CRINOID OSSICLES IN UPPER ORDOVICIAN BENTHIC MARINE ASSEMBLAGES FROM SNOWDONIA, NORTH WALES

by D. K. WRIGHT

ABSTRACT. Analyses of upper Ordovician (Caradoc) shelly faunas from Snowdonia, North Wales, reveal a remarkable diversity of crinoid columnals. So far, fifty-one columnal morphotypes have been recognized and these are listed, illustrated, and described. The morphotypes are categorized on the basis of earlier schemes of classification. The morphotype diversity implies that the original crinoid faunas were varied. Further applications of the columnal morphotype list include the potential recognition of morphotype combinations which originally comprised hetero- and xenomorphic columns and the possible use of the morphotypes in biostratigraphy.

BENTHIC palaeocommunity analysis is now an established sub-discipline within palaeontology. Although the holistic approach to community palaeoecology (Kauffman and Scott 1976) is accepted by many workers, the whole preserved fauna is rarely described (but see Jaanusson *et al.* 1979). In particular, taxa that are commonly found fragmented or dissociated are neglected, e.g. crinoids, bryozoans, cystoids, algae, and other groups, with the resultant loss of potentially valuable information.

The present paper is based on a study of upper Ordovician (Caradoc) shelly faunas from the Glanrafon Beds and Snowdon Volcanic Group, and their equivalents. The faunas were collected from several areas within Snowdonia (text-figs. 1, 2). Analyses of the poorly preserved and tectonically distorted faunas, including dissociated and fragmented taxa, reveal relatively diverse assemblages (Wright 1979). Brachiopods are the dominant element of the faunas. Brachiopod associations, similar to those described by Williams, A. (1963, 1973) and Pickerill and Brenchley (1979) are recognized. Crinoids, though not abundant, are a widespread element of the faunas. This account presents an illustrated descriptive list of the columnals of this palaeoecologically neglected group, in addition to associated problems and applications of the list.

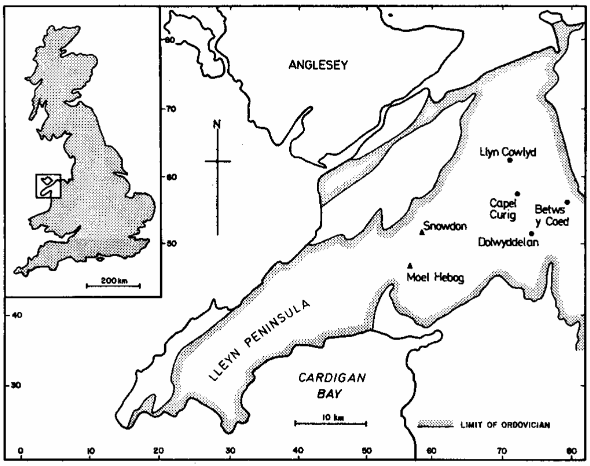
In the nineteenth century, the first systematic geological investigations of Snowdonia revealed 'encrinites' within shelly assemblages from Snowdon, Glyder Fawr, Moel Hebog, the Llyn Ogwen–Llyn Idwal area and Carnedd Llywelyn (Sedgwick 1838, p. 679; 1841, pp. 548, 549; 1843, p. 219; 1847, p. 138; Ramsay 1866, pp. 85, 88, 126, 173, 215, 262, 273, 283–284). Later, more detailed work discovered further assemblages yielding 'encrinites' and crinoid columnals from the Glanrafon Beds and Snowdon Volcanic Group of various areas within Snowdonia (Williams, H., 1927, p. 368; Williams, D., 1930, p. 206; Williams and Bulman 1931, p. 431; Shackleton 1959, pp. 233, 235, 241; Beavon 1960, p. 29; 1963, pp. 486, 487, 492, 508; Diggens and Romano 1968, p. 37; Romano and Diggens 1969, p. 603; Howells *et al.* 1978, pp. 67–70). Although earlier work indicates crinoids to be an important element of the Snowdonian benthic shelly assemblages, no detailed analyses of them have been undertaken. Figured specimens are deposited in the National Museum of Wales.

CRINOID COLUMNALS: *IN SITU* OR TRANSPORTED?

It is important to assess whether the fossil assemblages have been subjected to significant lateral transport prior to burial. Both physical and biological criteria are employed in this context, but the Palaeozoic palaeoecologist places greater reliance on such physical criteria as the fabric of the shelly

[Palaeontology, Vol. 26, Part 3, 1983, pp. 585–603, pl. 65.]

horizons, opposing valve ratios, articulation ratios, degree of abrasion and fragmentation, the enclosing lithology, and associated sedimentary structures (Pickerill and Brenchley 1979; Wright 1979). In the case of crinoid ossicles, physical criteria may not always prove to be so diagnostic, because low velocity currents, which would not affect the macrofauna, could transport such small biogenic particles. Most investigations reveal transportation only exerts a minor influence upon recent and fossil shelly assemblages (Ausich *et al.* 1979; Bretsky 1970*b*; Cadee 1968; Calef and Hancock 1968; Lane 1973; MacDonald 1976; Peterson 1976; Warme 1971; Warme *et al.* 1976). These investigations further suggest that whereas between-habitat transport is negligible, within-habitat small-scale transport is very likely. However, such studies usually are restricted to shelled macrofauna (in particular, brachiopods and bivalves), and have not included taxa which may disarticulate or fragment into many component parts.



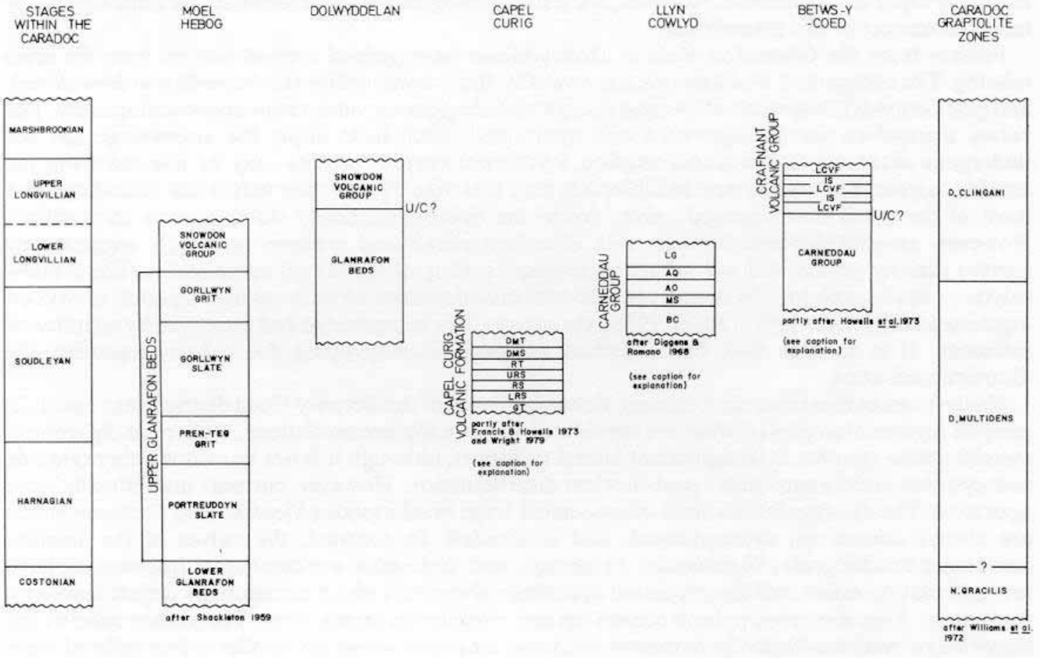
TEXT-FIG. 1. Regional setting of the study areas in Snowdonia.

