# PATTERNS OF DIVERSIFICATION AND EXTINCTION IN EARLY PALAEOZOIC ECHINODERMS

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ABSTRACT. It has been claimed that Cambrian and early Ordovician echinoderms show two phases of diversification as recognized by Sepkoski for marine taxa in general. However, a more critical assessment of the record, using cladistic analyses of all determinable echinoderm genera to identify sister group relationships, allows sampling deficits to be taken into consideration. It is shown that the Upper Cambrian dip in diversity amongst echinoderms is likely to be the result of preservation failure and that diversification more closely approximates to a continuous process of expansion during the Cambrian and early Ordovician. Taxonomic diversity cannot be used as a measure of morphological diversity because rank has been applied for a number of different and incompatible reasons. There is no evidence to support the claim that morphological evolution was occurring significantly faster during this period compared with later periods.

THE publication of the *Treatise on Invertebrate Paleontology* during the last three decades has provided a relatively comprehensive and authoritative data base summarizing the stratigraphical ranges for genera in most major groups of marine invertebrates. This in turn has made it relatively simple to carry out analyses of taxonomic ranges, and has stimulated the current interest in patterns of evolution and changes in taxonomic diversity during the Phanerozoic. The recent interest in patterns of evolution, as revealed by the available taxonomic data, dates back to the work of Simpson (1953). Further interest in large scale patterns was created by the publication of Valentine's (1969) analysis developing Simpson's thesis that different taxonomic levels showed different diversity patterns when plotted through geological time. Valentine found that, whereas generic diversity appears to have increased towards the present day, higher taxonomic groups reach their peak diversity further back in time; the higher the categorical rank of the taxon, the earlier it appears to have reached its maximum diversity. Thus phyla and classes were most numerous in the Lower Palaeozoic and have declined since then (see Raup 1972 for a clear analysis of this phenomenon). Valentine believed this pattern demonstrated that there was a rapid initial morphological diversification in the Cambro-Ordovician which was later followed by a protracted phase of competition in which the less successful groups were weeded out.

This general approach of using taxonomic data to interpret patterns of evolution has since been refined and expanded upon by several workers, notably by Sepkoski (1978, 1978, 1981a, b, 1986), Sepkoski and Raup (1986), and Raup and Sepkoski (1982, 1984), using a compilation of families of marine invertebrates that is as up-to-date as possible (Sepkoski 1982, plus supplements) and an as yet unpublished compendium of marine genera (see Sepkoski 1986). Various stimulating hypotheses have been generated in the last few years on the basis of these data, the most notable being the identification of cyclicity in extinction events with a periodicity of 26-28 million years (my) (Raup and Sepkoski 1984; Sepkoski and Raup 1986). Similar sorts of data have also been used to test a number of other hypotheses, including multiphase evolutionary diversification (Sepkoski 1979), the Red Queen's hypothesis (Van Valen 1973; Raup 1975), onshore-offshore community replacement (Sepkoski and Sheehan 1983; Jablonski and Bottjer 1986), changing levels of diversity within taxa through time (Flessa and Jablonski 1985). The ecological and genetic implications for these patterns have been explored by Valentine (1980, 1986).
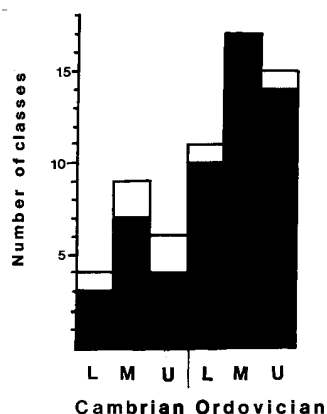
TEXT-FIG. 1. Plot of number of echinoderm classes in the early Palaeozoic (taken from Sprinkle 1980b). Questionable occurrences unshaded.

The record of echinoderms has also been examined in detail by specialists interested in documenting the pattern of evolution within this group (Paul 1977, 1979; Sprinkle 1980a, b, 1981, 1983) and has been shown to conform with that for invertebrate marine groups in general. Indeed, the record of echinoderms appears to show an initial diversification during the Cambrian and early Ordovician at class level which is more pronounced than in any other group. Paul (1979) was able to demonstrate that diversity, as measured in genera per million years, increased to a maximum in the Carboniferous then declined to a low at the Permo-Triassic boundary and then increased once more to the present-day levels. But analysis of diversity at class level demonstrated 'a clear early radiation' (Paul 1979, p. 417) with fifteen classes known from the Cambrian and nineteen from the Ordovician after which the numbers gradually decline to the present level of five extant classes. Sprinkle (1980b, 1983) confirmed this view of echinoderm evolution and claimed that 'no new classes [of echinoderm] appeared in the fossil record after the Middle Ordovician' (Sprinkle 1983, p. 5). Paul (1979) described this pattern as one of 'colonisation-radiation/competition-retrenchment' and discussed the biological causes that could produce this.

Sprinkle (1981, p. 221) argued that 'four of the five echinoderm subphyla probably crossed the pre-Cambrian–Cambrian boundary' and noted that 'new classes appeared suddenly in the record without obvious ancestors'. His (1980b) analysis of timing of appearance of echinoderm classes (text-fig. 1) showed that echinoderms appear to have undergone two or three phases of taxonomic diversification, precisely as described for invertebrate metazoans by Sepkoski (1979, 1981b). Campbell and Marshall (1986) have also analysed the record of echinoderms using higher taxonomic groupings and concluded that there were two phases of morphological diversification, one in the Lower to Middle Cambrian, the other in the Early Ordovician. They also believe that these classes were morphologically highly distinct from their inception. They speculate that the echinoderm genome might have been significantly different at this time to allow such jumps.

Thus analysis of the traditional taxonomic data base shows that echinoderms are not an aberrant group, in so far as they show a similar pattern of taxonomic diversification to other marine invertebrate groups and to the marine invertebrate biota as a whole. The question that I wish to address in this paper is—how real is this view of the early evolutionary history of echinoderms? Or, put another way, how much does it reflect taxonomic artefact? This question was first posed by Derstler (1981), in a short but interesting paper, where he briefly outlined evidence suggesting that much evolution in echinoderms occurred during the early Phanerozoic rather than in the Precambrian, and that accounts of the early Phanerozoic diversification were probably based on 'inappropriate assumptions about morphological change during evolution' (Derstler 1981, p. 74). In this paper I shall try to show how the assumptions and practice of taxonomists have indeed resulted in a very misleading view of the early evolution of echinoderms.

PROBLEMS IN ESTABLISHING TAXONOMIC DIVERSITY PATTERNS

1. Poor knowledge of the Cambrian fauna

Despite some really excellent and detailed work on selected primitive echinoderms (see for example Ubaghs 1953, 1963 a, b; Ubaghs and Robison 1985; Sprinkle 1973; Bell and Sprinkle 1978; Jell et al. 1985) our understanding of a large number of forms remains sketchy and incomplete. In the past there has been a tendency to describe new taxa based on very incomplete or badly preserved material simply because it comes from the Cambrian and therefore 'must be important'. Certainly the Cambrian fauna is of interest because it provides us with direct evidence on the earliest and most primitive echinoderms that existed. Yet all too often taxa are established on very scrappy material. This has caused workers to misinterpret basic anatomical organization, with the result that these taxa appear to have a morphology that is strikingly different from known echinoderms. Thus Cymbionites and Peridionites were described as new classes of echinoderm and united together in the subphylum Haplozoa by Whitehouse (1941), whereas they are now interpreted as fragments (basal circlets) of 'eocrinoids' (Smith 1982). Camptostroma, another echinoderm known from only a small number of distorted and badly preserved specimens, was initially described as a plated jellyfish (Ruedemann 1933), then as a new class of echinoderm with plated tube feet (Durham 1966) and more recently as either eocrinoid (Broadhead 1980) or edrioasteroid (Derstler 1981) or intermediate between eocrinoids and edrioasteroids (Paul and Smith 1984).

