching lumen*	*No. crenulae touching latus*	*Extras*
TCD.53253	5.11	2.33	0.45	91	9	1.2	23	about 24	about 46	Bin: ?
TCD.53052	8.4	3.6	1.2	86	14	1.4	17	30	about 90	Bin: IN1

Remarks. The paratype TCD.53253 is inferred to be an immature specimen of this columnal morphospecies.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 48 gp. nov.

Plate 82, figs a, b

Holotype. Specimen TCD.53053, a pluricolumnal of twelve ossicles, one end of which is broken. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Cylindrical columnals of symplectially articulating heteromorphic stem; latus weakly angulated, one to three ridges of irregular rounded tubercles extend around circumference; crenularium with simple, peripherally intercalated and bifurcating crenulae, lumen central and circular.

Description. The columnals are circular in outline and are symplectially articulating. The crenularium has simple, bifurcating and peripherally intercalated crenulae. Twenty-five originate on the inner boundary, which cannot be deciphered, and thirty terminate at the latus. They are medium in height, have rounded apices and troughs and are of differing widths. The remainder of the facet is unclear, but the outline of the lumen can be seen at the broken end of the specimen. It is circular in outline and is positioned centrally. Longitudinally it is straight.

The latus is slightly angulated in longitudinal profile. The ridge created is at

columnal mid-height and is composed of a row of tubercles. The tubercles are wide, low and rounded and are irregularly disposed. Higher ordered columnals may have two further rows of smaller tubercles, one each above and below the medial one, when space permits. The crenulate suture is open and irregular with a low amplitude.

Measurements, in mm, of all columnals of the holotype and paratype pluricolumnals and their inferred noditaxial orders are inserted in the following tables:

Holotype TCD.53053

KH	1.0	1.3	1.1	1.5	1.3	1.5	1.3	1.4	1.2	1.4	1.3
Order	3	2	3	1	2	N*	2	1	2	1	2

A single cirrus socket occurs on the nodal of the holotype. It is pointing obliquely outwards and facing upwards. The morphology of the articular facet is unclear, but its diameter is about half that of the height of the columnal itself.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*ZR*	*LD*	*Zi*	*Li*	*KH*	*KHi*	*No. crenulae originating on inner boundary*	*No. crenulae touching latus*	*Extras*
TCD.53053	2.45	0.88	0.69	72	28	1.0	41	25	30	Bin: IN3

Remarks. Where some of the wider crenulae occur it appears that they were about to bifurcate suggesting that the specimen is not fully mature.

A similar tuberculate keel is seen on the latus of *Graphosterigma grammoides* Moore and Jeffords, 1968 (Osagian (Lower Mississippian), Indiana) (Moore and Jeffords 1968, Plate 14, fig. 1*a*).

The holotype was scrubbed using a toothbrush with a weak solution of household detergent. It was then immersed for five minutes in 30% by volume hydrogen peroxide.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 49 gp. nov.

Plate 83, figs a, b

Holotype. Specimen TCD.53054, a single columnal. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks,

after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratypes TCD.53055, a pluricolumnal of five ossicles, TCD.53056, a pluricolumnal of five ossicles of which one terminal columnal is broken, TCD.53057, a pluricolumnal of three ossicles, TCD.53058, a pluricolumnal of five ossicles and TCD.53059, a pluricolumnal of two ossicles. All are taken from the same bulk sample as the holotype.

Diagnosis. Cylindrical columnals of distinctly heteromorphic stem, higher ordered columnals greater in height, may be cirriferous; latus with distinctive high tubercles, adjacent tubercles often merging forming small ridges between them, tubercles form horizontal rows on lower ordered columnals, randomly disposed on higher orders; articular facet with crenularium, circular outer and pentagonal inner boundary, crenulae mostly simple, directed normally inwards along long sides so that they are parallel, often intercalated at corners as bifurcating crenulae or as short inwardly directed crenulae from corner extremity, often corner crenulae are just thickened, pentagonal, smooth areola, steeply sloping ?rounded pentagonal claustrum, central ?rounded pentagonal lumen.

Description. The columnals are circular in outline and are symplectially articulating. The crenularium has a circular outline, but an evenly pentagonal inner boundary. It has fifty-six to sixty-five crenulae touching the areola and sometimes a few more touching the latus. They are mainly simple but may bifurcate at the corners or be disposed in the extremity of the corners, as seen on the holotype. The crenulae along the long sides are more or less parallel, except in the corners. Those nearest the corners often have their adaxial ends bent in towards the corners as these were the last to be formed. The corners of the crenularium are not as obvious on paratype TCD.53055 where crenulae are thickened instead of being intercalated. The crenulae are very high and deep with rounded apices and troughs. Their sides are parallel. They slope gradually downwards towards the areola in only their most adaxial portions. The areola is pentagonal on its outer boundary and appears pentagonal or rounded pentagonal on its inner boundary. The corners are coincidental with those of the crenularium. It is narrow, smooth and planar. The claustrum appears to have a coincidental pentagonal outline and it slopes at

about 45° downwards towards the lumen. The outline of the lumen is obscured in the paratypes, but it appears that it may be rounded pentagonal in the holotype.

The latus is straight with a sculpture of small, but high tubercles and ridges. These do not occur on its upper and lower extremities where the columnal recurves back to the suture. On the higher columnals they are apparently randomly disposed, but on the lower columnals they are disposed in irregular horizontal rows around the circumference. Erosion has meant that only a small amount of the sculpture remains on the holotype. The crenulate suture cannot be seen as it is obscured by matrix.

The paratype TCD.53055 has a probable noditaxis of 3231323N with higher ordered columnals being greater in height, but showing no lateral convexity. Measurements, in mm, of all columnals of the pluricolumnal specimens, paratypes TCD.53055, TCD.53056, TCD.53057 and TCD.53058, and their inferred noditaxial orders are inserted in the following tables:

Paratype TCD.53055

KH	1.1	1.8	1.1	1.5	1.1
Order	3	1	3	2	3

Paratype TCD.53056

KH	2.0	1.5	2.3	1.6
Order	2	3	1	3

Paratype TCD.53057

KH	1.7	1.5	2.0
Order	2	3	1

Paratype TCD.53058

KH	2.0	2.2	1.7	2.1	2.5
Order	1	1	2	1	N*

There is a slight depression on the articular facet of one of the terminal tertinternodals of paratype TCD.53055 where the cirrus socket from the adjacent columnal, probably a cirrinodal, impressed onto this columnal. As well as this a segment of the cirrus socket with four or five simple crenulae of the crenularium is seen on the latus. A single cirrus socket appears on the terminal nodal of paratype TCD.53058. It measures 2.7 mm in diameter, is overall concave and is disposed at columnal mid-height. There are about twenty-four crenulae around the crenularium, but the remainder of the facet cannot be seen. It is slightly raised away from the latus.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching areola*	*No. crenulae touching latus*	*Extras*
TCD.53058	5.90	1.10	?	?	?	37	?	?	?	2.0	34	?	48	Bin: ?IN1
TCD.53059	6.25	1.00	0.68	0.80	1.29	32	22	26	21	1.7	27	50	50	Bin: ?IN2 or 3
TCD.53055	7.55	1.52	0.40	?	?	40	11	?	?	1.1	15	56	56	Bin: ?IN3
TCD.53056	7.60	1.15	?	?	?	30	?	?	?	2.0	26	60	61	Bin: ?IN2
TCD.53057	8.30	2.10	0.70	?	?	51	17	?	?	1.7	20	51	59	Bin: ?IN2
TCD.53054	8.52	1.83	0.70	1.06	1.35	43	16	25	16	1.7	20	65	66	Bin: IN

Stereom. From specimen TCD.53057 the stereom appears to be galleried. The pores are smaller on the crenularium and areola than the claustrum.

Remarks. The sculpture seen on the holotype and paratype TCD.53055 is similar to that seen in Columnal Taxon Numbers 3 and 5 herein. The fact that the sculpture is seen on these two specimens and not the others is probably a simple a case of erosion. Even on the holotype the sculpture is only seen on part of the facet, so for it to be eroded away on other specimens is not unlikely.

A similar converging of crenulae into five radii on circular columnals is seen on articular facets of the Lower Jurassic species *Millericrinus*? *alpinus* (Gümbel, 1888) in Simms (1989*b*, Plate 14, fig 24).

The holotype and paratype TCD.53055 were immersed in 30% by volume hydrogen peroxide and then scrubbed using a toothbrush with a weak solution of household detergent.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 50 gp. nov.

Plate 84, figs a, b

Holotype. Specimen TCD.53060, a pluricolumnal of two ossicles, one end of which is partly broken away so that the articular facet cannot be fully seen. From Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (about 1 mm diameter) cylindrical columnals of heteromorphic stem, nodals higher than internodals and cirriferous; latus with small flare at both ends; articular facet with circular crenularium and steeply sloping claustrum, central, presumably circular lumen.

Description. The columnals are circular in outline and are as high as they are wide. Articulation is symplectial. The crenularium has twenty high and deep, simple crenulae with squared apices and troughs. The claustrum is smooth and steeply sloping downwards adaxially at about 45°. The lumen is central, apparently circular in outline and is straight longitudinally.

The latus is smooth and straight, except at the very edges where it flares out a small amount. The details of the crenulate suture cannot be deciphered.

The noditaxis is at least 1N with the nodal being cirriferous and higher than the internodal. The circular cirrus socket of the nodal is not disposed at columnal mid-height. It is raised away from the columnal latus, more so on the side that is adjacent to the articulated internodal, so that it is directed obliquely outwards and either upwards or downwards. The diameter of the cirrus socket is about half that of the articular facet. The nodicirral articulum has a small, peripheral crenularium with about twenty short, rounded and bulbous crenulae. The remainder of the facet is unclear.

Columnal morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53060	937	157	159	304	34	34	32	?	?	20	SEM: at least IN1

Stereom. The stereom is galleried. It appears that the pore diameters of the claustrum stereom are generally larger than those of the crenularium. This may have been to accommodate wider and stronger intercolumnal ligaments.

Stereom microstructure morphometrics, measurements in microns.

Specimen TCD.53060	*Bar widths*	*Pore diameters*
Crenularium	3.86	6.31
	5.12	6.95
	6.24	7.82
Claustrum	4.67	7.34
	5.07	7.85
	6.94	7.91
	7.78	10.60

Remarks. Although a join between the two ossicles cannot be seen it is inferred that the holotype is in fact two articulated columnals since there is a raised area around the circumference about halfway down the latus.

The holotype suffered a little cracking on its alteration from calcite to calcium fluoride following immersion in 3.6% hydrofluoric acid for one week. However, since its removal from the SEM. stub on which it was mounted a piece of the nodal has broken away.

Stratigraphical range. Arundian (Bundoran Shale Formation).

COLUMNAL PLESION D pln. nov.

Type species. Columnal Taxon Number 52a gp. nov.

Other species. Columnal Taxon Number 41 gp. nov.; Columnal Taxon Number 51 gp. nov.; Columnal Taxon Number 52b gp. nov.; Columnal Taxon Number 52c gp. nov.

Diagnosis. Ovate columnals of heteromorphic or homeomorphic stem, non-cirriferous; latus sculpture variable, one to two even or tuberculate ridges at, or close to, columnal mid-height around the whole, or part, of the circumference; crenularium with simple, bifurcating and peripherally intercalated crenulae, lumen dilobate to ovate in outline.

Stratigraphical range of plesion. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 41 gp. nov.

Plate 71, fig. b

Holotype. Specimen TCD.53042, a single columnal. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Columnal Plesion D morphospecies, columnal ovate; latus with narrow ridge

at columnal mid-height on widest half of columnal; crenularium with simple, bifurcating and peripherally intercalated crenulae, ovate outline, steeply sloping, slightly concave claustrum, circular outline, lumen dilobate in outline and central to the claustrum.

Description. The columnal is ovate in outline and has symplectial articulation. The crenularium has a wider radius at the narrow end of the columnal rendering its inner outline circular even though its outer one is ovate. It has mainly simple crenulae, but also a few bifurcating and peripherally intercalated ones. About forty-seven crenulae originate adjacent to the claustrum and fifty-six terminate at the latus. The crenulae are of medium height, have rounded apices and troughs and are of differing widths, some being relatively wide. They slope downwards towards the claustrum so that they have no relief when they reach it. The claustrum slopes steeply downwards at more than 45° towards the lumen and is slightly concave. It has a circular outer boundary with the crenularium, but the inner boundary follows that of the lumen. The lumen is dilobate in outline and is positioned centrally relative to the claustrum. The long axis coincides with that of the columnal.

The latus is straight to slightly angulated in longitudinal profile, the angulation being caused by a ridge disposed at columnal mid-height. The ridge extends around the wider end of the columnal only. The remainder of the latus is smooth.

There are no cirrus related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*CLR*	*LD*	*Ci*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae touching claustrum*	*No. crenulae touching latus*	*Extras*
TCD.53042	6.1	1.4	1.02	1.26	46	33	21	3.4	56	about 47	56	Bin: ?

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 51 gp. nov.

Plate 85, figs a, b

Holotype. Specimen TCD.53061, a single columnal. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben

Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Columnal Plesion D morphospecies with ovate columnals; latus concave, sculpture of row of tubercles on narrow half of columnals which bifurcates once at either side; crenularium with simple, bifurcating and peripherally intercalated crenulae, gently sloping claustrum, claustrum and lumen nearer to narrow end of columnal, all are ovate in outline.