With respect to crinoid ossicles, their open stereom meshwork (Marcurda *et al.* 1978) and low specific gravity, together with entrapped gases from organic decay (Cain 1968), makes them very light and thus susceptible to transport. Ossicles may undergo transient suspension transport (Schwarzacher 1963; Ruhrmann 1971; Herm 1972; Seilacher 1973) which would not produce abrasion. Thus it is occasionally difficult to differentiate indigenous from exotic ossicles purely on surface condition.

Recent studies show that post-mortem crinoid disarticulation starts at the arm tips and proceeds towards the calyx (Meyer 1971; Brower 1973; Liddell 1975). Examples from the fossil record confirm such a sequence of disarticulation (Brower and Veinus 1974). This process is accelerated by persistent wave and current activity (Anderson 1968; Brower and Veinus 1974; Liddell 1975; Muller 1979). The rate of sedimentation is a critical factor governing crinoid preservation. Rapid sedimentation ensures the preservation of complete crinoids and arms (Liddell 1975; Brower and Veinus 1978), whereas crinoids often become entirely disarticulated in areas of reduced sedimentation, even when current velocities are low (Lane and Matthews 1965; Anderson 1968; Brower 1973; Brower and Veinus 1978). Transport of crinoid debris is likely in those areas with reduced sedimentation, although probably only within-habitat transport occurs when low rates of sediment deposition are associated with low velocity currents.

Biological and physical criteria show that most crinoid remains within the Snowdonian assemblages are essentially *in situ*. Here, *in situ* implies little or no significant lateral transport of the crinoid material from their living sites, rather than the crinoids being still attached. Crinoid arms

(Pl. 65, fig. 3) from the Portreuddyn Slate of the Moel Hebog district (text-figs. 1, 2), several complete crinoids associated with complete detached arms and twisted pluricolumnals (Pl. 65, figs. 1, 2, 5) from the Gorllwyn Slate of the same district (text-fig. 2), together with rare crinoid crowns (Pl. 65, fig. 4) from the Glanrafon Beds at Dolwyddelan (text-figs. 1, 2), are unequivocally *in situ*. Transitory pulses of rapid sedimentation probably effected their preservation.



TEXT-FIG. 2. Stratigraphy for the study areas within Snowdonia. *Capel Curig area*: GT—Garth Tuff; LRS—Lower Racks Sandstone; RS—Racks Siltstone; URS—Upper Racks Sandstone; RT—Racks Tuff; DMS—Dyffryn Mymbyr Siltstone; DMT—Dyffryn Mymbyr Tuff. *Llyn Cowlyd area*: BC—Bwlch Cowlyd Formation; MS—Multiplicata Sandstone; AO—Adwyon Owen Beds; AQ—Arkosic Quartzite; LG—Llethr Gwyn Sandstones. *Betws-y-Coed area*: IS—Intercalated sediments; LCVF—Lower Crafnant Volcanic Formation.

The Portreuddyn Slate fauna is recovered from lenticular shelly concentrations displaying random orientations of the disarticulated brachiopod valves, within a fine-grained siltstone (Wright 1979). The two commonest components of the fauna are aegiromenine (*Sericoidea*) and dalmanellid (*Dalmanella* and *Onniella*) brachiopods. Almost 50% of these genera are still articulated and disarticulated opposing valve ratios approach unity. As the valves of *Sericoidea* probably disarticulated very easily (Bergström 1968), relatively low velocity currents could induce large-scale disarticulation, with consequent unequal valve dispersion resulting from their relative thinness and differing hydrodynamic properties. For *Sericoidea*, the relatively high degree of articulation, opposing valve ratios approaching unity and unabraded, unfragmented valves all suggest very little current activity and thus insignificant lateral transport. It is likely the fauna accumulated relatively quickly within sea floor sediment traps. These traps then became rapidly buried. The enclosing siltstone displays parallel laminations of variable thickness (usually less than 1 cm), with some slightly coarser grained laminae. No bioturbation is noted. Such laminations imply slow, uniform sedimentation in a low energy environment, the slightly coarser material being deposited from suspension in slowly moving waters (Harms and Fahnestock 1965). Therefore it is unlikely that this fauna has suffered any significant lateral transport, and thus can be regarded as being essentially *in situ*.

Entire crinoids and detached crinoid arms from the Gorllwyn Slate similarly indicate an *in situ* assemblage, as do associated unabraded, unfragmented ramose bryozoa and pluricolumnals. Thin (5–10 cm) fining-upwards sequences are noted within the enclosing siltstone, suggesting some level of fluctuating current activity and clastic input. Slight down-loading at certain horizons implies relatively rapid sedimentation. However, the palaeontological evidence seems to discount significant lateral transport of this assemblage.

Faunas from the Glanrafon Beds at Dolwyddelan have yielded crinoid calyces with the arms missing. The commonest brachiopods, e.g. sowerbyellids, dalmanellids (*Dalmanella* and *Howellites*), and plaesiomyids (*Dinorthis*), all possess disarticulated opposing valve ratios approaching unity. The valves themselves are unfragmented and unabraded. Such facts imply the assemblage has not undergone extensive lateral transportation, but minor current activity may be inferred from the armless calyces. The commonest brachiopods have less than 33% of their valves still articulated and most of the small disarticulated valves are in the hydrodynamically stable convex-up position. However, associated pluricolumnals with abundant cirrals and pinnates seemingly suggests any current activity present did not induce widespread sorting of the faunal components. The armless calyces could be explained by *in situ*, post-mortem disarticulation of the arms over a period of days on a quiet sea bed (Meyer 1971; Liddell 1975), the calyces then being buried and preserved by an influx of sediment. It is feasible that the abundant pinnates accompanying the calyces represent the disarticulated arms.

Shelly assemblages from the Crafnant Volcanic Group of the Betws-y-Coed district (text-figs. 1, 2) provide further examples of what are considered to be *in situ* accumulations. Collapsed diploporite cystoid thecae connote little significant lateral transport, although it is not known whether crinoids and cystoids underwent similar post-mortem disarticulation. However, currents undoubtedly were operative. The disarticulated valves of associated large brachiopods (*Nicolella* and *Orthambonites*) are always convex-up, unfragmented, and unabraded. In contrast, the valves of the smaller, commoner brachiopods (*Skenidioides*, *Protozyga*, and *Sericoidea*) are commonly fragmented, have low articulation ratios and disarticulated opposing valve ratios which occasionally depart markedly from unity. They are noted in both convex-up and concave-up orientations. The author believes the larger valves were unaffected by current activity and are *in situ*, whilst the smaller valves suffered some degree of within-habitat transport. The robust cystoids were relatively unaffected by the currents. No entire crinoids are noted in these assemblages, but a diverse assemblage of columnal morphotypes is present. Consequently, it appears likely that the post-mortem disarticulation rate of crinoids and cystoids differed.

The vast majority of shelly assemblages from Snowdonia only contain disarticulated crinoid ossicles. Physical criteria suggest that the assemblages have suffered only minor within-habitat transportation.

Irrefutable proof of transported crinoid material is surprisingly rare. Assemblages deposited under high energy regimes, e.g. from the *Multiplicata* Sandstone of the Llyn Cowlyd district and the Racks Sandstone at Capel Curig (text-figs. 1, 2) contain sparse crinoid material. Such absence is explained either by transportation away from the original depositional areas or that the original environments were inimical to crinoid colonization. Palaeoenvironmental interpretations enforce the latter proposal.