Leaving aside specimens that have been misinterpreted, there are also a number of Cambrian species (and the genera, families, and sometimes orders established for them) which are based on just one or a very few specimens and which remain incompletely known. There are only a handful of specimens of the genus Echmatocrinus, and much of its anatomy remains unknown (we do not even know how many arms it had), yet this is elevated to the rank of subclass (Sprinkle and Moore 1978). Some genera are so poorly known that they are for all intents and purposes unclassifiable. For example, the genus Volchovia, on which the record of ophiocistioids is extended back to the base of the Ordovician, is so incompletely known and shows so few features that it could just as easily be a mitrate, or a Rhipidocystis-like eocrinoid. The record of holothuroids is extended back to the Cambrian on even flimsier evidence. The supposed Cambrian record of holothuroids is based on one body fossil, Eldonia, from the Burgess Shale, which lacks even a single echinoderm character, and on microscopic spicules which are undiagnostic and could be juvenile elements of almost any echinoderm.

Thus, because of the 'mystique' of the Cambrian, there are a disproportionately large number of incompletely known taxa some of which have been elevated to high rank on the basis of misinterpretation.

2. Sampling, preservation, and Lagerstätten

Although some echinoderms such as echinoids have rigid skeletons that are readily preserved intact in the fossil record, most do not. Primitive echinoderms had a membrane-embedded skeleton that rapidly disarticulated upon death into individual plates to be scattered and lost. Whereas echinoderm debris is often an important element in bioclastic sands and limestones, whole fossils are rare. It requires special sedimentological conditions to preserve primitive echinoderms more or less complete and intact, and these conditions can produce the so-called 'starfish beds' (see Goldring and Stephenson 1972; Paul 1977). Sprinkle (1976a) has noted how rare echinoderm localities are in the Cambrian, despite the apparent abundance of echinoderm plates within the sediments at certain horizons. Occasionally a locality will yield only one or a few specimens of a single species by chance, but it is more usual for echinoderm localities to yield sometimes large numbers of well-preserved specimens of more than one species. These are deposits where conditions have been favourable for preserving the echinoderm fauna and which can be referred to as echinoderm Lagerstätten.

The distribution of echinoderm Lagerstätten will affect the apparent pattern of taxonomic origination and extinction, since periods when conditions were favourable for the formation of

TABLE 1. Localities at which two or more taxa of echinoderm or carpoid have been collected as articulated specimens.

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Arenig	
Schistes de St Chinian, Hérault, France	Ubaghs (1983)
Schistes de Landeyran, Hérault, France	Ubaghs (1983)
Gres de la Manerie, Hérault, France	Ubaghs (1983)
Anti-Atlas Mountains, Morocco	Chauvel (1966)
Asaphus Marl, Oslo, Norway	Bockelie (1984)
Whitland, Wales, UK	Fortey and Owens (1987)
Kunvald Formation, Estonia	Bassler and Moodey (1943)
Ramsey Island, Wales, UK	Spencer (1918), Bates (1968)
Llangynog, Wales, UK	Cope (1988)
Upper Tremadocian	
Fillmore Limestone, Nevada, USA	Lane (1970), Paul (1972)
Anti-Atlas Mountains, Morocco	Chauvel (1966)
Schistes de St Chinian, Hérault, France	Ubaghs (1983)
Lower Tremadocian	
—	
Trempealeauian	
Whipple Cave Formation, Nevada, USA	Sprinkle (1976a)
Franconian	
Chatsworth Limestone, Queensland, Australia	Jell et al. (1985)
Dresbachian	
—	
Upper Middle Cambrian	
Secret Canyon Formation, Nevada, USA	Sprinkle (1976a)
Marjum Formation, Utah, USA	Ubaghs and Robison (1985)
Jince Formation, Czechoslovakia	Pompeckj (1896)
Porth-y-Rhaw beds, Pembroke, Wales, UK	Jefferies et al. (1987)
Beds E, F, Ferrals-les-Montagnes, France	Courtessole (1973), Ubaghs (1987)
Median Middle Cambrian	
Chisholm Shale, Nevada, USA	Sprinkle (1976a)
Lead Bell Shale, Idaho, USA	Sprinkle (1976a)
Spence Shale, Idaho/Utah, USA	Sprinkle (1976a)
Burgess Shale, British Columbia, Canada	Sprinkle (1976a)
Oelandicus Shales, Norrtrop, Sweden	Berg-Madsen (1986)
Cateena Group, Tasmania	Jell et al. (1985)
Lower Middle Cambrian	
Beetle Creek Formation, Queensland, Australia	Jell et al. (1985)
Lower Cambrian, Bonnia-Olenellus Zone	
Upper Olenellus Beds, Newfoundland, Canada	Smith (1986)
Kinzers Formation, Pennsylvania, USA	Derstler (1981)
Lower Cambrian, Nevadella Zone	
Poleta Formation, Nevada, USA	Sprinkle (1976a)
Poleta Formation, California, USA	Durham (1967)

echinoderm Lagerstätten will tend to show falsely higher rates of origination and extinction of taxa than periods when conditions were less favourable and the fauna only patchily preserved. So rates of origination and extinction will be artificially depressed during times of low preservation potential brought about by factors such as major marine regression. Sprinkle (1981) was aware of this problem and pointed out that, although the Upper Cambrian appears to show a drop in total diversity, this may be at least partially due to non-preservation. Sprinkle pointed out that the Upper Cambrian was a period in which broad carbonate shelves formed, unfavourable for the preservation of echinoderms. Whereas echinoderm debris is often an important constituent of these Upper Cambrian limestones, whole specimens are particularly rare.

TEXT-FIG. 2. Abundance of echinoderm Lagerstätten (Table 1) through the Cambrian and early Ordovician. Superimposed is a graph of the number of family originations per time period—data taken from Sepkoski 1982, plus supplements.
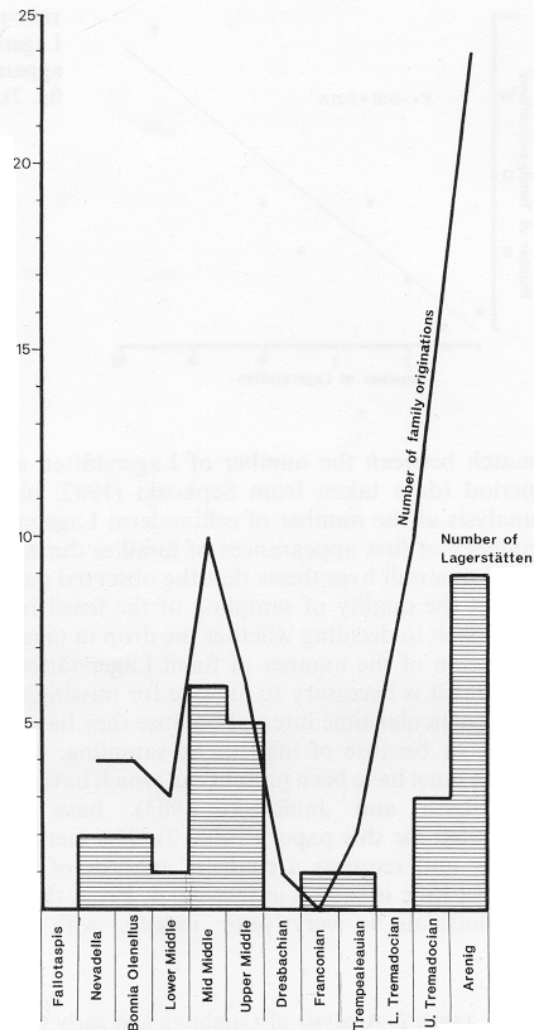
The rapid appearance of a number of groups at the base of the Ordovician may, therefore, be more apparent than real; the product of our poor knowledge of Upper Cambrian echinoderm faunas. Campbell and Marshall (1986), however, believed that it was not so, arguing that morphological innovation really was concentrated in two distinct phases. They based their argument on the observation that other groups (namely trilobites, brachiopods, and molluscs) continue to diversify through the Upper Cambrian, which for them proved that the observed pattern of taxonomic origination for echinoderms must be genuine. Whether the observed low diversity in echinoderms during the Upper Cambrian was a genuine phenomenon or is a result of sampling deficiency can, however, be tested.