Description. The columnal is ovate in outline, wider than it is high and symplectially articulating. The crenularium follows the ovate outline of the columnal itself. It has a larger radius at the widest end of the columnal. It has mainly simple, but also some bifurcating and peripherally intercalated crenulae. Bifurcations and intercalations occur especially on the 'corners' of the crenularium. The crenulae are widely distributed and fairly regularly disposed. They are of medium height with evenly rounded apices and troughs. The claustrum slopes gently downwards towards the lumen and has an ovate outline. The lumen also has an ovate outline. The claustrum and lumen are positioned nearer to the narrow end of the columnal.

The latus is slightly concave. On the narrower end of the columnal there is a sculpture of an irregular row of tubercles, some of which merge with adjacent ones at columnal mid-height. This row bifurcates twice, once each around each side of the latus so that two rows terminate where the columnal starts to widen.

There is no evidence of any cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FDx*	*FDy*	*FD*	*CR*	*CLR*	*LD*	*Ci*	*CLi*	*Li*	*KH*	*KHi*	*FSi*	*No. crenulae touching claustrum*	*No. crenulae touching latus*	*Extras*
TCD.53061	6.4	6.6	6.5	1.33	1.22	1.40	41	38	22	2.9	45	97	about 48	about 58	Bin: ?

Stereom. The stereom is galleried.

Remarks. The holotype was scrubbed with a toothbrush in a weak solution of household detergent then immersed for five minutes in 30% by volume hydrogen peroxide.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 52a gp. nov.

Plate 86, figs a, b; Plate 87, figs a, b

Holotype. Specimen TCD.53062, a pluricolumnal of two ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Material. Paratype TCD.53063, a pluricolumnal of three ossicles, taken from the same bulk sample as the holotype.

Diagnosis. Columnal Plesion D morphospecies with ovate columnals of heteromorphic stem, higher ordered columnals greater in height; latus with one to two ridges around circumference; crenularium with mainly simple crenulae, ?in two parts, lumen dilobate in outline and central.

Description. The columnals are ovate in outline with symplectial articulation. On neither specimen can the radii of the crenularium be measured. It has mainly simple, but also a few bifurcating or peripherally intercalated crenulae, which are fairly regularly disposed and quite narrow. They have rounded apices and troughs and are of medium height. Fifty-two to sixty-six crenulae terminate at the latus, which originate from fewer on the central part of the crenularium, but this part cannot be seen. However, on the holotype it appears that crenulae continue across a downward slope to the lumen, perhaps an inner crenularium. The lumen is dilobate in outline.

The latus is weakly convex. The columnals of the holotype have the same height of about 2.6 mm. However, the latus on the highest ordered columnal of the paratype is drawn into a point or nadir on two occurrences making measurement of its height difficult. They measure between 2 and 3 mm high. On the holotype there is a sculpture of two narrow, parallel continuous ridges either side of columnal mid-height. They are slightly wavering, but continue all around the circumference of the latus. On the paratype there is a single ridge at columnal mid-height which is sometimes interrupted. The ridge bifurcates at points where the latus increases in height. It is stronger at the narrow end of the columnal, erosion on the other half probably weakening any sculpture there. The

remainder of the lateral surface is smooth. The crenulate suture is fairly regular and of low amplitude, but coarse, with rounded apices and troughs.

The stem is heteromorphic, but the noditaxis is unknown. Three orders probably occur in the paratype. There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*FDx*	*FDy*	*CR*	*LD*	*Ci*	*Li*	*KH*	*KHi*	*FSi*	*No. crenulae originating on inner boundary*	*No. crenulae touching latus*	*Extras*
TCD.53062	6.65	6.3	7.0	?	?	?	?	2.6	39	90	less than 52	52	Bin: ?
TCD.53063	9.2	8.9	9.5	?	?	?	?	2.0 to 3.0	22 to 33	94	less than 66	66	Bin: ?

Remarks. The holotype was scrubbed with a toothbrush in a weak solution of household detergent and then immersed in 30% by volume hydrogen peroxide for five minutes. The paratype was immersed in 40-45% hydrofluoric acid for nine minutes.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 52b gp. nov.

Plate 88, figs a, b

Holotype. Specimen TCD.53064, a pluricolumnal of four ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Columnal Plesion D morphospecies with ovate columnals of homeomorphic stem; latus with sculpture of ridge at columnal mid-height on narrow half of columnal; crenularium with many simple, bifurcating and peripherally intercalated crenulae, lumen dilobate to ovate in outline.

Description. The columnals are ovate in outline and are symplectially articulating. The crenularium is ovate in outline and occupies almost 66% of the entire articular facet. There are many crenulae which are low with rounded apices and troughs. The simple crenulae maintain a similar width along their lengths, but if they are complex their widths

decrease. The remainder of the articular facet is unclear. It does not appear that there is a slope downwards towards the lumen. The lumen is unevenly dilobate or ovate in outline.

The latus has a sculpture on the narrower half of the columnal. There is a clear ridge at columnal mid-height which is straight, wavering only at the terminations on either side of the columnal. The remainder of the latus is weakly convex. The crenulate suture is uneven with a low amplitude, but with rounded apices and troughs.

The stem is apparently homeomorphic with all the columnals measuring about 1.9 mm high, and they all have the same diameter of about 6.15 mm. There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FDx*	*FDy*	*FD*	*ZR*	*LD*	*Zi*	*Li*	*KH*	*KHi*	*FSi*	*No. crenulae originating on inner boundary*	*No. crenulae touching latus*	*Extras*
TCD.53064	5.8	6.5	6.15	2.58	0.99	84	16	1.9	31	89	about 42	about 77	Bin

Remarks. More crenulae occur on this columnal morphotype than on Columnal Taxon Number 52a. In addition, the ridges occurring on this columnal morphotype is stronger and more even.

The holotype was scrubbed in weak solution of household detergent using a toothbrush.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

COLUMNAL TAXON NUMBER 52c gp. nov.

Plate 89, figs a, b

Holotype. Specimen TCD.53065, a pluricolumnal of four ossicles. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Columnal Plesion D morphospecies with ovate columnals of homeomorphic stem; latus with sculpture of discontinuous ridge of elongate tubercles close to columnal mid-height; wide, ovate crenularium with simple, bifurcating and peripherally

intercalated crenulae, remainder of facet unknown.

Description. The columnals articulate symplectially and are ovate in outline. The exact radii of the crenularium cannot be seen, but it occupies about 66% of the total diameter of the articular facet. There are about thirty-eight crenulae on the inner boundary which, as well as being to give forty-two crenulae terminating at the latus. The crenulae are of medium relief and have evenly rounded apices and troughs. The remainder of the articular facet cannot be deciphered.

The latus has a sculpture on the wider half of the columnal. It is a very discontinuous row of three or four elongate tubercles disposed close to columnal mid-height. The end members are often just small round tubercles. The remainder of the latus is smooth and straight. The crenulate suture has a very low amplitude, is coarse and has rounded apices and troughs.

The stem is homeomorphic, the columnals all measuring about 1.6 high. There are no cirrus-related structures.

Columnal morphometrics, measurements in mm.

Specimen number	*FDx*	*FDy*	*FD*	*CR*	*LD*	*Ci*	*Li*	*KH*	*KHi*	*FSi*	*No. crenulae originating on inner boundary*	*No. crenulae touching latus*	*Extras*
TCD.53065	3.8	4.0	3.9	?	?	about 66	?	1.6	41	95	about 38	42	Bin

Remarks. The holotype was scrubbed using a toothbrush in a weak solution of household detergent. It was then immersed in 30% by volume hydrogen peroxide for five minutes.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

Discussion. Columnals with similar ovate outlines, but with different articular facet sculptures to those in Columnal Plesion D morphospecies herein, are seen in *Desidiamphidia frondea* Moore and Jeffords, 1968 (Erian (Middle Devonian), New York) (Moore and Jeffords 1968, Plate 20, figs 9,10). Also, ovate columnals with eccentric lumina and a sculpture confined to one side of the latus belong to the genus *Eurax* Moore and Jeffords, 1968 (Upper Silurian, Tennessee) (Moore and Jeffords 1968, Plate 19).

COLUMNAL TAXON NUMBER 53 gp. nov.

Plate 90, fig. a

Holotype. Specimen TCD.53066, a single columnal, taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Circular columnals, may be cirriferous; latus smooth and straight; articular facet with crenularium, which has only simple crenulae, smooth areola, probably steeply sloping claustrum, central lumen, all are circular in outline.

Description. The columnal is essentially circular in outline, but due to the deposition of cirrus sockets has taken on a slightly rounded pentagonal form. The crenularium is circular in outline. It has sixty-one simple crenulae that are deposited regularly, but are of slightly varying widths. They are very low with flattened apices and troughs. They slope down gradually adaxially to the areola. The areola is smooth and planar. Some of it is lost due to erosion or the cleaning process. The claustral slope cannot be seen, but it is circular in outline and appears to be simple. The lumen circular in outline and is positioned centrally.

The latus is smooth and straight, except where cirrus sockets are disposed.

The holotype, which is probably a nodal, has four cirrus sockets disposed at positions that are consistent with pentaradiate symmetry. They are disposed close to columnal mid-height. Their full morphologies cannot be seen due to erosion, but on one socket there are seven simple crenulae around the crenularium and this probably occupies 66% of the total facet diameter. Inside this the articular facet is unclear.

Columnal morphometrics, measurements in mm.

Specimen number	*FD*	*CR*	*AR*	*CLR*	*LD*	*Ci*	*Ai*	*CLi*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53066	5.95	0.80	0.40	1.03	1.50	27	13	34	25	2.7	45	61	Bin: ?N

Remarks. A wheel-like holothurian spicule (Plate 107, fig. b) is attached to the claustrum of the holotype.

The holotype was immersed for four minutes in 40-45% hydrofluoric acid.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

6.3.1. DISCUSSION

Many circular columnals could be compared with many morphospecies of the genus *Cyclocyclicus* Yeltyschewa, 1955, with a circular articular facet, central, circular lumen, usually circular columnal outline, and usually symplectial articulation. They have 'basic' facets, *i.e.*, a crenularium with simple or bifurcating crenulae, an areola and a lumen, which may be similar, but may have different lateral sculpture.

6.4. DESCRIPTIONS OF CIRRALS AND PLURICIRRALS

CIRRAL TAXON NUMBER 1 gp. nov.

Plate 91, fig. a

Holotype. Specimen TCD.53067, a single cirral, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Diagnosis. Very small (< 1 mm diameter) circular cirrals, much higher than wide; latus smooth and concave, flared at ends; cirral articular facet with very wide, circular crenularium, remaining facet unknown.

Description. The cirral is circular in outline, and much higher than it is wide. Articulation is symplectial. The crenularium is very wide, covering most of the articular facet. Disposed on it are ten elongate, triangular-shaped simple crenulae with somewhat triangular profiles. The remainder of the facet adaxially is unclear.

The latus is concave and smooth. In the central section it is flat, but it flares outwards at both ends.

Cirral morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*LD*	*Ci*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53067	641	?	?	?	?	?	?	10	SEM

Remarks. The holotype suffered no damage following immersion in 3.6% hydrofluoric

acid for one week.

Stratigraphical range. Arundian (Bundoran Shale Formation).

CIRRAL TAXON NUMBER 2 gp. nov.

Plate 91, fig. b

Holotype. Specimen TCD.53068, a pluricirral of three ossicles, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Diagnosis. Very small (less than 1 mm diameter) cylindrical cirrals of heteromorphic cirrus, cirrals with high cirral height index; latus with two or three rounded protrusions at one, and always the same, end of cirrals, all are projecting in same direction and at an angle of less than 45° from latus; cirral articulum with crenularium, areola and central lumen, all are circular in outline.

Description. The outline of the cirrals is circular to flattened slightly along the margin where the protrusions occur. They are much higher than they are wide. Articulation is symplectial. They are all of a similar height at about 1.10 mm. The crenularium is peripheral with fourteen simple, irregularly disposed crenulae, which are wedge-shaped. Each radius is less than 1.0 mm across. The areola is smooth and flat. The lumen is central and circular in outline.

The latus is smooth and straight, but with strange, characteristic protrusions at one, and always the same, end of the cirral. The protrusions are small and rounded, extending at an angle of less than 45° from the latus and all projecting in the same direction. They may be wide or narrow, but in any case, they resemble the rooted area at the base of a tree trunk. Each cirral has two or three adjacent projections. They are confined to only one side, and always the same side, of each cirral. The crenulate suture is low and even.

A noditaxis cannot be determined.

Cirral morphometrics, measurements in microns.

Specimen number	*FD*	*CR*	*AR*	*LD*	*Ci*	*Ai*	*Li*	*KH*	*KHi*	*No. crenulae*	*Extras*
TCD.53068	784	?	?	?	?	?	?	1070	136.50	14	SEM

Remarks. The holotype is probably a pluricirral rather than a pluricolumnal. Moore *et al.* (1968, p. 11) mention that, down one side only, cirri may possess small 'spinelets' at their distal ends. The projections described herein are probably analogous to their spinelets. A pluricirral belonging to *Isocrinus* basaltiformis (Miller, 1821) (Carixian (Lower Jurassic)) figured in Simms (1989*b*, Plate 9, fig. 10) has a spinose, flaring distal margin. However, the spinelets are smaller than in the specimen TCD.53068. Indeed, many of the cirrals figured in Simms (1989*b*) have flared distal margins. The projections are likely to have helped in anchoring the crinoid in the substrate.

Stratigraphical range. Arundian (Bundoran Shale Formation).

CIRRAL TAXON NUMBER 3 gp. nov.

Plate 92, figs a, b

Holotype. Specimen TCD.53069, a pluricirral of seven ossicles, both ends of which are broken so that the articular facet cannot be seen. Taken from a large bulk sample of only columnals, which were hand-picked following their accumulation on sheep tracks, after they dropped out of interbedded muddy, calcareous shales and limestones of the Benbulben Shale Formation (Holkerian), near the base of the western tip of Benbulben Mountain, just east of Barnarobin, Co. Sligo, GR 6865 4570 (Locality BB).