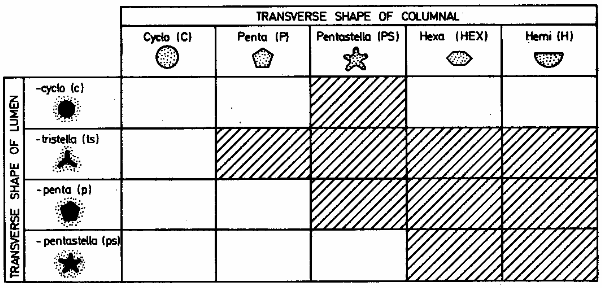
Re-examination of the shallow water sediments from locality 129 (SH 71445803) within the Upper Racks Sandstone at Capel Curig (text-figs. 1, 2) reveal microscopic, fragmentary, frequently abraded echinoderm (crinoid?) remains. The fauna and sediments from this locality are correlated with the slightly deeper water sediments and fauna from the Glanrafon Beds at locality 225 (SH 76125104), south-east of Dolwyddelan (text-figs. 1, 2). Crinoid material is common at the latter locality and is similarly preserved to that found at locality 129. Thus, in this case, crinoid debris apparently was transported onshore from an outer sublittoral environment, probably by onshore storm surge currents.

Previous treatment of crinoid columnals in faunal analyses

Crinoid columnals are accorded different types of treatment in faunal analyses. They are either apparently ignored (Bretsky *et al.* 1969; Hurst 1975*a*, *b*; Bretsky *et al.* 1977; Byers and Gavlin 1979) or only their presence is recorded (Bretsky 1969, 1970*a*, *b*; Bowen *et al.* 1974; Feldman 1980). Further levels of treatment are the quantification of columnals (Ziegler *et al.* 1968; Watkins 1978; Pickerill and Brenchley 1979) and the recognition of columnal morphotypes, which are sometimes quantified (Titus and Cameron 1976; Hurst 1979*a*, *b*). Arbitrary correction factors are used by some workers to estimate the relative numbers of crinoids represented by the columnals and these range from 5 to 300 columnals being equal to one crinoid (Watkins 1973; Thayer 1974; Berry *et al.* 1979; Wright 1979). However, such correction factors are sometimes regarded with scepticism, as the estimates '. . . defy reality' (W. I. Ausich, pers. comm.).

CRINOID COLUMNAL MORPHOTYPES

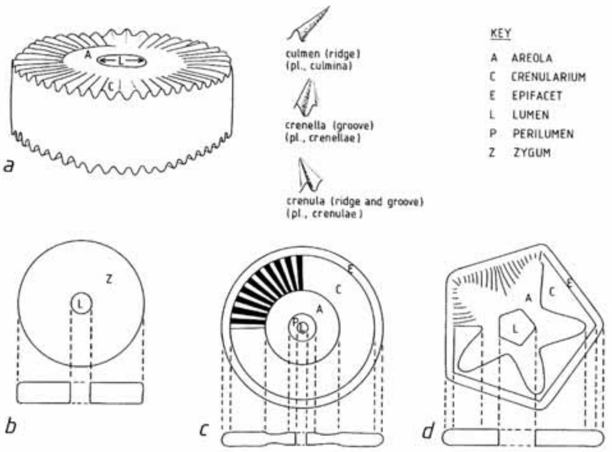
Analyses of the shelly assemblages revealed columnal diversity was not satisfactorily defined by the term 'crinoid columnals' (Wright 1979). It was necessary to devise a classification of the different columnal morphotypes. Each morphotype has been recognized within the Snowdonian shelly assemblages, in contrast to the morphotype lists of other workers (see Jeffords 1978, T928–T929). The basis for the categories employed in the list of morphotypes is taken from a classification proposed by Moore (1939), and later elaborated by Moore and Jeffords (1968) and Moore *et al.* (1968). Following Moore's classification, the morphotype categories of the following list are based on: (*a*) transverse outline of the articular facet; (*b*) transverse outline of the lumen; (*c*) features of the articular facet. Genus groups (text-fig. 3) and morphotypes are differentiated using these criteria, latinized binomina being applied to the genus groups (after Moore 1939), e.g. *Cyclocyclopa*. The 'prefix' (*Cyclo*/cyclopa) refers to the transverse shape of the articular facet, e.g.



TEXT-FIG. 3. Matrix illustrating the ten basic columnal genus groups found in the Snowdonian shelly assemblages. Shading denotes non-combination.

Cyclo-	circular articular facet
Penta-	pentagonal articular facet
Hexa-	hexagonal articular facet
Pentastella-	stellate five-armed articular facet
Hemicyclo-	semi-circular articular facet

The 'suffix' (Cyclo/*cyclopa*) pertains to the transverse outline of the lumen and follows the same nominations. This method generates cumbersome genus group names, so a coding scheme is implemented (see next section). Features of the articular facet govern morphotype subdivision within each genus group.



TEXT-FIG. 4. Morphological features of crinoid columnals. *a*, oblique view of single columnal showing features of articulation surface. Single ridge (culmen) and groove (crenella) together form a crenula. *b*–*d*, facetal views and median longitudinal sections of different columnal morphotypes to show various morphological features. All after Moore *et al.* 1968.

Of the three morphological features cited above, the transverse outline of the lumen is often regarded as being less variable than the other two features (Stukalina 1966), and thus possibly of greater importance when grouping the columnal morphotypes. The morphotypes in the following list are grouped primarily on the transverse outline of the articular facet. If, however, primary importance is attached instead to the transverse outline of the lumen and the morphotypes are grouped principally on the basis of this feature, a somewhat different system of groupings would result. Certain genus groups would become amalgamated, e.g. Cc with Pc; HEXc with HCc; Cp with Pp; Cps with Pps and PSps. Depending on preservation, pluricolumnals can be assigned to a columnal morphotype. Intercolumnal articulation is sometimes visible (Pl. 65, fig. 7) and is usually symplectic (Ubaghs 1978a, T77).

EXPLANATION OF PLATE 65

Fig. 1. Twisted pluricolumnal associated with detached crinoid arms. Gorllwyn Slate, south of Moel Hebog. NMW 83. 14G. 1, × 3·1.

Fig. 2. Complete crinoid. Bottom—stem; centre—poorly preserved theca; top—arm still attached to theca. Gorllwyn Slate, south of Moel Hebog. NMW 83. 14G. 2, × 3·4.

Fig. 3. Detached crinoid arm. Portreuddyn Slate, south of Moel Hebog. NMW 83. 14G. 3, × 5·8.

Fig. 4. *Balacrinus* sp. Theca. Glanrafon Beds, south-west of Dolwyddelan. NMW 83. 14G. 4, × 5·5.

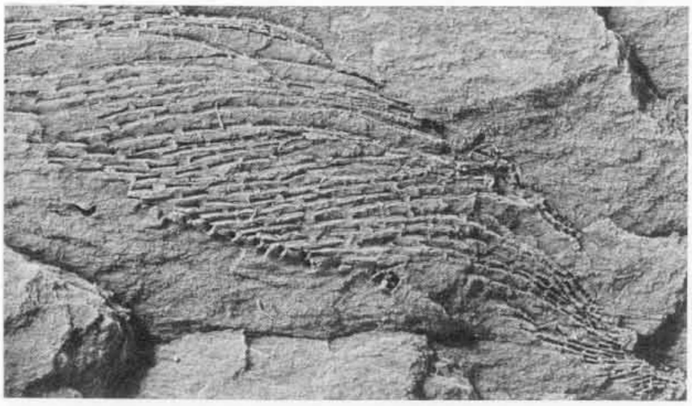
Fig. 5. Part of detached crinoid arm. Gorllwyn Slate, south of Moel Hebog. NMW 83. 14G. 5, × 5·5.