Table 1 lists all localities from the Lower Cambrian through to the Arenig that have yielded articulated specimens of two or more taxa of echinoderm or 'carpoid'. (As all previous analyses of echinoderm diversity patterns have treated 'carpoids' as echinoderms, here and throughout the paper carpoid and echinoderm data have been combined so that results are directly comparable. This does not imply that carpoids and echinoderms necessarily form a monophyletic group.) When plotted as number of Lagerstätten per time interval (text-fig. 2) there appears to be a very close

Y = -0·31 + 2·21X

Number of 'family originations'

24
18
12
6

2   4   6   8   10
Number of Lagerstätten
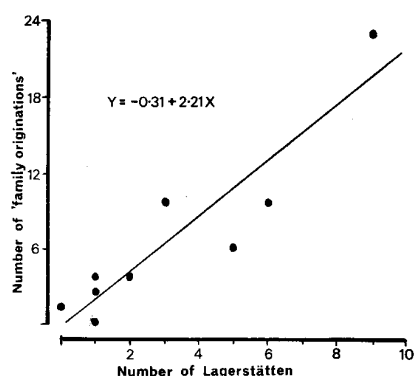
TEXT-FIG. 3. Regression analysis of number of echinoderm Lagerstätten for each time interval plotted against number of apparent family-level taxonomic originations (data as in text-fig. 2).

match between the number of Lagerstätten and the number of families originating during each period (data taken from Sepkoski (1982, plus supplements)). This is confirmed by regression analysis of the number of echinoderm Lagerstätten in each time interval plotted against apparent number of first appearances of families during that period (text-fig. 3).

Thus a null hypothesis that the observed pattern for family level originations does no more than reflect the quality of sampling of the fossil record cannot be rejected. However, a more positive approach to deciding whether the drop in taxa observed in the Upper Cambrian is a real event or a reflection of the number of fossil Lagerstätten can be adopted. To distinguish between these two options it is necessary to analyse for missing taxa (see Paul 1982). Taxa may disappear at the end of a particular time interval because they have gone extinct, because they have suffered a change of name or because of inadequate sampling: the latter two cases produce pseudoextinctions. Taxa which must have been present but which have not yet been found (named Lazarus taxa by Jablonski, in Flessa and Jablonski 1983), have been calculated using the generic data base compiled for this paper (Table 2). The method by which missing taxa was recognized is detailed below and requires a cladistic analysis of the taxa. A plot of known taxa plus Lazarus taxa against time is shown in text-fig. 4. From this it is clear that the fossil record of Upper Cambrian echinoderms is very poor indeed, with up to 80% of the taxa known to have been

TABLE 2. Analysis of Cambrian and early Ordovician echinoderm diversity, based on text-fig. 9. Figures in brackets = fauna excluding 'carpoids'.

	No. of genera recorded	No. of Lazarus genera	No. of originations	Minimum % genera not yet recorded
Arenig	43 (27)	6 (6)	39 (23)	12
Upper Tremadocian	8 (7)	16 (14)	5 (5)	67
Lower Tremadocian	1 (1)	16 (13)	12 (11)	94
Trempealeauian	5 (2)	13 (13)	7 (4)	72
Franconian	3 (3)	12 (10)	3 (3)	80
Dresbachian	3 (2)	10 (8)	3 (3)	77
Upper Middle	22 (12)	6 (5)	13 (7)	21
Median Middle	15 (11)	6 (4)	12 (7)	29
Lower Middle	8 (8)	4 (3)	7 (7)	33
Upper Bonnia–Olenellus	3 (3)	4 (3)	4 (4)	57
Lower Bonnia–Olenellus	5 (4)	0 (0)	4 (4)	—
Nevadella	2 (2)	1 (1)	3 (2)	33
Fallotaspis	0 (0)	1	1	—

TEXT-FIG. 4. Histogram of number of recorded genera (black) and 'Lazarus' taxa, those that are known to have been present but have not yet been discovered (stippled), in each time interval.
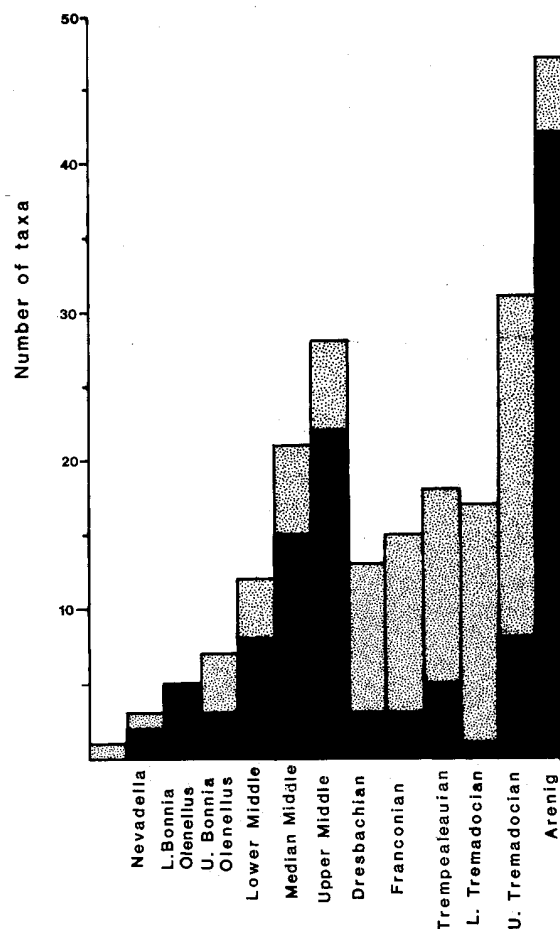
present still undiscovered (this is a minimum estimate). During the entire Upper Cambrian and Tremadoc, Lazarus taxa outnumber known taxa by more than two to one. The only other early Palaeozoic geological period where Lazarus taxa form more than 50 % of the 'total' fauna is during the Upper Bonnia-Olenellus Zone where they reach 57 %. (A comparable loss of taxa attributable to preservation failure was noted for Lower Silurian cystoids by Paul 1982.) Thus the apparent drop in taxonomic origination during this period is unlikely to be a real phenomenon, but a reflection of sampling. Any calculation of echinoderm patterns of standing diversity, origination, and extinction must take into account this artificial drop in diversity brought about through inadequate sampling of the fauna.

3. Taxonomic artefact

Whereas the poor knowledge of Cambrian echinoderms can be put right by further finds and more detailed revision of the taxa, and the effect of fluctuating levels of sampling produced by Lagerstätten distribution can be taken into account, a much more fundamental question can be raised about the comparability of the taxa analysed.