Diagnosis. Very small (less than 1 mm diameter) subcylindrical cirrals of homeomorphic cirrus; latus flares out down one side, opposing straight side with peg and socket joint; articular facet with ?circular, ?ellipse or ?dilobate central lumen.

Description. The cirrals are circular to slightly ellipse-shaped in outline. The cirral height index is high at about 67. The type of articulation cannot be deciphered. The lumen is the only part of the articular facet whose outline can be deciphered. It is either circular, ellipse-shaped or dilobate and is small and central. The mean cirral diameter is about 3.0 mm across.

The latus is straight down one side of the cirrals. On the opposite side the latus flares out at one end, always the same end, while the other end remains straight with the rest of the cirral. The flaring out initiates around the straight side of the cirral and is equal around both sides. The straight side has a 1.3 mm wide peg which inserts into a small socket on the adjacent cirral. The suture cannot be seen at any of the articulation points.

The height of each cirral is generally the same at about 2.0 mm high.

Remarks. The protruding edges were probably used as extra anchorage structures.

Stratigraphical range. Holkerian (Benbulben Shale Formation).

6.5. DESCRIPTIONS OF DISARTICULATED MATERIAL FROM PARTS OF THE CRINOID SKELETON OTHER THAN THE STEM AND CIRRI

6.5.1. INFRABASALS

Subclass CLADIDA Moore and Laudon, 1943

gen. et sp. indet. CLADIDA-TYPE INFRABASAL PLATES

Plate 93, fig. b; Plate 94, figs a, b; Figure 6.24.*e*

Holotype. Specimen TCD.53174 (Plate 1), a single infrabasal plate, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Other material. A single infrabasal (Plate 2), specimen number TCD.53227, was obtained from the same sample as the holotype.

Description. The plates are thin, slightly wider than high and pentagonal in lateral outline. The proximal ends bend under at right angles to form a base for the reception of part of the stem. The stem impression is circular and has symplectial articulation. The crenularium covers about 25% of the articular facet and has about thirty-five crenulae. The areola is planar. From specimen TCD.53174, the outline of the axial canal is pentagonal, but from specimen TCD.53227 the outline is circular.

Morphometrics of Plate 1 are outlined in Figure 6.24.*e*.

Remarks. Unfortunately, the holotype was broken whilst being prepared to go into the SEM for a second time.

Stratigraphical range. Arundian (Bundoran Shale Formation).

6.5.2. RADIALS

Subclass DISPARIDA Moore and Laudon, 1943

Superfamily ALLAGECRINACEA Carpenter and Etheridge, 1881

Emended d*iagnosis.* (Modified after Moore and Strimple 1973, p. 16; Moore, Lane *et al.* 1978, p. T537.) Radials upflaring, almost equally sized, or with *A* and *D* radials much larger than others, larger radials generally with multiple arm facets.

Family CATILLOCRINIDAE Wachsmuth and Springer, 1886

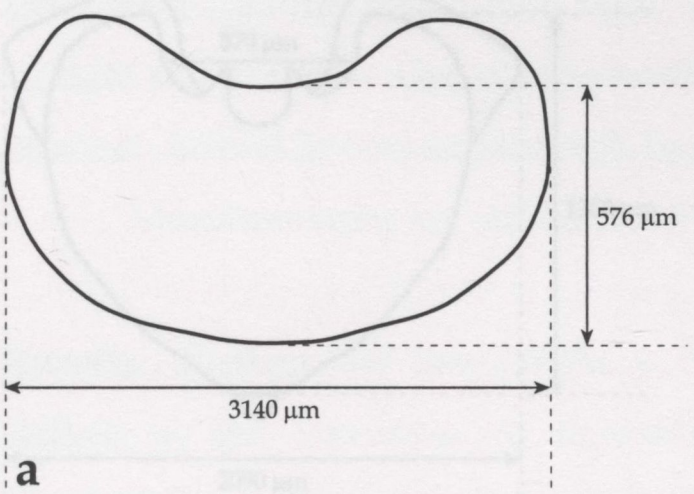
Diagnosis. (After Moore, Lane *et al.* 1978, p. T542.) Calyx low truncate conical or bowl-shaped to discoid, characteristic strong asymmetry owing to enlargement of *A* and *D* radials, large radials bear numerous unbranched slender arms, homocrinoid bilateral symmetry (*E-BC*) distinct and generally very well developed.

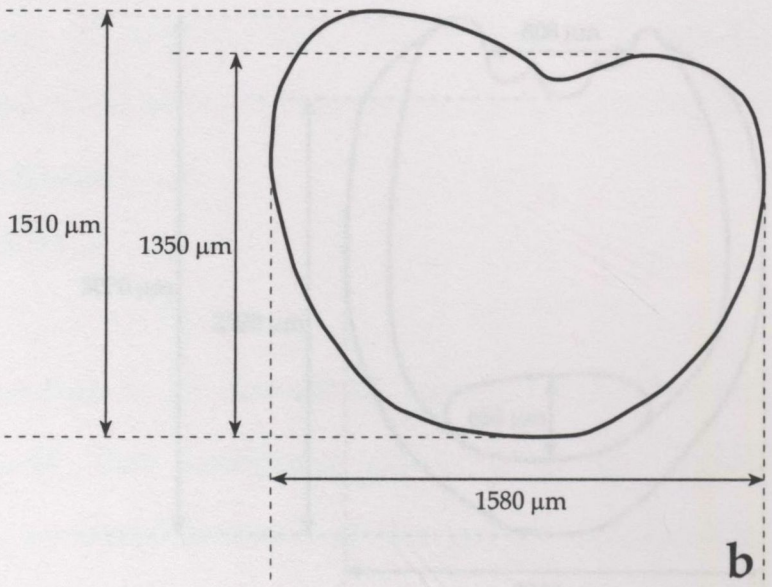
Stratigraphical range. Lower Ordovician; Lower to Middle Devonian; Lower Carboniferous; Lower to Middle Pennsylvanian; Upper Permian (Europe - USA - Indonesia - Czech Republic).

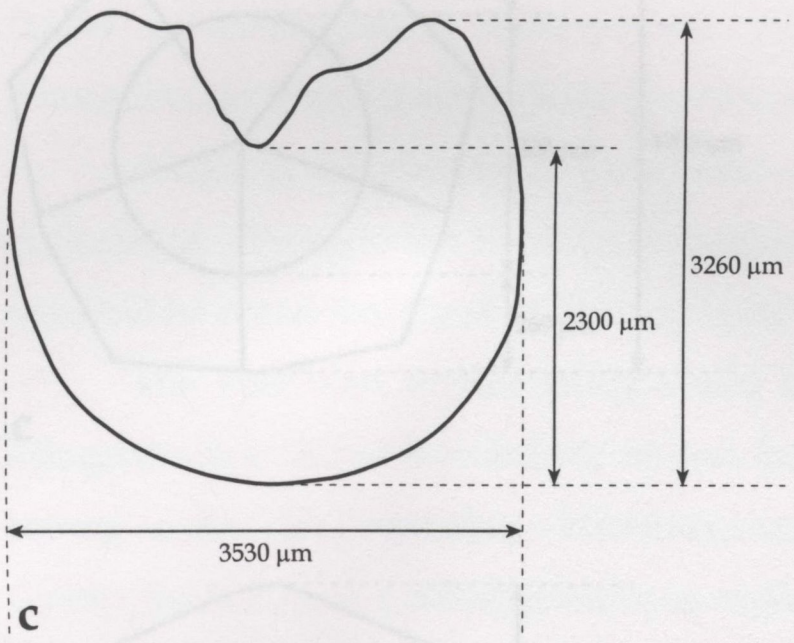
gen. et sp. indet. CATILLOCRINIDAE?-TYPE RADIAL PLATE 1

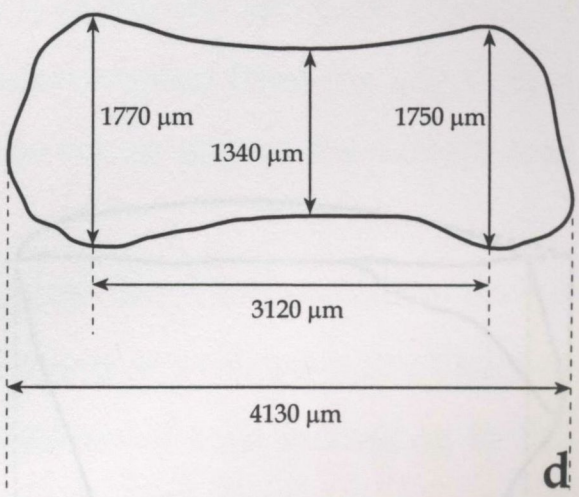
Plate 95, figs a, b; Figure 6.24.*d*

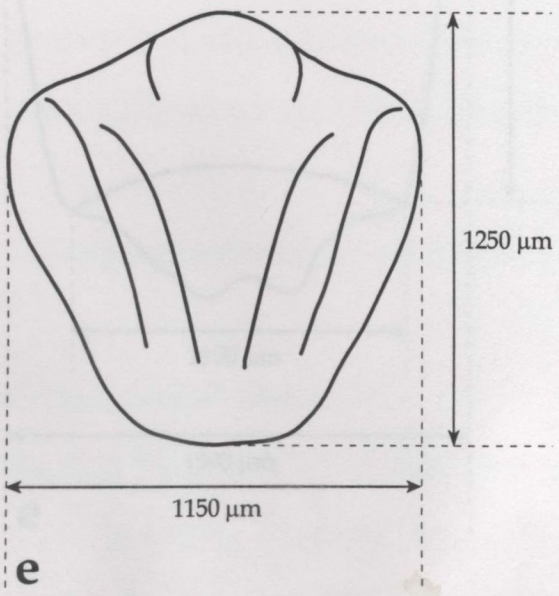
Holotype. Specimen TCD.53173, a single radial plate, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.











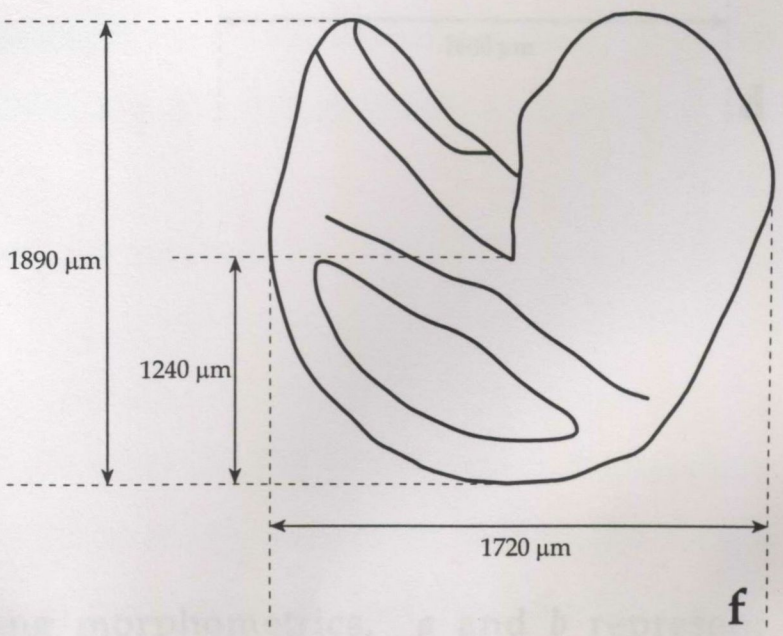


Figure 6.23. Outline sketches displaying morphometrics of brachials. *a* to *f* represent Cladida-Type Brachials 1 to 6 respectively.