Fig. 6. Pc 1 pluricolumnal showing nodals, three orders of internodals, and symplectic intercolumnal articulation. Glanrafon Beds, south-west of Dolwyddelan NMW 83. 14G. 6, × 8·1.

Fig. 7. Curved pluricolumnal showing different orders of columnals (nodals? and internodals) and symplectic intercolumnal articulation. Glanrafon Beds, south-west of Dolwyddelan. NMW 83. 14G. 7, × 9·6.

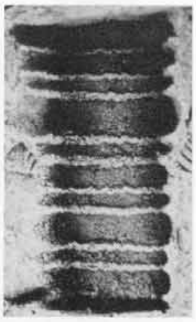

1


2


3


4


5


6


7

WRIGHT, Upper Ordovician crinoids

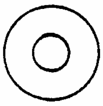
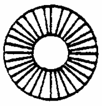
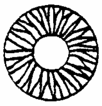
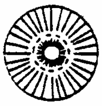
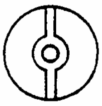
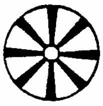
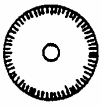
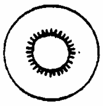
MORPHOTYPE LIST

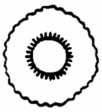
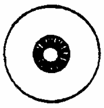
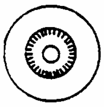
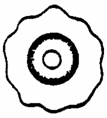
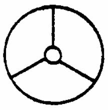
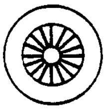
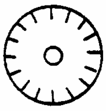
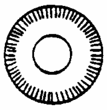
The columnals described and illustrated in the following list are all represented in the Caradoc shelly faunas of Snowdonia. In all cases, the morphological terms applied to the columnals are defined by Moore (1978, T229–T242) and Moore *et al.* (1968, pp. 27–30), and are depicted in text-fig. 4. A coding scheme is implemented to replace the cumbersome genus group names and is as follows:

Cyclo-	C	-cyclopa	c
Pentagono-	P	-pentagonopa	p
Pentastella-	PS	-pentastellatopa	ps
Hexagono-	HEX	-tristellatopa	ts
Hemicyclo-	H		

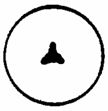
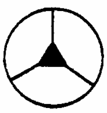
Group CYCLICI. Circular columnals.


Genus CYCLOCYCLOPA (Cc). Circular columnal with circular lumen.

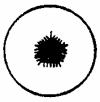
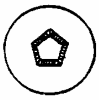
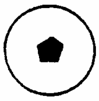
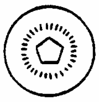
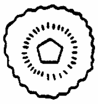
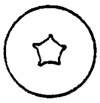
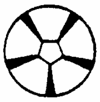
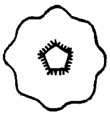
	Varieties	
	Cc 1	Variably sized lumen; smooth undifferentiated zygum.
	Cc 1a	Variably sized lumen; zygum composed of wide crenularium; well-defined radial crenulae unbranched.
	Cc 2	As for Cc 1a, except majority of culmina display centrifugal bifurcation.
	Cc 3	Wide crenularium divisible into inner narrow section with simple culmina, and outer broader section where most culmina branch. Narrow areola occasionally developed.
	Cc 4	Fulcral ridge extends across zygum and divides it into two smooth bifascial fields. Fulcral ridge may denote some degree of flexible articulation (synarthry) in crinoid stem.
	Cc 5	Wide crenularium with spaced, thick culmina which occasionally bifurcate centrifugally and thin centripetally.
	Cc 6	Wide areola; narrow peripheral crenularium of thin simple culmina; sides of columnal granulose.
	Cc 7	Variably sized lumen; narrow band ('perilumen') of simple fine crenulae rims lumen; remainder of zygum smooth.

	Cc 7a	As for Cc 7, except finely crenulate in transverse outline.
	Cc 8	Depressed, narrow, radially ornamented perilumen.
	Cc 9	Variably sized lumen; areola surrounded by narrow crenularium, in turn surrounded by smooth rim (?epifacet).
	Cc 9a	As for Cc 9, except undulose in transverse outline.
	Cc 10	Small lumen; three thin culmina traverse the otherwise smooth zygum.
	Cc 11	Variably sized lumen; crenularium of thick crenulae surrounded by wide smooth rim (?epifacet).
	Cc 12	Very small lumen; areola surrounded by peripheral crenularium of short, widely spaced crenulae.
	Cc 13	Wide lumen; areola surrounded by peripheral crenularium of short, fine, closely packed crenulae.

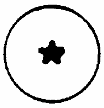
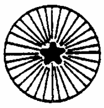
 Genus CYCLOTRISTELLATOPA (Cts). Circular columnal with tristellate–triangular lumen.

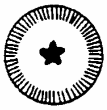
	Cts 1	Tristellate lumen; smooth undifferentiated zygum.
	Cts 2	Triangular lumen; zygum traversed by three culmina, each originating at one apex of triangular lumen.


Genus CYCLOPENTAGONOPA (Cp). Circular columnal with pantagonal-quinquelobate lumen.

	Varieties	
	Cp 1	Narrow band of fine unbranched crenulae rims lumen (?perilumen).
	Cp 2	Depressed narrow crenularium within groove rims lumen.
	Cp 3	Smooth undifferentiated zygum.
	Cp 4	Areola surrounded by narrow intermediate crenularium, in turn surrounded by smooth rim (?epifacet).
	Cp 5	As for Cp 4, except finely crenulate in transverse profile.
	Cp 6	Quinquelobate lumen.
	Cp 7	Zygum traversed by paired culmina, each pair originating at an apex of pentagonal lumen and thence diverging centrifugally.
	Cp 8	As for Cp 1, except undulose in transverse profile.

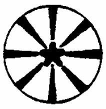

Genus CYCLOPENTASTELLATOPA (Cps). Circular columnal with pentastellate lumen.

	Cps 1	Smooth undifferentiated zygum.
	Cps 2	Wide crenularium; narrow areola may be developed.



Cps 3

Wide areola surrounded by narrow peripheral crenularium of fine unbranched crenulae.

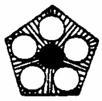


Cps 4

Crenularium of broad, widely spaced culmina which widen centrifugally.

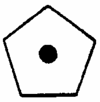
Group PENTAMERI. Pentagonal-quinquelobate columnals.

Genus PENTAGONOCYCLOPA (Pc). Pentagonal-quinquelobate columnal with circular lumen.



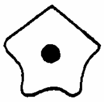
Pc 1

Complex zygum; areola subdivided into five discrete circular fields; a prominent culmen, slightly thickening centripetally, passes between adjacent fields, meeting columnal periphery approximately midway along each side of columnal; a crenularium partially surrounds each circular field, with simple culmina, separated by relatively broad crenellae, radially disposed at each apex of columnal but gradually becoming subparallel to one of the 'major' culmina.



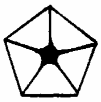
Pc 2

Smooth undifferentiated zygum.



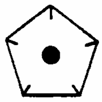
Pc 2a

As for Pc 2, except lower half of columnal is lobate, giving appearance of combined pentagonal and quinquelobate forms.