Prior to the advent of cladistics, the practice of taxonomy lacked any clear or agreed methodology and proceeded in a rather haphazard manner. In effect, taxonomic decisions about how to group species were arbitrary and basically authoritarian, and there was no objective criterion by which

to judge rival schemes. Echinoderm taxonomy during the last three decades has fared particularly badly with taxonomists tending to stress differences between taxa while ignoring shared derived characters, which form the basis for identifying relationships. Paraphyletic taxa which have some, but not all, characters of an established higher taxon have tended to be separated off as a new higher taxon (for example the creation of the Coronoidea by Brett *et al.* 1983). This has led to the creation of a plethora of taxa of high rank. I have criticized this approach elsewhere (Smith 1984) for side-stepping problems of relationships between taxa and for destroying the hierarchical nature of the classificatory system.

The lack of a clearly stated method that can be applied consistently in traditional systematics has resulted in a taxonomic data base that is riddled with inconsistency. Thus there are major problems in extrapolating evolutionary patterns from this sort of data, two of which will be explored below:

(i) *Extinctions and pseudoextinctions.* In traditional systematics there has been no clear distinction made between monophyletic and paraphyletic groupings, and paraphyletic groupings abound in the non-cladistic taxonomic data base (see Patterson and Smith 1987). Paraphyletic groupings, being arbitrary units whose upper boundary is created by a taxonomist's decision, tend to obscure evolutionary patterns and extinction patterns. Whereas the disappearance of a clade from the fossil record is a real event and represents the extinction of an evolutionary lineage, the disappearance of a paraphyletic group reflects a taxonomist's decision to change the group's name, usually because he/she thinks sufficient morphological change has taken place to merit this. Paraphyletic groups are created when a taxonomist removes a derived portion of a clade, leaving an 'ancestral group' characterized only by its 'primitive' features.

Where a number of more specialized members are removed from a clade the remaining primitive taxa are lumped together in a paraphyletic catch-all group. This is precisely what has happened in the creation of class Eocrinoidea (see Smith 1984). The traditional group Cystoidea was split during the 1960s into a number of classes based on apparently well-defined novel structures associated with gaseous exchange (Diploporita, Rhombifera, Paracrinoidea, Blastoidea, Parablastoidea, Coronoidea). The remaining primitive members were then grouped together within the class Eocrinoidea whose only uniting feature is their lack of those defining characters on which the more derived classes are recognized. The group has no reality in biological or evolutionary terms and probably contains ancestors to all of the more derived classes. Its extinction, and the extinction of the various lineages of which it is comprised, are taxonomic artefacts.

The arbitrariness of decisions about where a paraphyletic group should end is well demonstrated by the arguments surrounding the glyptocystitid rhombiferans. An analysis of the Cambrian fauna shows that typical glyptocystitid rhombiferans such as *Cheirocrinus* can be traced back through a sequence of 'eocrinoid' genera that includes *Macrocystella*, *Ridersia*, and probably to *Cambrocrinus* (see cladogram, text-fig. 6). Traditionally it has been the appearance of respiratory structures called pectinirhombs in the theca that has been used to define this group of rhombiferans (viz. Kesling 1967). These are present in *Cheirocrinus* but absent in the 'eocrinoid' members. However, Paul (1968*b*) argued that *Macrocystella* had all the characters associated with glyptocystitid rhombiferans (including the characteristic large lateral periproct, unique stem construction, and identical thecal plating) save for the pectinirhombs and should be classified as a glyptocystitid. Sprinkle (1976*b*) objected to this, arguing that pectinirhombs were the all-important character for the group. More recently, Jell *et al.* (1985) described the genus *Ridersia* which has the unique stem morphology of glyptocystitid rhombiferans and similar thecal plating but lacks the large lateral anal area, one of the circlets of thecal plates found in *Macrocystella* and *Cheirocrinus* and the pectinirhombs of *Cheirocrinus*. Jell *et al.* concluded that it was ancestral to the glyptocystitids but should remain classified as an eocrinoid because of its lack of pectinirhombs. Clearly then there is a clade defined by the shared presence of pectinirhombs and a more inclusive clade defined by the shared presence of a large lateral anus and a still more inclusive clade that is defined by the shared presence of the unique stem morphology. Whether this branch of 'eocrinoids' is made to go extinct by taxonomists

at the first appearance of a distinctive stem morphology (probably with *Cambrocrinus*), or the first appearance of a definitive thecal plating (*Ridersia*), or the first appearance of a lateral anus (*Macrocystella*), or the first appearance of pectinirhombs (*Cheirocystella*) is purely arbitrary. Furthermore, there is no reason why one character acquisition should be taken as a 'class-level jump', while another is treated as a 'genus-level' or 'family-level' jump as has been well illustrated by Runnegar (1987) for primitive molluscs. Designating one step within a sequence as marking the start of a 'class' only serves to mislead non-specialists as to the significance of such an event.

For any analysis that claims to be looking at rates and timing of taxonomic origination and extinction, it is absolutely crucial to have data which incorporate only real groups (i.e. monophyletic taxa) since paraphyletic groupings can, and usually do, introduce a large amount of taxonomic artefact into the analysis. In effect, this requires a cladistic data base.

(ii) *Taxonomic rank*. Whereas clades are real entities which have meaning in the biological world, the taxonomic rank which is assigned to them is arbitrary. The designation of taxonomic rank has in the past proceeded in a very haphazard way. Even Agassiz, who had a set of criteria for taxonomic rank, noted (1868, p. 110) that there was '. . . difficulty . . . in determining the natural limits of such groups . . . for individual investigators differ greatly as to the degree of resemblance existing between the members of many Families, and there is no kind of group which presents greater diversity of circumspection in the classification of animals'. Despite over 100 years of taxonomic endeavours this remains as true today as it ever was and traditional taxonomy has made little advance in defining how rank is to be assigned.

Yet despite this, there has continued a general and largely unspoken belief that taxonomic categories such as class, order, family represent approximately equivalent chunks of evolutionary trees that can be analysed meaningfully. So for example, Valentine (1980, 1986) and Campbell and Marshall (1986) are able to equate morphological distance to categorical rank and derive evolutionary models based on 'phylum-level' and 'class-level' jumps without considering how these ranks are defined in practice.

Whereas it is generally agreed that a species is recognized on the basis of a morphologically homogeneous sample population that is demonstrably discrete from other sample populations, there exist no rules or method by which higher ranks are designated. Thus taxonomists rarely agree about the precise composition of a taxon. Echinoderms have suffered particularly at the hands of traditional taxonomists and Paul (1979, p. 417) noted that 'echinoderm workers, unlike those of some other groups, have unashamedly created classes for many fundamentally different "designs" of echinoderms that appear early in the fossil record irrespective of their size (number of genera or species) or longevity'. Like most evolutionary taxonomists, Paul (1979, p. 427) argued for morphological distinctiveness as the guiding criterion on which higher taxonomic categories should be defined, not taxonomic size or longevity. Sprinkle (1983, p. 8) took a similar approach in trying to assess the 'real' number of classes into which echinoderms should be divided. He identified three factors of importance in determining whether high taxonomic rank should be given, morphological distinctiveness, success (measured by diversity and longevity), and survival to the present day.

Most recently, Campbell and Marshall (1986) have attempted to justify the use of taxonomic rank as some measure of morphological distinctiveness, claiming, amongst other things, that classes of echinoderm did not converge in morphology towards their time of origin. The analysis of specific and generic data presented here demonstrates that characters are hierarchically arranged and lends no support to their claim (see discussion on glyptocystitid rhombiferans, above).

Evolutionary systematists have assigned categorical rank arbitrarily and for reasons which are often unclear. Although morphological distinctiveness (perceived phenetic distance) is currently the most popular criterion on which this judgement is made, this certainly is not the only reason why high rank has been applied. In echinoderms a high taxonomic rank has been designated for at least five different reasons, outlined below, which means that taxa of the same rank are unlikely to be commensurate entities.