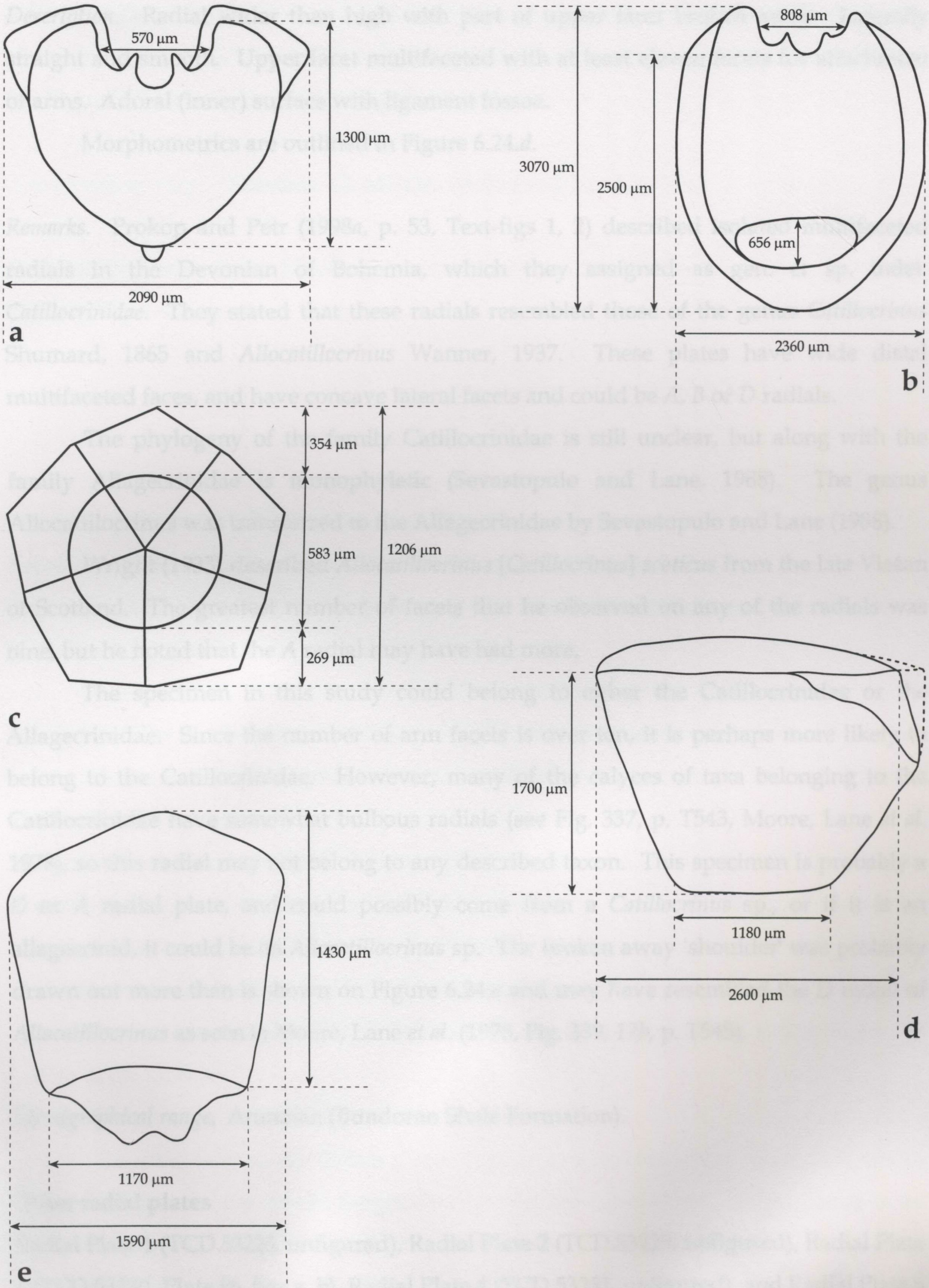


Figure 6.24. Outline sketches displaying morphometrics. *a* and *b* represent Flexibilia-Type Brachials 1 and 2 respectively, *c* represents Cladida-Type Infrabasal Circlet 1, *d* represents Catillocrinidae?-Type Radial Plate 1 and *e* represents Cladida-Type Infrabasal Plate 1.

Description. Radial wider than high with part of upper facet broken away. Laterally straight and smooth. Upper facet multifaceted with at least eleven facets for attachment of arms. Adoral (inner) surface with ligament fossae.

Morphometrics are outlined in Figure 6.24.*d*.

Remarks. Prokop and Petr (1998*a*, p. 53, Text-figs 1, 2) described isolated multifaceted radials in the Devonian of Bohemia, which they assigned as gen. et sp. indet. *Catillocrinidae*. They stated that these radials resembled those of the genus *Catillocrinus* Shumard, 1865 and *Allocatillocrinus* Wanner, 1937. These plates have wide distal multifaceted faces, and have concave lateral facets and could be *A*, *B* or *D* radials.

The phylogeny of the family Catillocrinidae is still unclear, but along with the family Allagecrinidae is monophyletic (Sevastopulo and Lane, 1988). The genus Allocatillocrinus was transferred to the Allagecrinidae by Sevastopulo and Lane (1988).

Wright (1933) described *Allocatillocrinus* [*Catillocrinus*] *scoticus* from the late Viséan of Scotland. The greatest number of facets that he observed on any of the radials was nine, but he noted that the *A* radial may have had more.

The specimen in this study could belong to either the Catillocrinidae or the Allagecrinidae. Since the number of arm facets is over ten, it is perhaps more likely to belong to the Catillocrinidae. However, many of the calyces of taxa belonging to the Catillocrinidae have somewhat bulbous radials (see Fig. 337, p. T543, Moore, Lane *et al.* 1978), so this radial may not belong to any described taxon. This specimen is probably a *D* or *A* radial plate, and could possibly come from a *Catillocrinus* sp., or if it is an allagecrinid, it could be an *Allocatillocrinus* sp. The broken away 'shoulder' was probably drawn out more than is shown on Figure 6.24.*e* and may have resembled the *D* radial of *Allocatillocrinus* as seen in Moore, Lane *et al.* (1978, Fig. 339, *12b*, p. T545).

Stratigraphical range. Arundian (Bundoran Shale Formation).

Other radial plates

Radial Plate 1 (TCD.53228, unfigured), Radial Plate 2 (TCD.53229, unfigured), Radial Plate 3 (TCD.53230, Plate 96, figs a, b), Radial Plate 4 (TCD.53231, unfigured), and Radial Plate 5 (TCD.53232), were found in the same sample as the Catillocrinidae?-Type Radial Plate 1 and remain undescribed.

6.5.3. BRACHIALS

See Figure 5.7 for measurement criteria of brachials.

Subclass CLADIDA Moore and Laudon, 1943

Emended diagnosis. (After Moore and Laudon 1943, p. 24, 32; Moore, Lane *et al.* 1978, p. T520, T578.) Arms simple or branched, free above radials, pinnulate or non-pinnulate.

gen. et sp. indet. CLADIDA-TYPE BRACHIAL 1

Plate 97, figs a-c; Figure 6.23.*a*

Holotype. Specimen TCD.53177, a single brachial, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The brachial is almost twice as high as it is long and almost twice as wide as it is long. It has a wide U-shape in transverse outline. It is symmetrical through a medial aboral-adoral line.

The articular facets both show symplectial articulation, but are of different widths and morphologies. Both have a wide U-shaped outline. The morphology of the smaller articular facet is unclear, but it is seen that there are some peripheral, radial crenulae. The wider facet has faint radial crenulae on its left and right sides that appear to graduate into a peripheral ridge along the base. From this ridge is a tooth, which is just below the centre of the facet.

The adoral groove is shallow and evenly curved.

The latus is concave. It has a sculpture of low, narrow, vein-like anastomosing ridges that mostly run almost longitudinally and are curved, but others appear to be randomly disposed. The stereom can be seen between these raised ridges.

Morphometrics are outlined in Figure 6.23.*a*.

Remarks. The sculpture of the articular facets in this type of brachial suggests immovable zygosynostosial or symplectial articulation.

Anastomosing ridges on the latera of these brachials are similar to those on the latera of pinnules belonging to *Shroshaecrinus obliquistriatus* Simms, 1989, and *Plicatocrinus inornatus* Simms, 1989 (Simms 1989*b*, Plate 14, fig. 8 and Plate 15, fig. 14 respectively).

Stratigraphical range. Arundian (Bundoran Shale Formation).

gen. et sp. indet. CLADIDA-TYPE BRACHIAL 2

Plate 98, figs a-c; Figure 6.23.*b*

Holotype. Specimen TCD.53178, a single brachial, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The brachial has an asymmetrical heart-shaped transverse outline. It is as wide as it is high and slightly wider than it is long.

Both articular facets have small tubercles and pits. They have the same asymmetrical heart-shaped outline.

The adoral groove is very shallow.

The latus is straight. Looking from one side the height of the brachial at both ends is the same, but looking from the other side it appears cuneate.

Morphometrics are outlined in Figure 6.23.*b*.

Remarks. Owing to the interlocking tubercles and pits on the articular facets, the type of articulation for this type of brachial is probably immovable zygosynostosy.

Stratigraphical range. Arundian (Bundoran Shale Formation).

gen. et sp. indet. CLADIDA-TYPE BRACHIAL 3

Plate 99, figs a, b; Figure 6.23.*c*

Holotype. Specimen TCD.53179, a single brachial, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation

(Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. Overall, the outline of this brachial is horseshoe-shaped in facetal view. It is symmetrical through a medial aboral-adoral line, except at the adoral apices where one shoulder is truncated and the other is pointed. The brachial is as wide as it is long, but is much lower than wide. It is cuneate.

Both articular facets are smooth and slightly concave. There is an uneven peripheral rim, but there is no obvious sculpture.

The adoral groove is asymmetrically V-shaped. A circular, shallow, crater-like pinnule socket is positioned halfway down the long side of the 'V' and is positioned more towards one articular facet.

The latus is straight and has a finely tuberculate to vermiculate sculpture.

Morphometrics are outlined in Figure 6.23.*c*.

Remarks. These brachials articulate by synostosy, which allows slight movement (Ubaghs 1978*a*, p. T171).

The outline of this type of brachial is similar to that of *Proallosocrinus glenisteri* Moore and Strimple, 1973 (see Moore, Lane *et al.* 1978, p. T743, Fig. 491, *2a, c*). This brachial probably originated from the distal arm of a cladid. It is similar to brachials of *Bundoranocrinus vermiculatus* gen. et sp. nov., but is not as high.

Stratigraphical range. Arundian (Bundoran Shale Formation).

gen. et sp. indet. CLADIDA-TYPE BRACHIAL 4

Plate 100, figs a-c; Figure 6.23.*d*

Holotype. Specimen TCD.53180, a single brachial, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The transverse outline of this brachial is a wide, angular U-shape. It is essentially symmetrical through a medial aboral-adoral line. It is much higher than it is wide and almost twice as wide as it is long.

The proximal articular facet has a thick transverse ridge, which pinches slightly in the centre. It is slightly oblique and separates a shallow, aboral ligament pit from an adoral muscular fossa.

The distal articular facet is unclear, but it has an oblique transverse ridge. It appears that his separates a shallow ligament fossa from a muscular fossa. A large pinnule socket appears to show synarthrial articulation.

The adoral groove is U-shaped and moderately deep.

The latus is concave with a sculpture of small, randomly disposed tubercles. The brachial height is greater on the side with the pinnule socket.

Morphometrics are outlined in Figure 6.23.*d*.

Remarks. The oblique transverse ridge indicates oblique muscular articulation (see Ubaghs 1978*a*, p. T163).

Stratigraphical range. Arundian (Bundoran Shale Formation).

gen. et sp. indet. CLADIDA-TYPE BRACHIAL 5

Plate 101, fig. a; Figure 6.23.*e*

Holotype. Specimen TCD.53181, a single brachial, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. This is an axillary brachial which, overall, is crescentic in adoral view. It is about as high as it is wide, and much higher than it is long. It is symmetrical through a medial aboral-adoral line.

All three articular facets appear smooth, but this is inconclusive. They do, however, all slope towards the adoral groove. The distal shoulders are moderately steeply sloping laterally and are slightly narrower than the proximal facet.

Overall, the adoral groove is a wide U-shape. Proximally, before branching, the floor of the adoral groove comprises three adjacent U-shaped grooves. On branching, the distal grooves have only two U-shaped floor grooves. It is not known what the sculpture of the adoral groove is distally from this point.

The latus is smooth and straight proximally becoming concave distally.

Morphometrics are outlined in Figure 6.23.*e*.

Remarks. The articulation of this brachial is not known, but it is probably immovable and non-muscular.

Stratigraphical range. Arundian (Bundoran Shale Formation).

gen. et sp. indet. CLADIDA-TYPE BRACHIAL 6

Plate 101, fig. b; Plate 102, figs a, b; Figure 6.23.*f*

Holotype. Specimen TCD.53182, a single brachial, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The brachial is cuneate, but unevenly shaped. It is slightly wider than it is long.

The proximal articular facet is unevenly U-shaped and has peripheral crenulae. The distal articular facet is a more evenly U-shaped. It has an oblique transverse ridge separating an aboral ligament pit and fossa from a muscular fossa. It cannot be seen if the muscular fossa is separated by an intermuscular ridge.

The adoral groove is U- to V-shaped. On one side, there is a shallow pinnule socket.

The latus is straight with some longitudinal striations on part of it. The brachial height is greater on the side with the pinnule socket.

Morphometrics are outlined in Figure 6.23.*f*.

Remarks. The proximal articular facet probably has symplectial articulation, while the distal has oblique muscular articulation.

A similar distal articular facet with muscular articulation is displayed in a brachial belonging to the comatulid *Himerometra* (Tertiary-Recent (USA, Eur., Pacific Ocean, Indian Ocean)) (Rasmussen 1978, p. T889, Fig. 593, 1*d*).

Stratigraphical range. Arundian (Bundoran Shale Formation).

Infraclass FLEXIBILIA Zittel, 1895

Diagnosis. (After Moore 1978, p. T765.) Arms non-pinnulate, uniserial, bifurcating isotomously or both isotomously and heterotomously, rarely atomous, incurved and tapering distally.

gen. et sp. indet. FLEXIBILIA-TYPE BRACHIAL 1

Plate 103, figs a, b; Figure 6.24.*a*

Holotype. Specimen TCD.53175, a single brachial, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. Aboral-adoral synarthrially articulating brachial. Overall, the brachial has a heart-shaped outline and is essentially symmetrical through a medial aboral-adoral line. It is about as high as the minimum length.

The proximal facet is rounded and has a wide horseshoe-shaped outline. The maximum width is greater than the maximum length. Crenulated areas lie either side of a central slightly depressed adoral ligament fossa. The crenulae are few in number, maybe seven, and are quite indistinct. The adoral ligament fossa has a slightly raised area near the adoral grove. An adoral lip, which is slightly narrower than the adoral groove, rises from the adoral extremity of the facet. It is rounded and moderately pronounced.

The distal facet has the same overall outline as the proximal facet. Crenulated areas occupy the same position. A transverse rim is situated on the aboral side of the widest part of the facet. Laterally and centrally, it is raised with two small depressions at either side of centre. The adoral ligament fossa is large and planar. The sides of the aboral ligament fossa slope steeply to form a deep socket for the reception of the lip from the adjacent distal brachial.