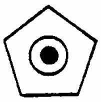
Pc 3

Zygum traversed by five fine culmina, which originate at lumen and terminate at each apex of columnal.



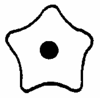
Pc 4

Five fine culmina originate at each apex of columnal, but do not extend to lumen.



Pc 5

Smooth undifferentiated zygum except for intermediate concentric groove.

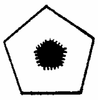


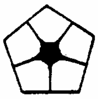
Pc 6

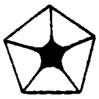
Columnal possesses quinquelobate transverse profile; smooth undifferentiated zygum.

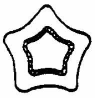

Genus PENTAGONOPENTAGONOPA (Pp). Pentagonal-quinquelobate columnal with pentagonal-quinquelobate lumen.

Varieties


Pp 1 Narrow band of fine unbranched crenulae rims lumen (?perilumen).

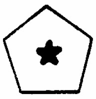

Pp 2 Pentagonal lumen is out of phase with respect to pentagonal shape of columnal in transverse profile; five fine culmina originate at each apex of lumen and meet columnal periphery approximately midway along each side of columnal.

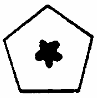

Pp 3 Lumen shape in phase with pentagonal columnal shape; five fine culmina originate at each apex of lumen and terminate at each apex of columnal.

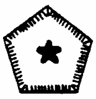

Pp 4 Quinquelobate columnal; very large quinquelobate lumen, bordered by slightly depressed groove possessing fine unbranched crenulae.

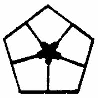

Pp 5 Narrow areola surrounded by narrow crenularium of short, fine, unbranched crenulae, in turn surrounded by smooth rim (?epifacet).

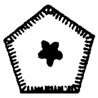

Genus PENTAGONOPENTASTELLATOPA (Pps). Pentagonal columnal with pentastellate lumen.


Pps 1 Apices of pentagonal columnal coincide with apices of lumen; smooth undifferentiated zygum.


Pps 2 Lumen orientation is rotated with respect to orientation in Pps 1.

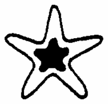

Pps 3 Wide areola surrounded by narrow peripheral crenularium of fine unbranched crenulae.


Pps 4 As for Pps 2, except five fine culmina originate at apices of rotated lumen and traverse zygum; culmina meet columnal periphery approximately midway along each side of columnal.


Pps 5 As for Pps 3, except lumen orientation is rotated.

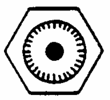

Genus PENTASTELLAPENTASTELLATOPA (PSps) Pentastellate columnal with pentastellate lumen.

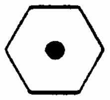
Varieties


PSps 1 Diagnosis as for genus; complex zygum smooth and undifferentiated.

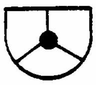
Group VARII. This group contains genera that do not find a place in the other two groups.


Genus HEXAGONOCYCLOPA (HEXc). Hexagonal columnal with circular lumen.


HEXc 1 Areola surrounded by narrow intermediate crenularium of fine unbranched crenulae, in turn surrounded by smooth rim (?epifacet).


HEXc 2 Smooth undifferentiated zygum.


Genus HEMICYCLOCYCLOPA (HCc). 'Trough-shaped' columnal with circular lumen; very rare.


HCc 1 Zygum traversed by three fine culmina, each disposed at an approximate angle of 120 degrees to each other.

It is likely that some of the illustrated columnal morphotypes are meric (i.e. segmented), e.g. Cc 10, Cts 2, ?Cp 7, Pc 3, Pp 2, Pp 3, Pps 4, and HCc 1. Stukalina (1966; 1968, fig. 1) considers segmented columnals to be primitive and illustrates two types of segmentation found in pentagonal columnals (Stukalina 1966, p. 553, fig. 2). In the first, the suture lines of the individual segments run from the angles of the lumen, whilst in the second type, the suture lines are perpendicular to the walls of the lumen and the side of the columnal. The first type is represented in the Snowdonian columnals, e.g. Pp 3, and therefore it is possible that this morphotype is meric. Of the second type described by Stukalina, no morphotypes have, as yet, been found that are exactly identical. Certain morphotypes, however, show probable suture lines which are perpendicular to the sides of the columnal but which run from the angles of the pentagonal or pentastellate lumen, e.g. Pp 2, Pps 4. Thus, these morphotypes may also be meric.

The Asegmentata group of Stukalina (1966) comprises morphotypes with a circular lumen and a circular articular facet, but no morphotypes included within this group are segmented. The Cc genus group from the Snowdonian list would be placed within the Asegmentata group, but Cc 10 may be meric, contradicting Stukalina's diagnosis of the group.

Discussion. The list demonstrates the diversity of the columnal morphotypes (51) within the Caradocian shelly assemblages from Snowdonia. Further work may reveal more. Such diversity obviously indicates that the original crinoid fauna was varied, even after accounting for taphonomic losses, as one crinoid species could not contribute over fifty differing columnal morphotypes. This diversity, however, must be interpreted with care. Certain species possess xenomorphic stems (Moore and Jeffords 1968; Moore *et al.* 1968; Ubaghs 1978*a*) in which columnals undergo shape changes along the stem (Manten 1970; Rasmussen 1978a). Proxisteles, mesisteles, andististeles often contain distinctive columnal morphotypes, e.g. *Scyphocrinites* (Ubaghs 1978*b*, T490), *Bathycrinus* (Macurda and Meyer 1976; Rasmussen 1978*b*, T843-T846), and *Archaetaxocrinus* (Lewis 1981). The ornament of the articular facets may differ in the proxistele, mesistele, and dististele. Columnals from the zone of maximum flexibility in the stem (middle 67–75% of the stem in camerates—Seilacher *et al.* 1968; Brower 1978) may possess specialised features on these facets.

Different types of ornamentation of the articular facets are observed during growth in isocrinid articulates (Rasmussen 1978*b*, T270) and *Bathycrinus* (Macurda and Meyer 1976). *Kallimorphocrinus* has smooth and nodose articular facets that are often found on opposing sides of the same columnal (Lane and Sevastopulo 1981). Crinoids with heteromorphic stems, i.e. stems composed of dissimilar columnals classifiable as nodals and one or more orders of internodals (Webster 1974), could potentially yield several distinctive columnal morphotypes. Preservation controls the precision of morphotype identifications. Poor preservation destroys delicate ornamentation and thus some morphotypes may be poorly preserved varieties of others.

After considering these factors, it is believed that the diversity of the columnals can be attributed to the presence of several crinoid species within the Caradocian sessile benthos and also to morphological differences between the columnals of these species.

FURTHER APPLICATIONS

The list of columnal morphotypes provides a method of quantifying the occurrence of crinoid columnals and a relative appreciation of their diversity. Other applications also present themselves. Through computerized techniques, temporally and spatially recurrent morphotype combinations may be recognized. Such combinations may represent the columnals originally comprising either the heteromorphic or xenomorphic stems of certain crinoid species. Once these combinations are statistically proven to be recurrent, it may be that these combinations could be assigned generic names. Certain morphotypes in the list are differentiated only on minor morphological details, e.g. Cc 7 and Cc 7a, Cc 9 and Cc 9a, Cp 4 and Cp 5, and Pc 2, Pc 2a, and Pc 6. Such combinations possibly represent original columnal transitions along stems. If, as Stukalina (1966) believes, the transverse outline of the lumen is a relatively stable morphological feature, it is feasible that, for example, the Cps or Pps genus groups were components of either a heteromorphic or xenomorphic stem. The abundance and diversity of the Snowdonian columnals favours them as biostratigraphical indicators and subsequently they may corroborate existing Snowdonian biostratigraphies (Wright 1979) although, like the shelly macrofauna, the crinoids were probably facies controlled. Morphotypes from contemporaneous rocks within the Anglo-Welsh province are easily accommodated within the list (S. Donovan, pers. comm.) and morphotype correlations may be possible between Snowdonia and these areas.