1. *A high categorical rank may be given to a species or small group of species which, because of poor preservation or misinterpretation of morphological structure, are not well understood.* This is equivalent to stating that the species are problematic. A number of echinoderm classes proposed in the past fall into this category, and are usually monotypic and based on scrappy material (e.g. 'Camptostromatoida', 'Haplozoa').

2. *A group is given a high categorical rank because it has achieved considerable diversity through time.* Such groups have to be given relatively high taxonomic rank because of the hierarchical nature of the Linnean classificatory system. All extant classes of echinoderm fall into this category. Crinoidea is a large group that includes a very large number of species and genera which are grouped into various higher categories. However, it is important to realize that high taxonomic rank here does not imply that there was significant morphological divergence at the initiation of the group (the differences between the crinoid *Echmatocrinus* and the cystoid *Lepidocystis* are slight), only that significant levels of diversity were achieved at some time *after* the establishment of the clade.

3. *A high categorical rank may be given to a group which is neither morphologically diverse, nor particularly distinctive morphologically, but which has as its closest relative a group which has achieved high internal diversity.* Thus, the subclass Echmatocrinea was created for the monospecific genus *Echmatocrinus*, not because it was so very different from other primitive echinoderms, but because it is supposed to have given rise to the crinoids. Since crinoids are given high rank, a similar rank was given to *Echmatocrinus*. Here *Echmatocrinus*, known from a handful of specimens from one locality and horizon, is the plesiomorphic sister group to all other crinoids.

4. *A high categorical rank may be given to well-defined groups on the grounds of perceived phenetic distinction.* Sprinkle (1981, p. 220) claimed that 'new classes appeared suddenly in the record without obvious ancestors'. Although morphological distinctiveness from the outset may be genuine, it is more commonly the result of an incomplete and patchy fossil record, or taxonomy in which differences are stressed and shared derived features ignored. An example of this is the newly erected class Concentricycloidea (Baker *et al.* 1986), where a single species, sister group to the highly derived asteroid family Caymanostellidae (Smith, in press) has been established on the basis of its unusual ambulacral arrangement. This represents the misuse of classificatory schemes to express an opinion, not to group species.

5. *A high categorical rank is given to what remains after abstracting a number of monophyletic groups from a larger group.* The Cystoidea (Blastozoa) are a large group which has subsequently been split into a number of groups, most of which are defined on derived character states (rhombiferans, diploporites, etc.). This has left a number of genera with only primitive morphological characters that have been grouped together in the Eocrinoidea, largely as a by-product of abstracting better-defined clades.

Because taxonomic rank can be assigned for such a variety of disparate reasons it seems untenable to believe that precise categorical rank can convey any meaningful biological significance. Groups may be given the same rank because of the diversity that they subsequently achieve, because of the morphological distance (apparent or real) separating them from other groups, because their nearest relatives subsequently achieved high diversity, or because they are poorly understood or misinterpreted.

Before leaving the problems of rank, it is worth pointing out that Raup (1983) demonstrated that it was an unavoidable product of tree topology that major groups appear early in the history of a clade. Consequently, as the Linnean system of nomenclature is also hierarchical in nature and high rank is inevitably given to major groups that have achieved high subsequent diversity, then it must also be true that most of the high ranking groups appear early in the history of a clade. This, however, certainly does not imply that these groups of high rank were separated by large morphological distances from their inception. Valentine's (1969, 1980) and Raup's (1983) observation that groups with high rank appear early in the Phanerozoic is thus a topological

feature of clade diversification and needs no biological explanation. To erect models in which taxonomic rank is equated with morphological distance at inception is misleading and the biological explanation spurious.

AN ALTERNATIVE APPROACH

If meaningful analyses are to be carried out on the pattern of specific diversity, origination, and extinction through time then the first step must be to construct a relatively artefact-free data base using cladistic methodology.

As an example, I present here an analysis of the early history of the echinoderms from the start of the Cambrian through to the Arenig. For comparison with the results based on the Sepkoski data base (1982, plus supplements) I have compiled a cladistic analysis and stratigraphic range chart for all known species of echinoderm from this interval. Because all previous analyses have treated carpoids as echinoderms I also include a stratigraphical range chart for this group, for comparable results. The same time-scale as used by Sepkoski (1979, 1982) is adopted here except that I have tried to use approximately equal-length geological periods of between 5 million years (using the time-scale presented in Conway Morris 1987) and 7-10 my (using the time-scale of Harland *et al.* 1982) each. Thus, the Tremadocian (17 my) is split into upper and lower Tremadocian, and the Atdabanian and Lenian (30 my on the Harland *et al.* time-scale) are split into the *Fallotaspis*, *Nevadella*, and lower and upper *Bonnia-Olenellus* Zones.

Although this has proved a difficult task, hindered by our current poor understanding of many of the taxa, a reasonable attempt can be made. Certain taxa posed major difficulties and no doubt some of the relationships suggested here will be proved wrong as new data on primitive echinoderms come to light. Indeed, my analysis is at variance in a small number of details with an independent analysis carried out by Paul (1988), and these details clearly need further investigation. But my aim here is not to provide a definitive phylogeny of Cambrian echinoderms, only to show that this sort of approach provides a more accurate method of assessing their evolutionary history. Hopefully though, the analysis provides a reasonable approximation to the evolutionary relationships of echinoderms during the early Palaeozoic. Every known species has another that is its closest relative and cladistic analysis is the best method for identifying these relationships. Combining the stratigraphic and cladistic data produces the best corroborated phylogenetic tree and places very specific constraints on the occurrence of Lazarus taxa. Comparison of the resultant patterns from these data with those derived from previous, less critical analyses occupies the last part of this paper.

Although this paper will deal primarily with radiate echinoderms, it has been necessary to consider the record of carpoids since they have a similar skeletal structure and are equally prone to the vagaries of preservation. The aims of this paper are to examine the diversification pattern of a major clade during the early Phanerozoic, so that whether carpoids are treated as primitive echinoderms, as by Ubaghs (1971*b*, 1975), Sprinkle (1983), and Philip (1979) or as primitive chordates (Jefferies 1986) is largely irrelevant for present purposes. If carpoids are treated as echinoderms then the pattern is one of 'phylum-level' diversification (in traditional taxonomic terms), if treated as chordates then it plots the initial diversification of a larger segment of the animal kingdom.

Cladistic analysis of Lower Cambrian to Lower Ordovician taxa

There are some eighty-five species of echinoderm and carpoid known from the Cambrian and Tremadocian and a further forty or so species in the Arenig (Table 3). The great majority of Cambrian and Tremadocian genera are monospecific, so that, with the exception of *Gogia*, analysis at generic level is more or less the same as a specific level analysis. Where a genus has more than one species, relationships of individual species have been examined to check for the possibility of paraphyly. In such cases, species or species clusters are treated separately, but where the species

TABLE 3. Echinoderm and 'carpoid' taxa from the Cambrian and Lower Ordovician.
Species are numbered for reference to text-fig. 9.