The adoral groove is overall a wide U-shaped. It comprises three smaller U-shaped furrows, which are all of equal width, the central one incising deeper into the

brachial.

The latus is smooth and planar. Two lateral spines, which are horizontally elongate, protrude normally from the adoral side of the widest part of the brachial and are disposed at mid-height. A single longer spine protrudes normally from the latus, but is positioned towards the distal facet and just to the left side of centre of the aboral fossa.

Morphometrics are outlined in Figure 6.24.*a*.

Remarks. The lip and socket on the facets of this brachial suggests that it came from a flexible crinoid.

Stratigraphical range. Arundian (Bundoran Shale Formation).

gen. et sp. indet. FLEXIBILIA-TYPE BRACHIAL 2

Plate 104, figs a, b; Plate 105, figs a, b; Figure 6.24.*b*

Holotype. Specimen TCD.53176, a single brachial, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Material. Several specimens were handpicked from the same sample as the holotype and are deposited in a cover slide, number TCD.53233. A single brachial, specimen TCD.53252, was taken from this slide (Plate 105). Further brachials are available for description in the sample.

Description. Aboral-adoral synarthrially articulating brachials. The brachial is elongate U-shaped in outline. It is almost symmetrical through a medial aboral-adoral line, but the right adoral 'shoulder' is slightly wider and more blunt. The left lateral edge of the facet is rounded while that of the right is moderately straight.

The distal facet is rounded oblong in outline the length coincident with the aboral-adoral line. The maximum facet length is almost twice the maximum facet width. Separating the facet adorally-aborally into three equal sections, the centre third is occupied by the adoral ligament fossa and the outer two by crenulated areas. The fossa is planar and is oblong in outline. The crenulae are distinct with rounded apices and

troughs. They are simple and about ten are disposed along each side. Near to the transverse rim, they are parallel with it, but moving adorally, their angle increases so that they almost radiate from the imaginary centre point of the facet. The transverse rim lies to the aboral side of the widest part of the facet. It is disposed at a slight angle, the higher side being on the left. It has a finely crenulate or vermiculate sculpture along its length. Transversely it is angulated so that adorally it slopes gently towards the adoral ligament fossa. It slopes more steeply on the aboral side where it is directly adjacent to the aboral ligament fossa. The sides of this fossa slope very steeply to form a very deep socket for the reception of the lip from the apposing facet. The aboral boundary with the latus is marked by a very sharp arcuate ridge.

The outline, adoral ligament fossa and crenulated areas of the proximal facet are similar to those of the distal facet. The aboral lip is very high and evenly rounded. A low transverse rim is positioned adorally to the lip and is at the same angle as that on the opposing facet. Tiny crenulae are disposed along the adoral side of the rim and are oriented perpendicular to it. Oblique crenulae lie in the lateral areas on the aboral side of the ridge and tiny pimples and depressions lie in the central area. The side of the lip which is part of the facet, *i.e.* the inner face, has three concentric half-rings which are coincident with the curve of the lip itself and which become larger outwards.

The adoral groove is U-shaped overall and it comprises three smaller U-shaped furrows. The middle one incises slightly deeper into the brachial than do the lateral ones, but they are all of about the same width.

The latus has a ridge at mid-height, but is only present on the left and right sides. The ridge apex is smooth on the right, but on the left irregular depressions are apparent. Aboral latus has a longitudinal ridge that continues from the depression marking the aboral ligament fossa to the lip apex. A few small tubercles are present at either side of the ridge.

Morphometrics are outlined in Figure 6.24.*b*.

Remarks. The lip and socket on the facets of this brachial suggests that it came from a flexible crinoid.

The individual brachials from cover slide TCD.53233 show a wide variation in heights, widths and lengths, although they retain the same overall morphology as the holotype. One of these morphotypes is shown in Plate 105, Figs a and b (TCD.53252).

Stratigraphical range. Arundian (Bundoran Shale Formation).

Discussion. Neither Flexibilia-Type Brachial 1 or 2 appear to have either the overall shape, dimensions or morphology, especially lateral, which would suggest that they are derived from any of the flexible genera described in Section 6.2. Brachials of *Onychocrinus polydactylus* (M'Coy), 1844, have a very finely tuberculate lateral sculpture. Similarly, *Amphicrinus scoticus* Springer, in Wright, 1914, has a lateral sculpture of fine pustules. The sculpture of spines, ridges and small tubercles on the aboral latera of the two current brachial types are quite distinct and clearly do not appear like the brachials of *O. polydactylus* and *A. scoticus*. It seems curious that the washed samples apparently produce no loose brachials of the species that are found as entire, or nearly entire, specimens.

6.5.4. INFRABASAL CIRCLETS

Subclass CLADIDA Moore and Laudon, 1943

Emended diagnosis. (After Moore and Laudon 1943, p. 24, 32; Moore, Lane *et al.* 1978, p. T520, T578.) Dicyclic aboral calyx composed of tightly sutured plates.

gen. et sp. indet. CLADIDA-TYPE INFRABASAL CIRCLET 1

Plate 93, fig. a; Figure 6.24.*c*

Holotype. Specimen TCD.53172, a single circlet of five infrabasal plates, from Bed BD:D1, a 3 m thick dark grey, calcareous, muddy, fissile shale. Taken from a bulk sample 2 m down from top of the bed and 3 m down from limestone marker bed x, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 8199 5958.

Other material. Three further specimens, numbers TCD.53224, TCD.53225 and TCD.53226, remain undescribed. They are from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The specimen comprises a circlet of five equally sized, fairly thick infrabasals. Each plate is about as high as it is wide. The proximal ends bend under at about 145° to

form a base for the attachment of the stem. The outline of the stem is circular and the impression left shows symplectial articulation. There are only five simple crenulae on the crenularium, which covers 66% of the total facetal diameter. A smooth areola surrounds the axial canal, whose outline cannot be clearly seen.

Morphometrics are outlined in Figure 6.24.*c*.

Remarks. The holotype suffered no damage following immersion in 3.6% hydrofluoric acid for one week.

Stratigraphical range. Arundian (Bundoran Shale Formation).

6.5.5. HOLDFASTS

Subclass and lower Plesion UNCERTAIN

HOLDFAST 1

Plate 90, fig. b

Holotype. Specimen TCD.53183, a holdfast attached to another type of pluricolumnal, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The holdfast is attached to a pluricolumnal (2580 μm) of slightly smaller diameter (616 μm), appearing like a clutched hand. It has a proximal columnal-like articular facet (921 μm diameter) that shows symplectial articulation. The smaller pluricolumnal also articulates symplectially, but has a different articular facet morphology.

Remarks. This type of holdfast does not appear to be described by Brett (1981, 1984), although 'virgate', which he describes as 'radices composed of a few asymmetrically developed rootlets' (1981, p. 349), but does not figure, could be similar. It may also be a cirrus-bearing type holdfast where cirri carry 'fingerlike projections' that attach to firm objects (Ubaghs 1978*a*, p. T88).

Stratigraphical range. Arundian (Bundoran Shale Formation).

6.5.6. ANAL TUBE PLATES

Subclass CLADIDA Moore and Laudon, 1943

Emended diagnosis. (After Moore and Laudon 1943, p. 24, 32; Moore, Lane *et al.* 1978, p. T520, T578.) Up to four anal plates in calyx, prominent anal sac.

gen. et sp. indet. CLADIDA-TYPE ANAL TUBE PLATE 1

Plate 106, fig. a

Material. Specimen number TCD.53185, a single anal tube plate, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a 3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The plate is hexagonal with a straight proximal and distal facet. Two lateral sides are straight and two are denticulate, the latter being drawn out further into a sharper angle. Longitudinally, the plate is slightly curved outwards. The inner and outer surfaces are essentially smooth, except for in the vicinity of the denticulation where they are vaguely corrugated, the apices 'in phase' with the denticle apices.

Remarks. This is a typical anal sac plate of a cladid. However, the denticulate edge is not unlike that found on a primary cover plate of an edrioasteroid with a multicyclic cover plate series (A. Smith, pers. comm. 2000).

Stratigraphical range. Arundian (Bundoran Shale Formation).

gen. et sp. indet. CLADIDA-TYPE ANAL TUBE PLATE 2

Plate 106, fig. b

Material. Specimen number TCD.53221, a single anal tube plate, collected in 1972 by Professors G. D. Sevastopulo and N. G. Lane from the 'flexible shale' (FX) (=Bed BD:D1), a

3 m thick dark grey, calcareous, muddy, fissile shale, near the base of the Bundoran Shale Formation (Arundian), Bundoran, Co. Donegal, GR 819 595.

Description. The plate is unevenly hexagonal. The distal and proximal facets are smooth, narrow and concave. The other four faces are uneven and this is caused by corrugations that originate on the outer and inner surfaces of the plate. These corrugations radiate from a little way in from the plate edges and continue to the four lateral sides. The corrugations are slightly bent so that they do not necessarily run exactly perpendicular to the sides. The plate is fairly strongly convex outwards.

Remarks. It is not known from which crinoid this plate originated. It is similar to the anal sac plates of *Linocrinus arboreus* (Worthen) (see Ubaghs 1978*a*, p. T187, Fig. 159, *3*).

Stratigraphical range. Arundian (Bundoran Shale Formation).

Other anal tube plates

A third type of anal tube plate, specimen TCD.53241, remains undescribed.

6.6. DESCRIPTIONS OF SOME OTHER FAUNA

All the following specimens were found at Bundoran in the 'flexible shale' (FX) or Bed BD:D1.

6.6.1. BRYOZOANS

Two types of bryozoan are described. The first specimen (number TCD.53184, Plate 108, fig. b) is *Fistulipora incrustans* (Phillips, 1836) (Wyse Jackson, pers. comm. 2000), which is encrusting the entire circumference of the latera of a pluricolumnal and giving the entire specimen a bulbous appearance. The second specimen (number TCD.53223, unfigured) is *Sulcoretepora parallela* (Phillips, 1836) (Wyse Jackson, pers. comm. 2000), which has a pluricolumnal attached to it. Part of the colony is grown around the pluricolumnal and the remaining part is growing along side it at a slightly oblique angle.

The encrustation of *F. incrustans* on the pluricolumnal is likely to have occurred when the crinoid was alive and the stem still in its life position. The colonies are usually found

encrusting such organic substrates (Bancroft and Wyse Jackson 1995). The occurrence of the *S. parallela* specimen with the pluricolumnal probably came about by part of the flexed stem of the live crinoid growing in close proximity to the erect bryozoan colony and, thus, the colony growing around part of the stem (Wyse Jackson, pers. comm. 2000). It is unlikely that the pluricolumnal was lying on the substrate and became enmeshed by the growing colony because the short postmortem survival of the stem ligaments means it would be expected that the columnals would completely disarticulate within a relatively short period of time.

6.6.2. BLASTOID OSSICLES

Two similar series of plates were found. Both of the specimens taper and comprise biserially arranged pentagonal plates, which are crescentic in outline, the outer side of each plate being slightly concave. A zigzag suture is formed where they meet and both rows of plates slope downwards towards the zigzag to form a very low V-shaped channel centrally. The plates have an sculpture of tiny peripheral crenulae that extend normal from each side, except the outer one. The plates are lower than they are high. The first specimen (number TCD.53186, Plate 107, fig. a) has six plates in one row and seven in the other. The second specimen (number TCD.53222, unfigured) is slightly shorter, but has the same number of plates and it is slightly warped. On the opposite side of this specimen, at least two ridges continue along its length.

These ossicles are the fused flooring plates of a blastoid ambulacrum (A. B. Smith, pers. comm. 2000). In Beaver *et al.* (1967) the portion shown as the 'lancet' (p. S322, Fig. 190, *1*) and 'exposed ambulacral plates' (p. S322, Fig. 190, *2*) seems to represent this part. He comments that the sides of the V-shaped median groove are marked by tiny crenulations for articulation with the covering plates.

6.6.3. ECHINOID OSSICLES

These specimens were immersed in 3.6% hydrofluoric acid for one weekend and underwent no breakages or cracking.

Specimen TCD.53242 (Plate 108, fig. a) is a series of ambulacral plates probably originating from *Maccoya*. *Maccoya* has tubercles whereas *Palaechinus*, the other echinoid common in the Arundian, lacked them.

Specimen TCD.53244 is a thick, hexagonal echinoid plate with a verrucate outer sculpture. It is probably an interambulacral plate also from *Maccoya*.

6.6.4. BORED PLURICOLUMNAL

This specimen (TCD.53070) was immersed in 3.6% hydrofluoric acid for one week and did not break or crack.

This pluricolumnal is swollen (Plate 28, fig. e) and has a hole surrounded by a depression on its lateral surface. The swelling of this pluricolumnal has closest affinity to a Type A barrel-shaped inflation of the stem described by Franzén (1974, p. 294-295, Fig. 10, A). It was probably caused by the parasitic, epizoic *Phosphannulus* Müller, as described by Welch (1976, Plate 1, Fig. 6).

CHAPTER 7

PALAEOECOLOGY, TAPHONOMY AND DIVERSITY

7.1. PALAEOECOLOGY

7.1.1. INTRODUCTION

The majority of extant crinoids are stemless feather-stars which live in clear, shallow coastal waters down to about 200 m. Living stalked crinoids live in deep water, the majority usually from 100 m (Simms 1989*b*), down to about 1000 m depth, but a small number may range to 6000 m below sea level. Geographically, they have a wide distribution being found in warm tropical seas to cold arctic waters (Black 1970).

The majority of Palaeozoic crinoids had a stem which was attached to the sea floor, or any other suitable surface, by means of various pelmatic structures. Such crinoids were geographically widespread and, while the greatest diversity was probably in equatorial latitudes, high latitude faunas are known, particularly from the Permian of Australasia.