To demonstrate these applications, the presence and absence of columnal morphotypes, from assemblages collected from the Glanrafon Beds and Snowdon Volcanic Group to the south-west of Dolwyddelan, are plotted. The resultant plot (text-fig. 5) shows several features:

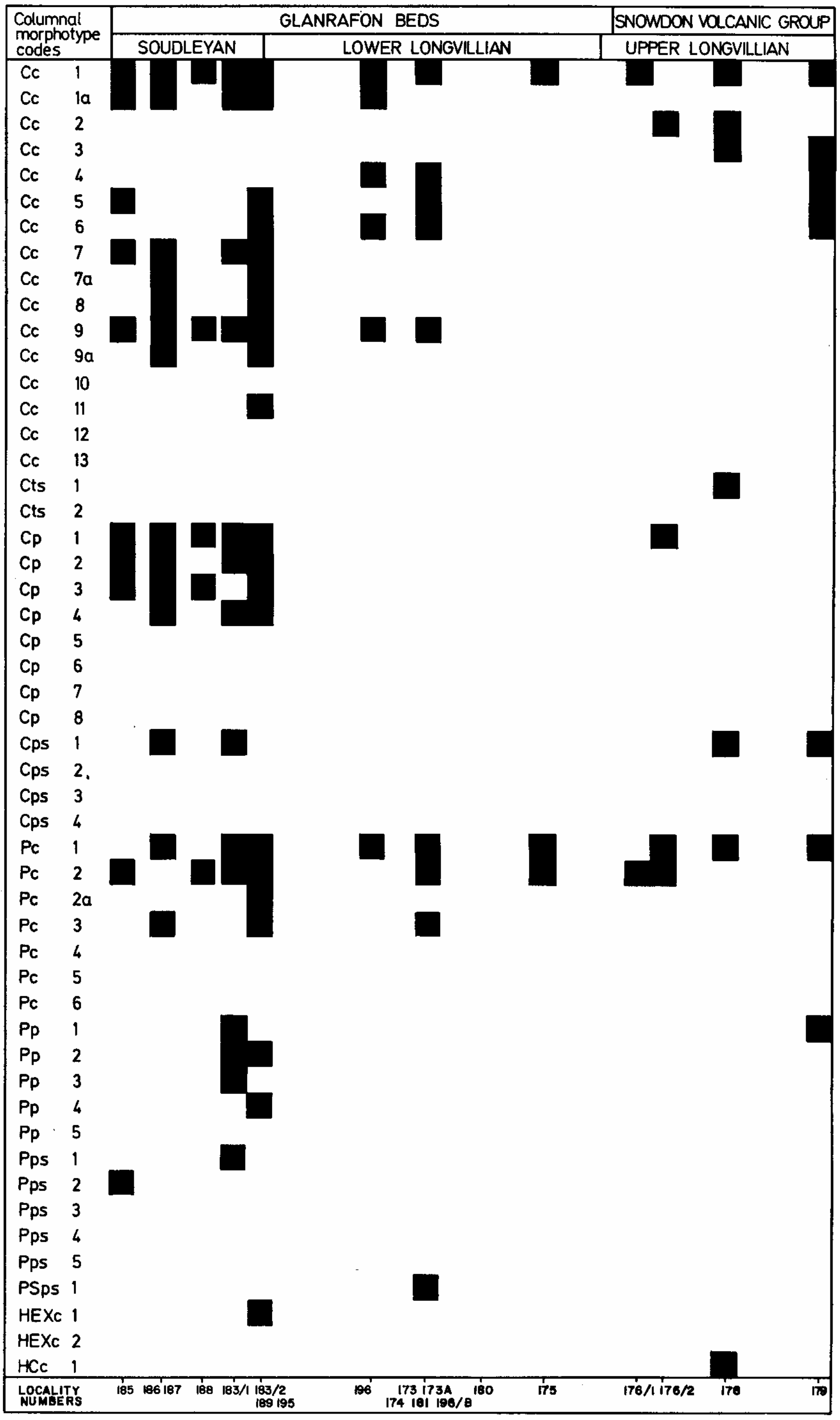
(*a*) Certain morphotypes appear potentially useful biostratigraphical indicators, as they seem restricted either to one horizon or Stage, e.g. Cc 2, Cc 3, Cc 7, Cc 7a, Cc 8, Cc 9a, Cc 11, Cts 1, and Cp 1–4.

(*b*) Certain morphotypes appear to cluster together, e.g. Cc 4–6, Cp 1–4, and Pc 1–2, and may represent original morphotype combinations from xenomorphic or heteromorphic stems.

(*c*) The Soudleyan–lower Longvillian stage boundary was derived from the shelly macrofauna, prior to the plotting of the presence–absence data. These data reveal a significant change in the stratigraphical distribution of morphotypes at this horizon.

SUMMARY

In contrast to many similar analyses, dissociated crinoid columnals and other fragmented fossils are incorporated within faunal analyses of the Caradoc shelly assemblages from Snowdonia. A list is compiled for the different columnal morphotypes encountered within the Snowdonian shelly faunas, which aids identification and highlights columnal diversity (fifty-one morphotypes). Taking into account xenomorphism, heteromorphism, taphonomic losses, and the vagaries of preservation, it is considered that several crinoid species comprised part of the sessile benthos in the outer



TEXT-FIG. 5. Presence-absence plot of columnal morphotypes from the Glanrafon Beds and Snowdon Volcanic Group to the south-west of Dolwyddelan.

sublittoral-offshore environments of the north-western part of the Welsh Basin. Further applications of the list include the potential recognition of columnal combinations which originally may have comprised either heteromorphic or xenomorphic stems and the possible use of columnals in biostratigraphy and resultant correlations.

Acknowledgements. The paper has been greatly improved by the constructive criticism and helpful comments of Drs. J. S. W. Penn, R. T. J. Moody, R. B. Stokes, P. J. Brenchley, A. W. A. Rushton, W. I. Ausich, Mr. S. Donovan, Mr. D. T. J. Smith, and an anonymous referee. Miss L. Parry and Mr. D. Bayliss prepared the diagrams and photographs, respectively.

REFERENCES

ANDERSON, E. J. 1968. Pelmatozoan limestone fabrics: an indicator of current and wave persistence and intensity. *Abstr. geol. Soc. Am.* (*Spec. Pap. geol. Soc. Am.* **115**), **5**, 97.

AUSICH, W. I., KAMMER, T. W. and LANE, N. G. 1979. Fossil communities of the Borden (Mississippian) delta in Indiana and northern Kentucky. *J. Paleont.* **53**, 1182–1196.

BEAVON, R. V. 1960. 'The geology of an area east of Beddgelert (North Wales).' Unpublished Ph.D. thesis, University College of Wales, Aberystwyth.

—— 1963. The succession and structure east of the Glaslyn River, North Wales. *Q. Jl. geol. Soc. London*, **119**, 479–512.

BERGSTRÖM, J. 1968. Some Ordovician and Silurian brachiopod assemblages. *Lethaia*, **1**, 230–237.