Lower Cambrian, Nevadella Zone
   (Poleta Formation)
     Helicoplacus gilberti Durham and Caster   Durham and Caster (1963)
     H. curtisi Durham and Caster   Durham and Caster (1963)
 1 *H. everndeni* Durham   Durham (1967)
     H. firbyi Durham   Durham (1967)
     H. nelsoni (Durham)   Durham (1967)
 2 *Polyplacus kilmeri* Durham   Durham (1967)

Lower Cambrian, Bonnia–Olenellus Zone
   (Kinzer Formation)
 3 Unnamed solute   Paul and Smith (1984)
 4 *Camptostroma roddyi* Ruedemann   Paul and Smith (1984)
 5 *Kinzercystis durhami* Sprinkle   Sprinkle (1973)
 6 *Lepidocystis wanneri* Foerste   Sprinkle (1973)
 7 stromatocystitid   Derstler (1981)

   (Upper Olenellus Beds)
 8 *Stromatocystites walcotti* Schuchert   Smith (1986)
 9 *S. pentangularis* Pompeckj   Smith (1986)

   (*Bristolia* subzone)
10 *Gogia ojenai* Durham   Durham (1978)

Lower Middle Cambrian
   (*Plagiura–Poliella* Zone, North America)
11 *G. prolifica* Walcott   Sprinkle (1973)
12 *Gogia* sp. 1   Sprinkle (1973)
   (*Albertella* Zone, North America)
13 *G. hobbsi* Sprinkle   Sprinkle (1973)
   (Coonigan Formation, Australia)
14 *Cambaster* sp. (isolated plates)   Jell *et al.* (1985)
   (Beetle Creek Formation, Australia)
15 *Edriodiscus primotica* (Henderson and Shergold)   Jell *et al.* (1985)
16 ?*Stromatocystites* sp.   Jell *et al.* (1985)
   (basal Middle Cambrian, north-eastern Australia)
17 *Cymbionites craticula* Whitehouse   Smith (1982)
18 *Peridionites navicula* Whitehouse   Smith (1982)

Median Middle Cambrian
   (*Glossopleura* Zone, North America)
19 unnamed cothurnocystid   Sprinkle (1976*a*)
20 *Ctenocystis utahensis* Robison and Sprinkle   Sprinkle and Robison (1978)
21 *Gogia palmeri* Sprinkle   Sprinkle (1973)
22 *G. granulosa* Robison   Sprinkle (1973)
23 *G. guntheri* Sprinkle   Sprinkle (1973)
24 *G. longidactylus* (Walcott)   Sprinkle (1973)
25 *G. multibrachiatus* (Kirk)   Sprinkle (1973)
26 *Totiglobus nimius* Bell and Sprinkle   Bell and Sprinkle (1978)
   (*Bathyuriscus–Elrathina* Zone, North America)
(21) *G. palmeri* Sprinkle   Sprinkle (1973)
27 *G. kitchnerensis* Sprinkle   Sprinkle (1973)
(22) *G. granulosa* Robison   Sprinkle (1973)
(23) *G. guntheri* Sprinkle   Sprinkle (1973)
28 ?*G. radiata* Sprinkle   Sprinkle (1973)

29	*Echmatocrinus brachiatus* Sprinkle	Sprinkle (1973)
30	?trachelocrinid arms	Sprinkle (1973)
31	*Walcottidiscus typicalis* (Walcott)	Smith (1986)
	(Cateena Group, Australia)	
32	*Cambraster tastudorum* Jell, Burrett and Banks	Jell *et al.* (1985)
33	*Ctenocystis jagoi* Jell, Burrett and Banks	Jell *et al.* (1985)
	(*E. oelandicus* Zone, Sweden)	
34	*Ceratocystis* sp.	Franzén, in Berg-Madsen (1986)
35	*Cigara* sp.	Franzén, in Berg-Madsen (1986)
(16)	*Stromatocystites* sp.	Franzén (pers. comm. Jan. 1987)

Upper Middle Cambrian
(*Bolaspidella* Zone, North America)

36	*Castericystis vali* Ubaghs and Robison	Ubaghs and Robison (1985)
37	*Marjumicystis mettae* Ubaghs and Robison	Ubaghs and Robison (1985)
38	*Gogia spiralis* Robison	Sprinkle (1973)
39	*Eustypocystis minor* Sprinkle	Sprinkle (1973)
40	*Walcottidiscus lloydi* (Sprinkle)	Sprinkle (1985)
	(Jince Formation, Czechoslovakia)	
41	*Etoctenocystis bohemica* Fatka and Kordule	Fatka and Kordule (1985)
42	*Trochocystoides parvus* Jaekel	Ubaghs (1967*b*)
43	*Trochocystites bohemicus* Barrande	Ubaghs (1967*b*)
44	*Ceratocystis perneri* Jaekel	Jefferies (1969)
45	*Cigara dusli* Barrande	Ubaghs (1967*a*)
46	*Acanthocystites briareus* Barrande	Fatka and Kordule (1984)
47	*A. jani* (Prokop)	Prokop (1962)
48	*Acathocystites nuntius* (Prokop)	Prokop (1962)
49	*Luhocrinus monicae* Prokop and Fatka	Prokop and Fatka (1985)
50	*Lichenoides priscus* Barrande	Ubaghs (1953)
(9)	*Stromatocystites pentangularis* Barrande	Smith (1986)
	(Beds E, F, Montagne Noire, France)	
51	*Ctenocystis smithi* Ubaghs	Ubaghs (1987)
52	*Ceratocystis vizcainoi* Ubaghs	Ubaghs (1987)
53	*Gogia gondi* Ubaghs	Ubaghs (1987)
54	'*Eocystites*' *languedocianus* Ubaghs	Ubaghs (1987)
55	*Trochocystites theronensis* (Cabibel *et al.*)	Cabibel *et al.* (1958)
56	*Gyrocystis barrandei* (Munier-Chalmas and Bergeron)	Ubaghs (1967*b*)
57	*Decacystis hispanicus* Gislén	Ubaghs (1967*b*)
	(two other genera of cinctan from here are of dubious status)	
58	*Cambraster cannati* (Miquel)	Smith (1986)
59	Undescribed genus resembling *Cambraster* but with annular aboral plating like a cyclocystoid	
	(Beds G, H, Montagne Noire, France)	
60	*Gyrocystis pardailhanicus* (Termier and Termier)	Termier and Termier (1973)
	(upper *Paradoxides paradoxissimus* Zone, St Davids, Wales, UK)	
61	*Protocystites meneviensis* (Hicks)	Jefferies *et al.* (1987)
62	ctenocystoid	Jefferies *et al.* (1987)

Middle Cambrian (undifferentiated)
(Pirineo, Spain)

(57)	*Decacystis hispanicus* Gislén	Meléndez (1954)
	(Atlas Mountains, Morocco)	
(43)	*Trochocystites bohemicus* Barrande	Chauvel (1971*a*)

Upper Middle Cambrian or Lower Upper Cambrian
(Siberia, USSR)

63	*Pareocrinus ljubzovi* Yakovlev	Ubaghs (1967*a*)

TABLE 3 (cont.)

Dresbachian
    (*Cedaria* Zone, North America)
  64 unnamed solute   Bell and Sprinkle (1980)
  65 *Nolichuckia casteri* Sprinkle   Sprinkle (1973)
    (*Olenus* Beds, Holy Cross Mountains, Poland)
  66 *Cambrocrinus regularis* Orlowski   Orlowski (1968)

Franconian
    (*Conaspis-Prosaukia* Zones, North America)
  67 *Trachelocrinus resseri* Ulrich   Sprinkle (1973)
    (Chatsworth Limestone, *Peichiashania secunda/Prochuangia glabella* Zone, Australia)
  68 *Ridersia watsonae* Jell, Burrett and Banks   Jell *et al.* (1985)
  69 unnamed isorophid   Jell *et al.* (1985)

Trempealeauian
    (Whipple Cave Formation, USA)
  70 *Minervaecystis* sp.   Ubaghs (1963b)
  71 *Nevadaecystis americana* Ubaghs   Ubaghs (1963b)
  72 cornute   Ubaghs (1963b)
  73 possible rhombiferan   Paul (1968a)
    (Montana, USA)
  74 hybocrinid-like crinoid   Derstler (1981)