7.1.2. PALAEOECOLOGY OF CARBONIFEROUS CRINOIDS DESCRIBED BY PREVIOUS AUTHORS

Lane (1972) discussed the synecology of Mississippian crinoid communities in the Borden Delta of Indiana. The Borden delta advanced, prograding south, then receded and ceased eventually to be replaced by shallow water with carbonate deposition. He identified two crinoid communities in the oldest part of the sequence (Crawfordsville), both living in quiet, deeper waters on the foreset of the Borden Delta. The first community lived on the interdistributary slopes in clear water and was dominated by monobathrid camerates (*Macrocrinus, Agariocrinites, Actinocrinites, Uperocrinus* and *Eretmocrinus*) with fewer disparids (*Halysiocrinus*) (Lane 1972; Lane and Matthews 1965). Typically, the slowly deposited sediments here (where crinoids are disarticulated) consisted of laterally restricted interbedded bioclastic limestone lenses and silty claystones, with uncommon fine, terrigenous material. The second community lived offshore from distributaries in quiet, turbid water where there was rapid silt sedimentation and was dominated by small poteriocrine inadunates (*Scytalocrinus, Decacrinus* and *Histocrinus*). Also, the large flexibles *Taxocrinus* and *Onychocrinus*, and the cladid *Barycrinus* resided here. None of them, however, lived on the soft, rapidly accumulating bottom sediments. Although this

community was laterally restricted in distribution, it contained a more abundant and diverse fauna than the first. It was thought that the reasons that these different groups thrived in different areas was due to their food capture capabilities, nutrient levels and productivity, although both communities were tiered (see Section 7.1.3 below). Long-stemmed crinoids were less abundant, diverse and widespread. The succeeding community lived on the topset of the delta in shallower, agitated water, and the next on the post-delta carbonate banks. The diversity of the community decreased up through this succession. Also, differences in water depth and rate of sedimentation affected different genera which belonged to the same family.

Cluster analysis enabled Ausich and Lane (1985) to determine that a monobathrid-disparid assemblage prevailed from the Burlington through Warsaw formations in bioclastic carbonate substrates. In the Keokuk Formation a poteriocrine inadunate assemblage occurred in siltstones and fine-grained sandstones with an equitable diversity fauna in mudstones. Geographic endemism was displayed around the Illinois Basin.

Ausich *et al.* (1979) recognised three main communities (including other fauna as well as crinoids) associated with the Borden Delta on the east side of the Illinois Basin; these were delta platform, delta slope and prodeltaic communities. Each was separated into different subcommunities. The delta platform community had a vertically tiered component and a trace fossil component. Three epifaunal communities were recognised in the tiered component. The crinoids of the carbonate bank community contained *Alloprosalocrinus*, *Halysiocrinus* and *Eretmocrinus*, the distributary channel community contained *Scytalocrinus*, *Abrotocrinus* and *Cribanocrinus*, and the interdistributary mudstone community contained *Halysiocrinus*, *Platycrinites*, *Cyathocrinites* and *Barycrinus*.

Ausich and Sevastopulo (1994) described the taphonomy and faunal composition of assemblages of crinoids from Tournaisian rocks at Hook Head, County Wexford. The shallower water assemblages were dominated by camerates and the deeper water assemblages by cladids, similar to the story in the Borden Delta.

7.1.3. TIERING MODEL

The concept of vertical structuring or niche partitioning of invertebrates in ancient benthic marine communities has been described by several authors (Lane 1963, 1972; Ausich 1979,

1980; Ausich and Bottjer 1982, 1985*a*, 1985*b*, 1991; Bottjer and Ausich 1986; Sprinkle 1992). Lane, Sprinkle and Ausich have elaborated the idea with echinoderms mainly from the Carboniferous, and Ausich and Bottjer extended the model to include the whole of the Phanerozoic. Ausich (1980) termed the vertical partitioning '*tiering*'. For their lateral distribution crinoids are energy controlled, but in tiering they are primarily controlled by vertical distribution and secondarily by food-particle size capture capability.

Ausich (1980) described a tiering model in the Keokuk-aged rocks of the Edwardsville Formation, southern Indiana, which is approximately the same age as the Arundian of Great Britain and Ireland. The fauna of the entire suspension feeding community was considered in his model. Three tier-levels were proposed: low level between 0 m and 0.2 m above the substrate; intermediate level between 0.2 m and 0.5 m above the substrate and high level between 0.5 m and 1.0 m above the substrate, although these were not intended to be taken as strict boundaries.

The measurements made by Ausich for his tiering model were of the stem plus the roots, but did not include the calyx (W. I. Ausich, pers. comm. 1996). He made no measurements of the stem diameters, but noted that Lane had previously stated that stem diameter was not important. Not until he started to look at stem flexibility did he measure diameters of stems (W. I. Ausich, pers. comm. 1996).

A stem section of 1.89 m in length was discovered in a shale parting at Bundoran (Locality BD:C, Bed BD:C2). It was overlain by, and intertwined with its neighbour of 1.60 m in length (Plates 56 and 57). The stem is composed of columnals belonging to Columnal Taxon Number 28 (p. 214). With the discovery of these long stem sections another tier (upper crinoid tier) was proposed by Mannifield and Sevastopulo (1998) approximately spanning the space between 1 and 2 m above the substrate (Figure 7.1). In the lower (between 0.2 m and 0.5 m), intermediate (between 0.5 m and 1.0 m) and upper (between 1.0 m and 2.0 m) crinoid tiers competition was between crinoids only, but in the lowest communal tier (between 0.0 and 0.2 m), other benthic suspension feeders were also competing for food.

Lane (1963) described a flexible *Onychocrinus* stem as being at least 0.79 m in length and a camerate *Gilbertsocrinus* stem as being 0.81 m. These specimens came from

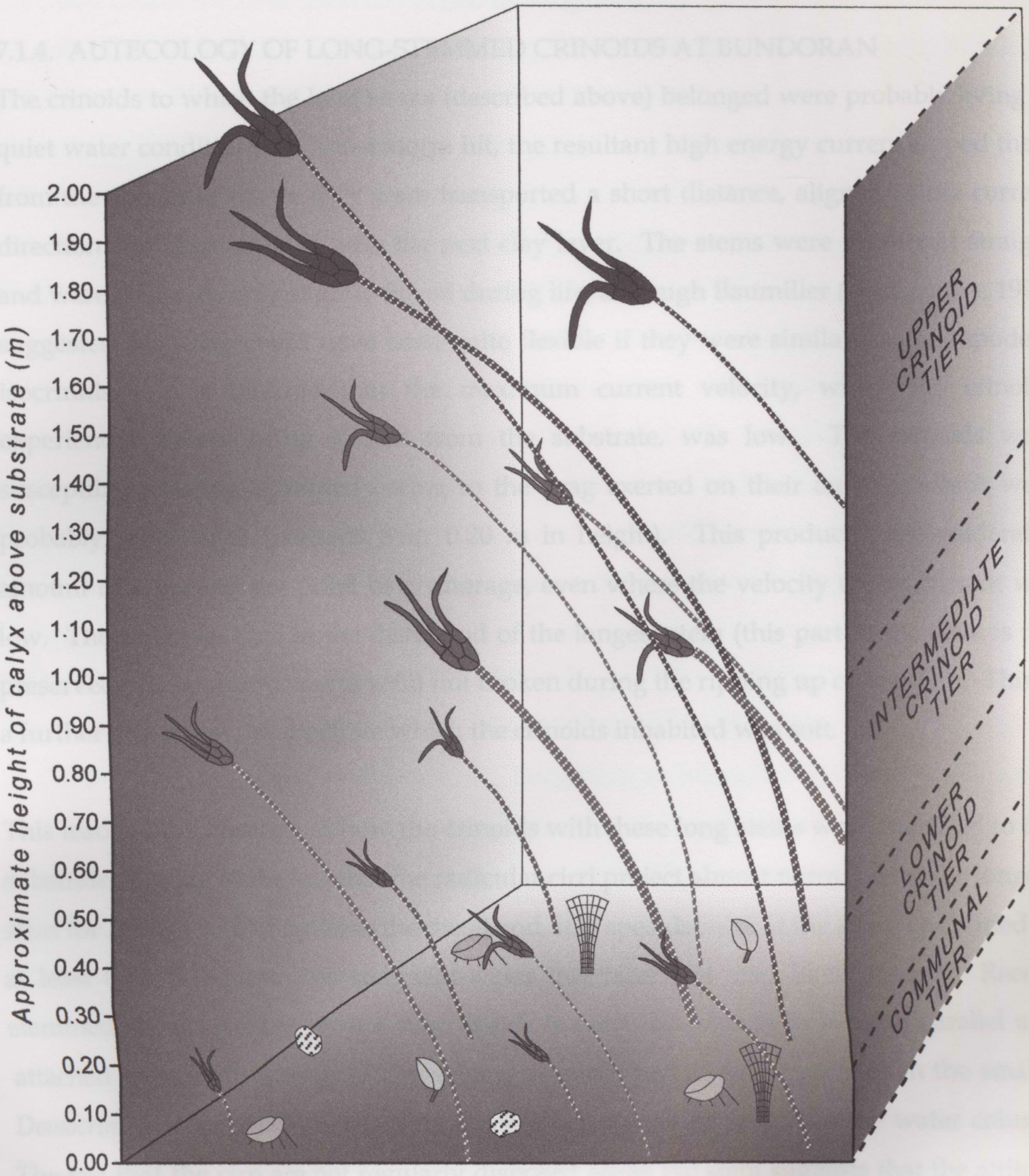


Figure 7.1. Tiering model for Dinantian marine communities in which crinoids were the dominant fauna. It is thought that four tiers were created by the different species of crinoids whose different stem lengths brought their calyces to various heights above the substrate for feeding (Mannifield and Sevastopulo 1998 (modified after Ausich 1980)).

Crawfordsville, Indiana (Viséan). The stems found in Bundoran are the longest Palaeozoic crinoid stems described thus far (in fact, only the stems of the Jurassic *Seirocrinus* are longer) and alter the tiering boundaries suggested by Ausich.

7.1.4. AUTECOLOGY OF LONG-STEMMED CRINOIDS AT BUNDORAN

The crinoids to which the long stems (described above) belonged were probably living in quiet water conditions. When a storm hit, the resultant high energy current ripped them from the substrate where they were transported a short distance, aligned to the current direction and then covered with the next clay layer. The stems were preserved straight and were probably only slightly flexed during life, although Baumiller (pers. comm. 1997) suggested that they could have been quite flexible if they were similar to some modern isocrinids. It is inferred that the maximum current velocity, which the crinoids experienced before being ripped from the substrate, was low. The crinoids were susceptible to being uprooted owing to the drag exerted on their crowns, which were probably quite large (perhaps over 0.20 m in height). This produced a considerable amount of torque at the point of anchorage, even where the velocity of the current was low. The radicular cirri at the distal end of the longest stem (this part of the stem is not preserved on the shorter stem) were not broken during the ripping up of the stem. This is a further indication the substrate which the crinoids inhabited was soft.

This leads to the question of how the crinoids with these long stems were anchored to the substrate. Owing to the fact that the radicular cirri project almost normal from the longest stem for at least 0.10 m up from the distal end, it is speculated that the stem was buried to at least 0.10 m beneath the sediment-water interface, and very likely deeper. Recent stemmed crinoids either have a stem which is erect then bends to become parallel and attached to the substrate as in *Cenocrinus*, or one which is sub-vertical as in the smaller *Democrinus*. Presumably these both reach about the same height in the water column. The fact that the cirri are not regularly disposed along the stem suggests that the attitude of the Bundoran crinoid was upright and more-or-less straight, like *Democrinus*, so probably reached a considerable height up into the water column.

It is clear to see that there are advantages of a crinoid having a stem so much longer than others and thus elevating its crown to a greater height. Firstly, there would be less trophic competition since there were few other attached, benthic suspension feeders

which reached to such a height in the water column. Secondly, when excessive currents disturb bottom sediments the calyx would be high enough above the level of disturbance to evade pollution. However, there are also disadvantages. Firstly, the effective torque at the distal end of the stem must have been much greater than that for a crinoid with a stem of only 1 m in length. Secondly, the long stems were probably prone to attack by predators (see Waters and Maples 1991) such as fish.

7.2. PALAEOCOMMUNITIES

Caldwell (1959) discussed how certain types of limestones and shales in northwest Ireland yielded certain faunal associations and showed that these lithologies are linked with and distinguished by the taxa (or their proportionate numbers) that they contain. He recorded that thinly bedded limestones and shales characteristically include an association of zaphrentids, caninioids, spinose athyrids, pustulose productoids and laminose spiriferids. Such associations, together with bryozoans and echinoids, occur in both the Bundoran Shale Formation (Section 2.4.2) and the Benbulben Shale Formation (Section 2.4.4).

7.2.1. PALAEOECOLOGICAL INTERPRETATION OF CRINOIDS AND FAUNAL ASSEMBLAGES IN THE BUNDORAN SHALE FORMATION

In the lower beds of the Bundoran Shale Formation at Bundoran there was a rich and diverse fauna, the echinoderms including crinoids, echinoids, blastoids, ophiuroids and asteroids, and other fauna including various brachiopods, fenestrate bryozoans, sponges and horn corals. The echinoderms were the dominant fauna, especially the crinoids. The community lived on a soft muddy substrate. Large productoids with spines for anchorage on such a substrate were common, as were long-hinged spiriferids. Erect fenestrate bryozoans, which cemented to small objects such as shell fragments to prevent their sinking into the mud, were also common. [Colonies of *Fistulipora incrustans* (Phillips) are particularly abundant in carbonate platform lithofacies in association with other bryozoan, crinoid, coral and brachiopod abundant communities (Bancroft and Wyse Jackson 1995), and are found in pure carbonate lithologies (in the lower parts of the Bundoran section).] Horn corals, for example *Zaphrentites*, lay recumbent on the substrate, the wide shape of the corallum prevented its sinking and kept the polyp above the sea-floor. These fauna were undisturbed. Higher energy conditions including storm events, represented by the limestones, were apparently unfavourable for most fauna to

thrive in, except for some large solitary corals. Crinoids were susceptible to being uprooted due to the soft substrate they inhabited. They recolonised the muddy bottom each time following the return to quiet water conditions.