BERRY, W. B. N., LAWSON, D. A. and YANCEY, E. S. 1979. Species diversity patterns in some Middle Ordovician communities from California-Nevada. *Palaeogeogr., Palaeoclimat., Palaeoecol.* **26**, 99–116.

BOWEN, Z. P., RHOADS, D. C. and MCALESTER, A. L. 1974. Marine benthic communities in the Upper Ordovician of New York. *Lethaia*, **7**, 93–120.

BRETSKY, P. W. 1969. Central Appalachian late Ordovician communities. *Bull. geol. Soc. Am.* **80**, 193–212.

—— 1970*a*. Upper Ordovician ecology of the Central Appalachians. *Bull. Peabody Mus. nat. Hist.* **34**, 1–150.

—— 1970*b*. Late Ordovician benthic marine communities in north central New York. *Bull. N.Y. St. Mus. Sci. Serv.* **44**, 1–34.

—— BRETSKY, S. S. and SCHAEFFER, P. J. 1977. Molluscan and brachiopod dominated biofacies in the Platteville Formation (Middle Ordovician), upper Mississippi Valley. *Bull. geol. Soc. Denmark.* **26**, 115–132.

—— FLESSA, K. W. and BRETSKY, S. S. 1969. Brachiopod ecology in the Ordovician of eastern Pennsylvania. *J. Paleont.* **43**, 312–321.

BROWER, J. C. 1973. Crinoids from the Girardeau Limestone (Ordovician). *Paleontogr. Am.* **7**, 263–499.

—— 1975. Silurian crinoids from the Pentland Hills, Scotland. *Palaeontology*, **18**, 631–656.

—— 1978. Camerates. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*. Part T, Echinodermata 2 (vol. 1). Geological Society of America and University of Kansas Press, T244–T263.

—— and VEINUS, J. 1974. Middle Ordovician crinoids from southwestern Virginia and eastern Tennessee. *Bull. Am. Paleontol.* **66**, 1–125.

—— and —— 1978. Middle Ordovician crinoids from the Twin Cities area of Minnesota. Ibid. **74**, 369–506.

BYERS, C. W. and GAVLIN, S. 1979. Two contemporaneous equilibrium communities in the Ordovician of Wisconsin. *Lethaia*, **12**, 297–307.

CADEE, G. 1968. Molluscan biocoenoses and thanatocoenoses in the Ria de Arosa, Galicia, Spain. *Zool. Verh.* **95**, 1–121.

CAIN, J. D. B. 1968. Aspects of the depositional environment and palaeoecology of crinoidal limestones. *Scott. J. Geol.* **4**, 191–208.

CALEF, C. E. and HANCOCK, N. J. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderlands. *Palaeontology*, **17**, 779–810.

DIGGENS, J. N. and ROMANO, M. 1968. The Caradoc rocks around Llyn Cowlyd, North Wales. *Geol. J.* **6**, 31–48.

FELDMAN, H. R. 1980. Level-bottom brachiopod communities in the Middle Devonian of New York. *Lethaia*, **13**, 27–46.

FRANCIS, E. H. and HOWELLS, M. F. 1973. Transgressive welded ash-flow tuffs among the Ordovician sediments of NE Snowdonia, N. Wales. *J. geol. Soc. London*, **129**, 621–641.

HARMS, J. C. and FAHNESTOCK, R. K. 1965. Stratification, bed forms, and flow phenomena (with an example from the Rio Grande). *In* MIDDLETON, G. V. (ed.). Primary sedimentary structures and their hydrodynamic interpretation. *Spec. Publ. Soc. econ. Paleontol. Mineral. Tulsa.* **12**, 84–115.

HERM, D. 1972. Pitfalls in paleoecologic interpretation—an integrated approach to avoid the major pits. *24th Int. geol. Congr. Montreal.* **7,** 82–88.

HOWELLS, M. F., FRANCIS, E. H., LEVERIDGE, B. E. and EVANS, C. D. R. 1978. *Capel Curig and Betws-y-Coed: Description of 1:25000 sheet SH 75.* Classical areas of British geology, Institute of Geological Sciences. Her Majesty's Stationery Office, 73 pp.

HURST, J. M. 1975*a*. Wenlock carbonate, level bottom, brachiopod dominated communities from Wales and the Welsh Borderland. *Palaeogeogr., Palaeoclimat., Palaeoecol.* **17,** 227–255.

——1975*b*. Some observation on brachiopods and the level-bottom community ecology of Gotland. *Forh. geol. Foren. Stockholm.* **97,** 250–264.

——1979*a*. Evolution, succession and replacement in the type upper Caradoc (Ordovician) benthic faunas of England. *Palaeogeogr., Palaeoclimat., Palaeoecol.* **27,** 189–246.

——1979*b*. The environment of deposition of the Caradoc Alternata Limestone and contiguous deposits of Salop. *Geol. J.* **14,** 15–40.

JAANUSSON, V., LAUFELD, S. and SKOGLUND, R. (eds.). 1979. Lower Wenlock faunal and floral dynamics—Vattenfallet section, Gotland. *Sver. geol. Unders.* Ser. C, **762,** 1–294.

JEFFORDS, R. M. 1978. Dissociated crinoid skeletal elements. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology.* Part T, Echinodermata 2 (vol. 3). Geological Society of America and University of Kansas Press, T928–T929.

KAUFFMAN, E. G. and SCOTT, R. W. 1976. Basic concepts of community ecology and paleoecology. *In* SCOTT, R. W. and WEST, R. R. (eds.). *Structure and classification of paleocommunities.* Dowden, Hutchinson & Ross, Inc., Stroudsberg, Pennsylvania, 1–28.

LANE, N. G. 1973. Paleontology and paleoecology of the Crawfordsville fossil site. *Univ. California Publ. geol. Sci.* **99,** 1–141.

——and MATTHEWS, J. L. 1965. Evolution of the Crawfordsville, Indiana, fossil community. *Abstr. geol. Soc. Am.* (*Spec. Pap. geol. Soc. Am.* **87**), 93.

——and SEVASTOPULO, G. D. 1981. Functional morphology of a microcrinoid: *Kallimorphocrinus punctatus* n. sp. *J. Paleont.* **55,** 13–28.

LEWIS, R. D. 1981. *Archaetaxocrinus*, new genus, the earliest known flexible crinoid (Whiterockian) and its phylogenetic implications. Ibid. **55,** 227–238.

LIDDELL, D. W. 1975. Recent crinoid biostratinomy. *Geol. Soc. Am. Abstr.*, **7,** 1169.

MacDONALD, K. B. 1976. Paleocommunities: towards some confidence limits. *In* SCOTT, R. W. and WEST, R. R. (eds.). *Structure and classification of paleocommunities.* Dowden, Hutchinson & Ross, Inc., Stroudsberg, Pennsylvania, 87–106.

MACURDA, D. B., Jr., and MEYER, D. L. 1976. The morphology and life habits of the abyssal crinoid *Bathycrinus aldrichianus* Wyville Thomson and its paleontological implications. *J. Paleont.* **50,** 647–667.

————and ROUX, M. 1978. The crinoid stereom. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology.* Part T, Echinodermata 2 (vol. 1). Geological Society of America and University of Kansas Press, T217–T228.

MANTEN, A. A. 1970. Palaeoecology of Silurian crinoids of Gotland (Sweden). *Palaeogeogr., Palaeoclimat., Palaeoecol.* **7,** 171–184.