Tremadocian
    (Lower and Upper: Wales, UK)
  75 *Macrocystella mariae* Callaway   Paul (1968b, 1984)
    (Lower: Hérault, France)
 (75) *Macrocystella* sp.   Ubaghs (1983)
    (Czechoslovakia)
 (75) *M. ?bavarica* (Barrande)   Ubaghs (1983)
    (Australia)
 (75) *Macrocystella* sp.   Jell *et al.* (1985)
    (Upper: Fillmore Limestone, USA)
  76 *Cheirocystella antiqua* Paul   Paul (1972)
  77 '*Hybocrinus*' sp.   Lane (1970)
  78 *Pogonipocrinus antiquus* Kelly and Ausich Kelly and Ausich (1978)
    (Upper: Anti-Atlas Mountains, Morocco)
  79 *?Aristocystites* sp.   Chauvel (1966)
  80 *Palaeosphaeronites* sp.   Chauvel (1966)
 (75) *Macrocystella bohemica* Barrande   Chauvel (1969)
 (75) *M. tasseftensis* Chauvel   Chauvel (1969)
 (75) *M.* cf. *mariae* Callaway   Chauvel (1969)
  81 *Rhopalocystis destombesi* Ubaghs   Ubaghs (1963a), Chauvel (1971b)
    (Uppermost Tremadocian/basal Arenig: Hérault, France)
  82 *Aethocrinus moorei* Ubaghs   Ubaghs (1969a, 1972b)
  83 *Minervaecystis vidali* Ubaghs   Ubaghs (1969b)

Arenig
    (Basal: Schistes de St Chinian, Hérault, France)
 (83) *Macrocystella vidali* Ubaghs   Ubaghs (1969b)
  84 *Phyllocystis blayaci* Thoral   Ubaghs (1969b)
 (84) *P. crassimarginata* Thoral   Ubaghs (1969b)
  85 *Cothurnocystis fellinensis* Ubaghs   Ubaghs (1969b)
 (85) *C. courtessolei* Ubaghs   Ubaghs (1969b)
  86 *Chauvelicystis spinosa* Ubaghs   Ubaghs (1983)

87	*Thoralicystis griffei* (Ubaghs)	Ubaghs (1969*b*)
88	*Amygdalotheca griffei* (Ubaghs)	Ubaghs (1969*b*)
89	*Galliaecystis lignieresi* Ubaghs	Ubaghs (1969*b*, 1983)
90	*Chinianocarpos thorali* Ubaghs	Ubaghs (1969*b*)
91	*Peltocystis cornuta* Thoral	Ubaghs (1969*b*)
92	*Balantiocystis thorali* Ubaghs	Ubaghs (1972*a*, 1983)
93	*Chinianaster levyi* Spencer	Spencer (1951)
94	*Villebrunaster thorali* Spencer	Spencer (1951)
95	*Pradesura jacobi* Thoral	Spencer (1951)
(75)	*Macrocystella azaisi* (Thoral)	Paul (1968*b*)
96	'*Hemicystis*' *boehmi* Thoral	Thoral (1935)

(Lower: Schistes de la Maurerie, Hérault, France)

(85)	*Cothurnocystis primaeva* Thoral	Ubaghs (1969*b*)
(93)	*Chinianaster levyi* Spencer	Spencer (1951)
(95)	*Pradesura jacobi* Thoral	Spencer (1951)
(75)	*Macrocystella azaizi* (Thoral)	Paul (1968*b*)
(76)	*Cheirocystella languedociana* (Thoral)	Paul (1968*b*, 1972)

(Lower: Gres du Foulon, Hérault, France)

97	*Lingulocystis elongata* Thoral	Ubaghs (1960)

(Lower: Schistes du Landeyran, Hérault, France)

(92)	*Balantiocystis* sp.	Ubaghs (1983)
(85)	*Cothurnocystis melchiori* Ubaghs	Ubaghs (1983)
98	*Ramseyocrinus vizcainoi* Ubaghs	Ubaghs (1983)

(Lower: Ramsey Island, Wales, UK)

(98)	*R. cambriensis* (Hicks)	Bates (1968)
99	*Petraster ramseyensis* (Hicks)	Spencer (1918)

(Lower: Anti-Atlas Mountains, Morocco)

(86)	*Chauvelicystis ubaghsi* (Chauvel)	Chauvel (1971*a*)
(84)	*Phyllocystis* sp.	Chauvel (1971*a*)
(92)	*Balantiocystis regnelli* Chauvel	Chauvel (1971*a*)
(87)	*Thoralicystis zagoraensis*	Chauvel (1971*a*)

(Lower: Llangynog, Wales, UK)

100	*Blastoidocrinus antecedens* Paul and Cope	Paul and Cope (1982)
(98)	*Ramseyocrinus* sp.	Cope (1988)

(Greenland)

101	*Compagicrinus fenestratus* Jobson and Paul	Jobson and Paul (1979)

(Upper: Estonia, USSR)

102	*Glyptosphaerites leuchtenbergi* (Volborth)	Jaekel (1899)
103	'*Cheirocrinus*' *giganteus* (Leuchtenberg)	Paul (1972)
104	*Cheirocystis radiatus* (Jaekel)	Paul (1972)
105	*Blastocystis rossica* Jaekel	Jaekel (1918)
106	*Echinosphaerites aurantium* (Gyllenhahl)	Bockelie (1981*b*)
107	*Echinoencrinites angulosus* (Pander)	Bassler and Moodey (1943)
108	*Cryptocrinites similis* Bockelie	Bockelie (1981*a*)
109	*Rhipidocystis* sp.	Bockelie (1981*a*)
110	*Asteroblastus sublaevis* Jaekel	Jaekel (1899)
111	*Bolboporites* spp.	

(Upper: Sweden)

112	*Sphaeronites pomum* Eichwald	Paul and Bockelie (1983)
(112)	*S. minor* Paul and Bockelie	Paul and Bockelie (1983)

(Upper Asaphus Marls, Oslo, Norway)

113	?*Hemicosmites* sp.	Bockelie (1979*a*)
114	?*Bockia* sp.	Bockelie (1981*a*)
115	*Volchovia norvegica* (Regnell)	Regnéll (1945)

TABLE 3 (cont.)	
(Upper Arenig, Whitland, Wales, UK)	
(85) *Cothurnocystis* sp.	Jefferies, *in* Fortey and Owens (1987)
116 *Reticulocarpos* sp.	Jefferies, *in* Fortey and Owens (1987)
117 *Lagynocystis* sp.	Jefferies, *in* Fortey and Owens (1987)
118 *Balanocystites* sp.	Jefferies, *in* Fortey and Owens (1987)
119 *Guichenocarpos* sp.	Jefferies, *in* Fortey and Owens (1987)
120 *Anatifopsis* sp.	Jefferies, *in* Fortey and Owens (1987)
121 *Mitrocystites* sp.	Jefferies, *in* Fortey and Owens (1987)
122 *Mitrocystella* sp.	Jefferies, *in* Fortey and Owens (1987)
(other localities)	
123 *Protocrinites* sp.	Bockelie (1984)
124 *Monocycloides oelandicus* Berg-Madsen	Berg-Madsen (1987)
125 *Perritocrinus transitor* (Beyrich)	Ubaghs (1971a)

are differentiated on only minor variations and appear as a polychotomy when analysed cladistically, (i.e. they are, so far as our resolution allows us to determine, all equally related to their sister group) then the genus is treated as a terminal taxon. This cladistic analysis has been carried out only for radiate echinoderms.