Moving up the Bundoran Shale Formation at Bundoran the shale becomes less calcareous and less commonly are silty. Limestones occurred only as thin ribs and thin siltstones appeared. There was a reduction in the diversity of fauna overall and only horn corals, a few brachiopods and some bryozoans appeared to thrive in this environment, together with the generator of *Skolithos* burrows. Only very few crinoids could tolerate the less calcareous, more silty environment. At this time the cleaner, deeper waters which the crinoid fauna preferred, moved southwards as the terrigenous input increased from the northwest. Crinoids reappeared for a short while as the delta front regressed slightly again and the waters became cleaner. On evidence of columnal material, some of the crinoid taxa which returned were the same, but there were also some new taxa and some taxa which apparently disappeared.

Once the environment became deltaic with the input of clastics of the Mullaghmore Sandstone Formation the crinoid fauna changed again. Only few taxa could tolerate this kind of environment, indicated by the low number and diversity of columnals found. As the shoreline moved to the southeast the crinoid fauna stayed in the cleaner waters in front of the delta.

In the hinge at Portmore (Locality CM:Hinge), the depositional environment was similar to that at Bundoran from the lithology: calcareous, clay-rich shales and limestones, although the shales do not get noticeably siltier as they do at Bundoran. The fauna consisted of only shelly organisms which dominated only a few thin beds. Crinoids were apparently lacking in this area. This is probably because the environment was unsuitable for their survival.

Overall, there were subtle changes in taxa moving up through section, as well as lateral ones, because some appear in some places, but not it others. [See Section 2.4.2 for more on general palaeoecology and environment of deposition.]

7.2.2. PALAEOECOLOGICAL INTERPRETATION OF CRINOIDS AND FAUNAL ASSEMBLAGES IN THE BENBULBEN SHALE FORMATION

The regression of the delta front back towards the north west meant the return of deeper water conditions and this is represented by a major flooding surface of the Benbulben Shale Formation. Quiet conditions again dominated, and the shales produced were more calcareous and clay-rich than in the older Bundoran Shale Formation. These shales also held a diverse fauna with the same groups of organisms, but many of which were represented by different taxa. The fauna had similar attributes as those at Bundoran; to prevent sinking in a soft muddy substrate. Crinoids were again the most diverse and abundant preservable component in the community. The quiet conditions were ideal for the crinoid community to thrive with little competition for feeding. A similar tiering structure to that inferred to be in place at Bundoran was probably in operation, although the tier heights are not known since long stem sections were not recovered from this formation. Geographically, it seems that crinoids were more widely spread during the Holkerian since at all the localities where the Benbulben Shale Formation was seen crinoids were present, diverse and fairly abundant. [See Section 2.4.4 for more on general palaeoecology and environment of deposition for the Benbulben Shale Formation.]

7.2.3. PALAEOECOLOGICAL INTERPRETATION OF CRINOIDS AND FAUNAL ASSEMBLAGES ELSEWHERE IN THE VISÉAN

Crinoids were common throughout the rest of the Sligo succession in northwest Ireland, although they never thrived as much in the study area as they did during the time of deposition of the Bundoran and Benbulben Shale formations. Initially, during the time of deposition of the Ballyshannon Limestone Formation, the clear, warm waters were an ideal environment for crinoids to live in and they were present in large numbers. However, the fully deltaic environment of the Mullaghmore Sandstone Formation was not suitable for crinoids to survive in since the energy was high and the salinity was not high enough, although there are a few crinoids found from times when energy was lower with less clastic input. The Glencar Limestone Formation housed a crinoid fauna. The shales between the higher energy limestones were subordinate so that the crinoid fauna could not really get established between each period of limestone deposition. In the Dartry Limestone Formation crinoids were present in reduced numbers in the bedded limestones. They were also a significant component in the mudmounds.

7.3. INTERPRETATION OF SYNECOLOGY OF CRINOIDS FROM DISARTICULATED MATERIAL

Although disarticulated crinoid stems are extremely common within shale units, it is rare that it can be determined from which taxa they were derived. However, disarticulated crown material (brachials from the arms and calycal plates) can often be identified down to at least subclass or infraclass, or sometimes a lower level.

In the present study the majority of disarticulated crown material originated from cladid crinoids as can be seen from the descriptions of brachials in Chapter 6. Disarticulated flexible material also occurs in moderate amounts (mostly brachials) and disarticulated camerate crown material is very rare. The large proportion of disarticulated cladid material suggests that they were better suited to the muddy, calm environment than the other groups. However, on comparing the articulated crown material it appears that disparids and flexibles were also present, probably in a significant proportion, as were camerates, for example, *Platycrinites*.

An observation which stands out from looking through all the material is that crinoid taxa which have been described from articulated material herein are not found as disarticulated material. *Platycrinites*, with its large, easily identifiable radials, is commonly found preserved as cups or thecae, yet it is only their columnals which have been commonly found as disarticulated material (Section 6.3). Likewise, *Amphicrinus* ossicles have not been found as disarticulated material even though the presence of a relatively large number of their calyces have been found (Section 6.2). This is probably due in part to a dominance of cladids in the crinoid community, but also the nature of the calyx of these crinoids, burial and taphonomic processes (see Section 7.4 below).

The Borden Delta can be considered analogous to the environment seen in northwest Ireland from the Arundian to the Holkerian-Asbian. It had thriving communities with crinoids being the dominant fauna. The Crawfordsville community is the most comparable to that in northwest Ireland. What is immediately apparent is the difference in the overall crinoid fauna. In Bundoran, in the turbid water palaeoenvironment, cladids were by far the most abundant group (*Bundoranocrinus* and *Phanocrinus*), whereas monobathrids of the Crawfordsville fauna dominated the equivalent environment, as they

did in Hook Head (Ausich and Sevastopulo 1994). Flexibles (*Amphicrinus* and *Onychocrinus*) probably contributed more to the fauna than the disparids, which are essentially represented only by microcrinoids (*Litocrinus* and ?*Catillocrinus*). The greatest contrast is in the camerates. In the Borden group monobathrid camerates hold the largest percentage of the crinoid fauna. At Bundoran, however, they are represented by only a few genera (*Platycrinites*). So, in similar environments cladids are dominant in Ireland and monobathrids in the United States. This is probably due to the camerate extinction which followed soon after this time which affected Europe before the United States (Sevastopulo, pers. comm. 2000). The cladids, mainly advanced poteriocrinitids, diversified as the camerates approached their demise (Lane and Sevastopulo 1987).

7.4. TAPHONOMY

7.4.1. DISARTICULATION OF THE CRINOID SKELETON

Some parts of the crinoid skeleton are more susceptible to post-mortem disarticulation than others. The order of complete disarticulation would most likely start with the pinnules, followed by cirri, arms, tegminal plates, calycal plates and finally complete disarticulation of the stem (see Figure 4.1).

7.4.2. BURIAL RATES AND PRESERVATION

After death, in normal marine environments benthic crinoids are susceptible to rapid disarticulation. This occurs through the bacterial decay of the soft tissues, current action, and the activities of scavengers and other vagile benthos (Meyer 1971; Liddell 1975). The discovery of fully articulated specimens is comparatively rare with regards to the discovery of disarticulated material. Preservation of these articulated specimens is the result of death through rapid burial by an influx of sediment, and to a sufficient depth to prevent subsequent bioturbation (Meyer 1971; Liddell 1975). This must also be the way in which some long sections of stem are preserved since they probably disarticulate completely into individual ossicles within about two weeks (see Baumiller and Ausich 1992). Nevertheless, because crinoid ossicles are composed of calcium carbonate they have a high potential for fossilisation, especially in limestones. In the soft shales of the Benbulben and Bundoran Shale formations, although the stems may be partly (as pluricolumnals) or completely disarticulated, they are not fragmentary due to the lower energy conditions. However, in limestones they are seen as completely disarticulated and

fragmentary due to the higher energy depositional conditions. Dixon (1972), in studying the fossils of the Bricklieve Mountains, commented that abrasion and breakage of many of the larger bioclastic components (presumably in the limestones) indicated that there was substantial bottom turbulence.

7.4.3. SHAPE OF AND ARTICULATION BETWEEN COLUMNALS AND THEIR INFLUENCE ON PRESERVATION

Stems with an elliptical outline and which articulate synarthrially may be more prone to disarticulation than circular ones since they are not as closely united and the ligaments will be more exposed and therefore more susceptible to decay and attack from small organisms and bacteria.

Columnals with a large lumen are prone to being crushed under burial if they are positioned on their side (see crushed columnals on Plate 3, fig. a).

7.4.4. PRESERVATION OF MATERIAL

Preservation of the majority of crinoid material found during the study is of unaltered original calcite. At some localities, however, replacement by pyrite or silica has occurred. For example, at Lackavarna, faunal elements are pyritised due to the emplacement of directly adjacent dykes reacting with the high ferric content in the shale. Silica replacement occurred due to the chemistry of the sediment in which the organism was buried in, even if this was limestone.

7.5. DIVERSITY

7.5.1. THE USE OF CROWNS - VS - DISSOCIATED OSSICLES AS AN ESTIMATE OF CRINOID DIVERSITY

During the Lower Carboniferous crinoids had a rapid turnover of taxa, so they were diverse. Since different crinoid taxa can be identified relatively easily, an estimate in their diversity should be fairly simple. However, well preserved crowns or partial crowns are quite scarce. In his monograph Wright (1950) described Tournaisian and Viséan crinoid taxa from Ireland and Great Britain using the most complete specimens available. Below is a table showing the numbers of taxa which were described:

Subclass	Inadunata		Flexibilia	Camerata	TOTAL
	Cladids	Disparids			
Order	1	1	2	2	6
Family	16	3	3	7	29
Genus	36	6	11	19	72
Species	101	10	23	116	250

The numbers may seem fairly large, especially for the cladids at the species level. However, some of the genera were unnecessarily split further into species (Mannifield 1995; G. D. Sevastopulo, pers. comm. 1996), particularly amongst the camerates, for example, *Amphoracrinus* and *Actinocrinites*. In reality only about four of Wright's species from the Arundian can be considered valid taxa.

Every crinoid always has a fixed, and known, number of plates in the calyx (typically ten or fifteen), whereas the number of columnals is highly variable and unknown (M. Simms, pers. comm. 2000). In addition, the plates of the calyx are only released to become fossils once the crinoid has died, while the stem may shed columnals throughout the life of the crinoid, giving a very distorted idea of abundance (M. Simms, pers. comm. 2000). Dissociated thecal plates and brachials can be useful for diversity estimates as they can often be taxonomically identified, to a certain level at least, even though they are not as abundant as dissociated columnals. The following table shows how diversity estimates can be more reliable using dissociated brachials and thecal plates for the Bundoran Shale Formation:

Group	Cladids	Disparids	Camerates	Flexibles	TOTAL
Diversity using entire calyces	1	1	1	1	4
Diversity using dissociated thecal plates and brachials	8	1	0	2	11

Columnals are morphologically diverse and can also be distinguished easily. In the present study sixty columnal morphospecies have been described from the Arundian and Holkerian-Asbian alone. There are many more which have not been described and probably many more for the remaining Tournaisian and Viséan. Subclasses or even species cannot be differentiated from stem material alone, so in no way is this meant to represent the real species diversity. However, the inferred diversity estimate using columnal morphospecies is less biased, since the fossils are so much more abundant, and therefore likely to be closer to the real amount of species than if just calyces were used.

CHAPTER 8

CRINOID BIOSTRATIGRAPHY

8.1. INTRODUCTION TO BIOSTRATIGRAPHY

Holland (1990, p. 461) described biostratigraphy as "*the use of fossils in stratigraphic correlation*". The concept was first realised by Smith (Holland 1990) in the early nineteenth century. He noticed that fossils contained in sedimentary rocks could be used as indices for correlation. d'Orbigny (1842) used the term zone, describing it as "*such and such a stage was the zone of such and such fossils*". Oppel (1856-1858) (*fide* Dunbar and Rodgers 1957) developed this concept by stating that a certain assemblage of species marked defined stratigraphical horizons. These are biozones (see below).

8.1.1. ZONE AND INDEX FOSSILS

Moore (1939) stated that a fossil is useful in stratigraphical studies if it is;

- confined to a definite part of the geological column, *i.e.* is short ranging.
- widely distributed geographically.
- abundantly represented by individuals.
- readily and reliably identifiable.
- has a readily preservable skeleton.

An animal with a high potential to be preserved would exclude, for example, soft bodied taxa, except in exceptional circumstances such as the Burgess Shale. Fossil taxa, preferably at species level, which can be used as biostratigraphical markers because they fulfil the above criteria, are called index fossils or zone fossils. Each stratigraphical horizon, which can be identified by its specific taxon content, is termed a biozone. A biozone should be named after one or more characteristic index or zone fossil of the assemblage. The index fossil may also be present in a different assemblage above and below the zone after which it is named, and it may be absent from an assemblage in a zone which was originally named after it (Dunbar and Rodgers 1957).