MEYER, D. L. 1971. Post mortem disarticulation of Recent crinoids and ophiuroids under natural conditions. *Geol. Soc. Am. Abstr. Progm.* **3,** 645–646.

MOORE, R. C. 1939. The use of fragmentary crinoidal remains in stratigraphic paleontology. *J. Sci. Lab. Denison Univ. Ohio,* **33,** 165–250.

——1978. Glossary of crinoid morphological terms. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology.* Part T, Echinodermata 2 (vol. 1). Geological Society of America and University of Kansas Press, T229–T242.

——and JEFFORDS, R. M. 1968. Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns. *Paleontol. Contrib. Kansas Univ.* **46,** *Echinodermata,* Article 9, 1–86.

————and MILLER, T. H. 1968. Morphological features of crinoid columns. Ibid. **45,** *Echinodermata,* Article 8, 1–30.

MULLER, A. H. 1979. Fossilization (taphonomy). *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology.* Part A, Introduction. Geological Society of America and University of Kansas Press, A2–A78.

PETERSON, C. H. 1976. Relative abundances of living and dead molluscs in two Californian lagoons. *Lethaia,* **9,** 137–148.

PICKERILL, R. K. and BRENCHLEY, P. J. 1979. Caradoc marine benthic communities of the south Berwyn Hills, North Wales. *Palaeontology,* **22,** 229–264.

RAMSAY, A. C. 1866. The geology of North Wales. *Mem. geol. Surv. G.B.* **3,** 381 pp.

RASMUSSEN, H. W. 1978*a*. Articulates. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*. Part T, Echinodermata 2 (vol. 1). Geological Society of America and University of Kansas Press, T268–T274.

——1978*b*. Systematic descriptions—Articulata. *In* MOORE, R. C. (ed.). Ibid. T813–T927.

ROMANO, M. and DIGGENS, J. N. 1969. Longvillian shelly faunas from the Dolwyddelan area, North Wales. *Geol. Mag.* **106,** 603–606.

RUHRMANN, G. 1971. Riff-ferne sedimentation unterdevonischer krinoidenkalke im Kantabrischen Gebirge (Spanien). (Off-reef sedimentation of Lower Devonian crinoid limestones in the Cantabrian Mountains, Spain.) *Neues Jahrb. Geol. Palaeontol. Abhandlungen.* **137,** 422–442.

SCHWARZACHER, W. 1963. Orientation of crinoids by current action. *J. sediment. Petrol.* **33,** 580–586.

SEDGWICK, A. 1838. A synopsis of the English series of stratified rocks inferior to the Old Red Sandstone—with an attempt to determine the successive natural groups and formations. *Proc. geol. Soc. London.* **2** (for 1833–1838), 675–685.

——1841. Supplement to a 'Synopsis of the English series of stratified rocks inferior to the Old Red Sandstone' with additional remarks on the relations of the Carboniferous System and Old Red Sandstone of the British Isles. Ibid. **3,** 545–554.

——1843. Outline of geological structure of North Wales. Ibid. **4,** 212–224.

——1847. On the classification of the fossiliferous slates of North Wales, Cumberland, Westmoreland and Lancashire. *Q. Jl. geol. Soc. London.* **3,** 133–164.

SEILACHER, A. 1973. Biostratinomy: the sedimentology of biologically standardised particles. *In* GINSBURG, R. N. (ed.). *Evolving concepts in sedimentology*. John Hopkins University Press, Baltimore, 159–177.

——DROZDZEWSKI, G. and HAUDE, R. 1968. Form and function of the stem in a pseudoplanktonic crinoid (*Seirocrinus*). *Palaeontology*, **11,** 275–282.

SHACKLETON, R. M. 1959. The stratigraphy of the Moel Hebog district between Snowdon and Tremadoc. With a note on the Caradoc shelly faunas by J. C. Harper. *Liverpool Manchester geol. J.* **2,** 216–252.

STUKALINA, G. A. 1966. O printsipakh klassifikatsii stebley drevnikh morskikh liliy. *Paleont. Zhurnal.* **3,** 94–102. (Translated—Principles of classification of stems of ancient sea lilies. *Int. geol. Rev.* **9,** 549–555, 1976.)

——1968. K sistematike gruppy Pentamerata. *Paleont. Zhurnal.* **1,** 81–91. (Translated—Systematics of the Pentamerata (Crinoidea) Group. *Paleont. Zh.* **1,** 73–82, 1968.)

THAYER, C. W. 1974. Marine paleoecology in the Upper Devonian of New York. *Lethaia*, **7,** 121–155.

TITUS, R. and CAMERON, B. 1976. Fossil communities of the Lower Trenton Group (Middle Ordovician) of central and northwestern New York State. *J. Paleont.* **50,** 1209–1225.

UBAGHS, G. 1978*a*. Skeletal morphology of fossil crinoids. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*. Part T, Echinodermata 2 (vol. 1). Geological Society of America and University of Kansas Press, T58–T216.

——1978*b*. Camerata. *In* MOORE, R. C. (ed.). Ibid. T408–T519.

WARME, J. E. 1971. Paleoecological aspects of a modern coastal lagoon. *Univ. California Publ. geol. Sci.* **87,** 1–131.

——EKDALE, A. A., EKDALE, S. F. and PETERSON, C. H. 1976. Raw material of the fossil record. *In* SCOTT, R. W. and WEST, R. R. (eds.). *Structure and classification of paleocommunities*. Dowden, Hutchinson & Ross, Inc., Stroudsberg, Pennsylvania, 143–169.

WATKINS, R. 1973. Carboniferous faunal associations and stratigraphy, Shasta County, northern California. *Bull. Am. Assoc. Petrol. Geol.* **57,** 1743–1764.

——1978. Silurian marine communities west of Dingle, Ireland. *Palaeogeogr., Palaeoclimat., Palaeoecol.* **23,** 79–118.

WEBSTER, G. D. 1974. Crinoid pluricolumnal noditaxis patterns. *J. Paleont.* **48,** 1283–1288.

WILLIAMS, A. 1963. The Caradocian brachiopod faunas of the Bala district, Merionethshire. *Bull. Br. Mus. nat. Hist.* (Geol.) **8,** 327–471.

——1973. Distribution of brachiopod assemblages in relation to Ordovician palaeogeography. *In* HUGHES, N. F. (ed.). Organisms and continents through time. *Spec. Pap. Palaeontology*, **12,** 241–269.

——STRACHAN, I., BASSETT, D. A., DEAN, W. T., INGHAM, J. K., WRIGHT, A. D. and WHITTINGTON, H. B. 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. London*, **3,** 1–74.

WILLIAMS, D. 1930. The geology of the country between Nant Peris and Nant Ffrancon (Snowdonia). *Q. Jl geol. Soc. London.* **86,** 191–233.

WILLIAMS, H. 1927. The geology of Snowdon (North Wales). Ibid. **83,** 346–431.

——and BULMAN, O. M. B. 1931. The geology of the Dolwyddelan syncline (North Wales). Ibid. **87,** 425–458.

WRIGHT, D. K. 1979. 'A faunal analysis of Soudleyan/Longvillian rocks in Snowdonia, North Wales.' Unpublished Ph.D. thesis, C.N.A.A. (2 vols.).

ZIEGLER, A. M., COCKS, L. R. M. and BAMBACH, R. K. 1968. The composition and structure of Lower Silurian marine communities. *Lethaia*, **1**, 1–27.

D. K. WRIGHT
School of Geology
Kingston Polytechnic
Kingston upon Thames KT1 2EE

Typescript received 1 February 1982
Revised typescript received 1 September 1982