It is often more reliable to use assemblages of taxa to create and recognise biozones rather

than using just individual markers. Sampling bias, especially when collecting large specimens, may mean that taxa are missed when they are actually there, implying that they do not exist there. This can lead to an incorrect identification of stratigraphical age.

Different geological periods have characteristic faunal groups which are used in biostratigraphy depending on which fauna were diverse and abundant at the time. For example, graptolites are used as the main biozonal indicators in the Ordovician and Silurian, but only in a restricted range of lithologies which accumulated in quiet palaeoenvironments where they were readily preservable. Other useful groups used in biostratigraphy are ammonoids, brachiopods, bryozoans, conodonts, corals, foraminiferans, ostracods, plant miospores and trilobites, all of which are used in the Carboniferous. Miospore Biozones have been listed to recognise stratigraphical units within this study (see Sections 2.4 and 2.5 and Figure 2.3).

8.2. THE USE OF CRINOIDS IN BIOSTRATIGRAPHY

On describing the stratigraphical significance of crinoids, Moore and Jeffords (1968, p. 16) made the following statement; "*Few, if any, index fossils rival crinoids as trustworthy indicators of geologic age and dependable markers for precise stratigraphic correlations*".

This is true since they fulfil all the criteria listed above by Moore (1939). On their World Wide Web site (see 'References') W. I. Ausich and C. G. Messing stated that "*many [crinoid] species have short stratigraphical ranges making them important, at least locally, as biostratigraphical index taxa*". Previous work on the use of crinoid ossicles in biostratigraphy of the British Isles has been carried out by Rasmussen (1961), Simms (1989) and Donovan (1986-95).

Crinoids have evolved to live in a wide range of marine environments and most species of crinoids have a very narrow stratigraphical range, so in some instances they may be useful for stratigraphical correlation (Ubaghs 1978*a*, p. T61), but they are facies controlled. They range from the Ordovician and are still in existence at the present day. Because crinoids were so abundant during the Carboniferous, when they reached their acme of diversity, it might be expected that they would have a rapid turnover of taxa, and this is

the case.

Almost any specimen that is reasonably complete can be identified with reasonable ease and confidence. These are highly desirable attributes from the point of view of stratigraphical palaeontology. A factor that limits usefulness of crinoids in defining and tracing faunal zones is the general scarcity of specimens that are sufficiently complete for identification. This is because of the way in which the crinoid skeleton is organised; it comprises many ossicles which disarticulate readily and rapidly after death (see Chapter 7). It means that an entire, or nearly entire fossil crinoid specimen is rarely discovered.

8.3. THE USE OF DISSOCIATED COLUMNALS AS BIOSTRATIGRAPHICAL TOOLS

8.3.1. WHY USE COLUMNALS IN BIOSTRATIGRAPHY?

8.3.1.1. Abundance

We are limited in using complete crinoids for biostratigraphy because they are so uncommon, even though we know that the crinoid animals themselves were abundant. Indeed, in the present study only about ten complete or incomplete crowns (not including micro crinoids) have been found during the three field seasons over which this study took place. The situation was similar for Strimple (1948*b*) whom, over twelve years of collecting, found only about one hundred complete or partial crowns. In strong contrast to a general dearth of reasonably complete crinoid calyces and crowns (probably thousands; Moore and Jeffords 1968) is an abundance of fragmentary crinoidal remains (probably trillions; Moore and Jeffords 1968) in many formations. Dissociated ossicles are a chief constituent of numerous marine deposits of middle and late Palaeozoic age, as well as being common in many additional deposits over wide areas. Many Carboniferous rocks especially have a large component of dissociated columnals, as well as other dissociated parts of the crinoid skeleton. It therefore seems logical to use dissociated ossicles in biostratigraphy.

8.3.1.2. Preservation

The columnals are very well preserved. Most of the morphological detail of the articular facet and latus is retained in the fossil, and the stereom microstructure can often be seen.

Distortion and crushing of columnals and pluricolumnals is usually minimal, and even distortion does not prevent a columnal morphospecies being identified. This means that after cleaning columnals are in excellent condition for description under the microscope or in the SEM.

8.3.1.3. Morphological diversity

Columnals have a large amount and variation of morphological features (see Chapter 5), therefore it is easy to distinguish between them.

8.3.2. MICROFOSSILS

A large proportion of the disarticulated material described herein consists of microscopic ossicles. Commonly ossicles which are easily washed out of bulk samples in moderately large numbers measure about 1 mm in diameter. These can be used in the same way biostratigraphically as the macroscopic specimens. Identifiable microcrinoid thecae have been found in washed samples in relatively higher numbers than macroscopic crinoid theca and crowns. Using microcrinoids as biostratigraphical markers is probably more reliable than using macrocrinoids as the former are more abundant and more likely to be preserved entire.

8.4. THE BIOSTRATIGRAPHY OF THE ARUNDIAN TO HOLKERIAN-ASBIAN USING CRINOID COLUMNAL MORPHOSPECIES

The Bundoran Shale Formation, which is of Arundian age, and the Benbulben Shale Formation, which is younger (Holkerian to Asbian in age), are lithologically similar, and are separated by an incursion of deltaic siliciclastics (the Mullaghmore Sandstone Formation). They both consist of alternating sequences of dark grey, clay-rich, calcareous shales and bioclastic limestones. Few crowns have been recovered from either formation ruling out the possibility of using these for biostratigraphy. Radial plates from the calyx would be useful, but even they are relatively rare. However, dissociated columnals and pluricolumnals are abundant and so have the potential to be good biostratigraphical tools. Because these two formations of the Viséan in the area studied contain the most crinoid fossil material, and because any differences in crinoid faunal composition is likely to reflect differences in age rather than in facies, they were used as a test of the use of

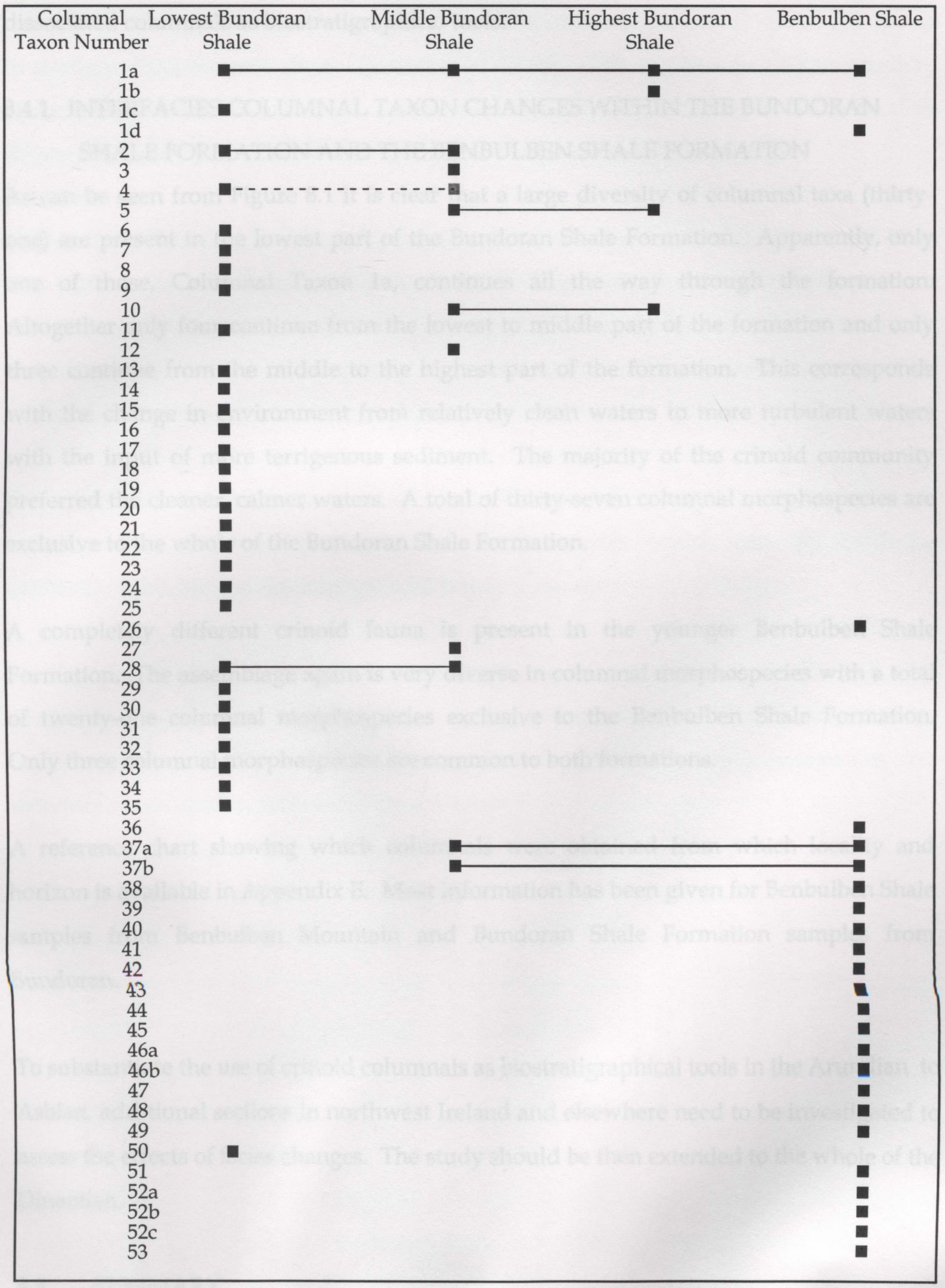


Figure 8.1. Biostratigraphical range chart for Columnal Taxa in the Bundoran Shale Formation (Arundian) to Benbulben Shale Formation (Holkerian to Asbian).

dissociated columnals as biostratigraphical tools.

8.4.1. INTERFACIES COLUMNAL TAXON CHANGES WITHIN THE BUNDORAN SHALE FORMATION AND THE BENBULBEN SHALE FORMATION

As can be seen from Figure 8.1 it is clear that a large diversity of columnal taxa (thirty-one) are present in the lowest part of the Bundoran Shale Formation. Apparently, only one of those, Columnal Taxon 1a, continues all the way through the formation. Altogether only four continue from the lowest to middle part of the formation and only three continue from the middle to the highest part of the formation. This corresponds with the change in environment from relatively clean waters to more turbulent waters with the input of more terrigenous sediment. The majority of the crinoid community preferred the cleaner, calmer waters. A total of thirty-seven columnal morphospecies are exclusive to the whole of the Bundoran Shale Formation.

A completely different crinoid fauna is present in the younger Benbulben Shale Formation. The assemblage again is very diverse in columnal morphospecies with a total of twenty-one columnal morphospecies exclusive to the Benbulben Shale Formation. Only three columnal morphospecies are common to both formations.

A reference chart showing which columnals were obtained from which locality and horizon is available in Appendix E. Most information has been given for Benbulben Shale samples from Benbulben Mountain and Bundoran Shale Formation samples from Bundoran.

To substantiate the use of crinoid columnals as biostratigraphical tools in the Arundian to Asbian, additional sections in northwest Ireland and elsewhere need to be investigated to assess the effects of facies changes. The study should be then extended to the whole of the Dinantian.

8.5. SUMMARY

If characters of ossicles (specifically columnals since these are the most abundant remains) differ from one horizon to another, in a manner corresponding to changes in species of

crinoids as determined from study of articulated specimens, the usefulness of this group in stratigraphical research should be increased greatly. This is a reasonable presumption, and extensive collection of crinoid ossicles from many Upper Palaeozoic rocks in the USA shows conclusively that they do have value in stratigraphical palaeontology.

Each described ossicle is a record, even though incomplete, of the crinoid animal from which is was derived (Moore and Jeffords 1968). This gives us an indication as to which crinoids were living at the time. But, when applying biostratigraphical rules to columnals they can almost be seen as completely removed from crinoids and treated as a separate entity, cf. conodonts.

With the recurrence of similarly morphological columnals throughout the crinoid fossil record, it is not individual columnal morphospecies which can be used for biostratigraphy, but the assemblages which they make up.

As a general observation it is obvious looking through the literature that columnals with similar morphologies have been repeated during geological history. This is more likely to be the case than say for arms or calycal plates since there are fewer parameters, and therefore combinations, achievable in columnals.

CHAPTER 9

CONCLUSIONS

9.1. SUMMARY OF CONCLUSIONS

- In contrast to complete, or partially complete crowns, disarticulated crinoid ossicles are extremely common in the Lower Carboniferous limestones and shales of Ireland.
- Columnals display distinct morphological features, which can be used to easily distinguish crinoid morphospecies.
- Descriptions of fossil columnals have been imperfect in the past. They should be precise and clear so that future authors can compare and contrast material.
- Owing to their abundance, dissociated crinoid ossicles offer distinct advantages over using entire calyces in terms of diversity estimates. Dissociated thecal ossicles can be used to estimate group diversity where an entire crown is not available.
- Palaeoecologically, certain crinoid groups inhabited particular environmental niches in the prodelta environment.
- Comparing the crinoid columnal morphospecies from the Bundoran Shale Formation (Arundian) and the younger Benbulben Shale Formation (Holkerian-Asbian), certain columnal morphospecies are exclusive to either one or the other of these formations, and some are common to both.
- The potential for the use of fossil crinoid columnals as biostratigraphical tools has not yet been fully realised.
- Some crinoid columnals can be considered as microfossils, and as such may offer more potential in terms of biostratigraphy than large columnals.

9.2. FURTHER WORK

To substantiate the use of crinoid columnals as biostratigraphical tools in the Arundian to Asbian, additional sections in northwest Ireland and elsewhere need to be investigated to assess the effects of facies changes. The study should be then extended to the whole of the Dinantian.

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