The genus *Gogia* has been subdivided into a number of species or species clusters as follows: (i) the *G. spiralis* group (*G. ojenai, G. granulosa, G. guntheri*, and *G. spiralis*), for species with spiral brachioles. The spiralling of the brachioles is a shared derived feature and is found in no other echinoderm; (ii) the *G. prolifica* group (*G. prolifica* and *G. palmeri*), for species with extensively developed epispires forming prominent external grooves on plate margins; (iii) the *G. hobbsi* group (*G. hobbsi* and *G. gondi*), species in which the holdfast is considerably reduced in size; (iv) *G. multibrachialis*, a species in which there is no apparent holdfast differentiated; (v) the *G. kitchnerensis* group (*Gogia* sp. 1 of Sprinkle 1973, *G. longidactylus*, and *G, kitchnerensis*), for species in which the epispires are greatly reduced and confined to the oral area of the theca. *G. radiata* Sprinkle appears to represent yet another group, but it is so poorly known that its assignment to a genus is impossible. However, from what little we do know of this species, it closely resembles *Eocystites languedocianus* (Ubaghs 1987) and the two have been grouped together.

Previous cladistic analyses of Cambrian echinoderms or carpoids are few. Paul and Smith (1984) produced a cladogram for Lower Cambrian taxa, Jefferies (1986) has published an analysis of mitrate and cornute carpoids, and Smith (1986) has published an analysis of eleutherozoan taxa. A cladistic analysis for blastozoan echinoderms is in press (Paul 1988), as is one for primitive crinoids (Donovan 1988). But nowhere previously have all Cambrian taxa been drawn together before in such an analysis. No cladistic analysis is attempted here for Cincta or Ctenocystoida; much work on these groups remains to be done.

Text-figs. 5 to 8 present the character analyses on which the phylogenetic groupings have been based. Individual character states are listed below and discussed where necessary. Table 3 provides a list of all known taxa, with reference to the most informative description available.

Discussion of characters

1. *Skeletal histology composed of stereom.* (Secondarily lost in some more derived groups—synaptid holothurians, ?chordates.)

2. *Larval development asymmetrical.* This is inferred in fossil forms from the presence of a single asymmetrically positioned hydropore/gonopore (solid circles), as opposed to the paired openings in hemichordates.

3. *Radial symmetry.* This is most prominently displayed in the arrangement of the radial water vessels around the peristome. It is three-fold in helicoplacoids and primitively five-fold in more derived echinoderms, although there is a great deal of variation in later forms.

TEXT-FIG. 5. Cladogram of early Cambrian echinoderms. For a discussion of characters 1–11 see text.
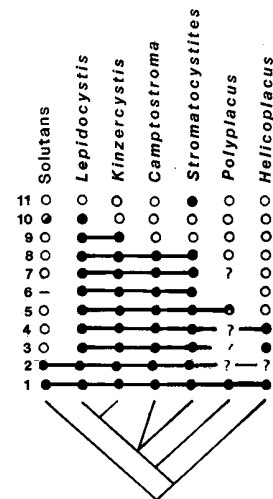
4. *Ambulacra integrated into body wall*. In helicoplacoids and in most crown group echinoderms the ambulacra form an integrated part of the main body of the animal. In crinoids and in some cystoid groups, however, the distal portion of ambulacra extend free of the body as arms (see character 9). In solutes the solitary ambulacrum is a free appendage and does not form part of the body wall.

5. *Differentiation of an aboral and oral plated surface*. In *Helicoplacus* the entire body is composed of spirally arranged rows of plates. *Polyplacus* appears to show a zone of non-spiral plating which may coincide with the oral area, although the anatomy of this genus is still largely unknown. In all other primitive echinoderms there are well-defined oral and aboral plated surfaces that differ in their organization. Again this feature is variably developed in some later cystoid groups.

6. *Pentaradial symmetry*. Present in all primitive crown group echinoderms (see Paul and Smith 1984) but not uncommonly modified in more derived groups (see from example Bockelie 1982). This is expressed as a 2:1:2 pattern in the arrangement of ambulacra around the mouth.

7. *Mouth and anus situated close together at the thecal summit*. In most carpoids, and in larval echinoderms, the mouth and anus are at opposite poles of the body. Helicoplacoids have a laterally positioned mouth and may or may not have a terminally positioned anus. In other primitive echinoderms the mouth or anus has rotated so that the two openings lie close together on the oral surface. This is true of primitive eleutherozoan echinoderms but not for some derived groups, such as echinoids and some asteroids.

8. *Epispires on oral surface*. A derived character by outgroup comparison.

9. *Brachioles*. Paul and Smith (1984) have argued that brachioles are derived from ambulacral cover plate series. As Sprinkle (1973) has previously pointed out, they cannot be considered as homologous with arms.

10. *Ambulacra extend free of the theca as arms*. Here the arms of fistuliporite cystoids, coronates, aristocystitids, crinoids, and some primitive 'eocrinoids' (e.g. *Nolichuckia* and *Trachelocrinus*) are treated as homologous structures derived from extension of the ambulacra outside the theca as free appendages.

11. *Loss of aboral holdfast*. In primitive eleutherozoan echinoderms the aboral and oral surfaces are of similar extent and there is no attachment holdfast. In *Camptostroma* the aboral surface is conical and shows evidence of having had spirally arranged musculature (Paul and Smith 1984).

12. *Food gathering appendages composed of brachioles only*. Food is gathered via appendages which may be composed of brachioles arising from ambulacra on the theca, or may incorporate brachiole-bearing ambulacra that extend free of the theca.

13. *Aboral surface extended into a stalk*. The absence of a stalk in some cystoids is treated here as a secondary loss, on the strength of other characters.

14. *Cup plating is clearly differentiated from holdfast plating*. Only in some of the most primitive members is there little differentiation between the plating of the stalk and the cup.

15. *Stalk supported by holomeric columnals*. The recent discovery that *Acanthocystites* has holomeric columnals draws into question the distinction between this genus and *Akadocrinus*. Furthermore, the newly created genus *Luhocrinus* may also turn out to be a juvenile form of *Acanthocystites*.
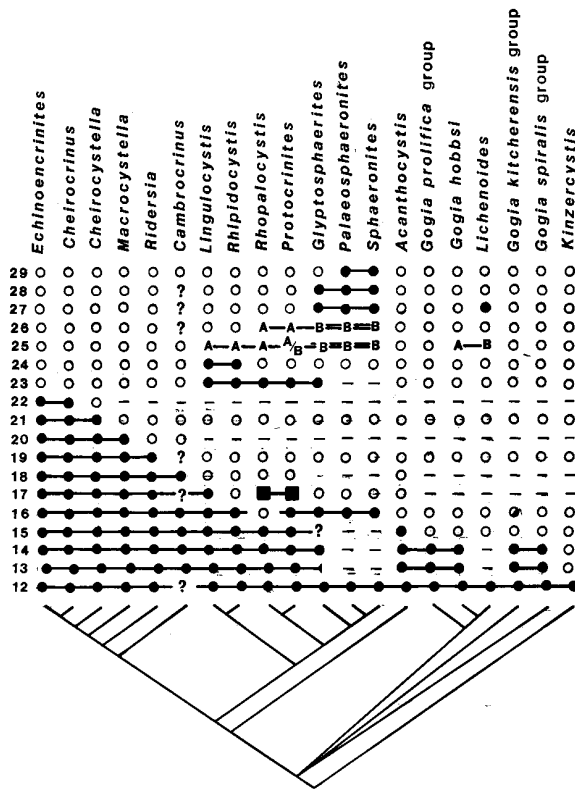
TEXT-FIG. 6. Cladogram of selected Cambrian to Lower Ordovician cystoid groups. For a discussion of characters 12–29 see text.

16. *Loss of epispires*. *Camptostroma* and primitive pelmatozoans such as *Kinzercystis* and *Gogia* all have well-developed epispires over their oral surface. In the *G. kitchnerensis* group epispires are greatly reduced in size and extent. In other groups the epispires are either lost or have been replaced by more sophisticated respiratory structures.

17. *Basal circlet fused (solid squares) or composed of four basals (solid circles)*.

18. *Xenomorphic stem*. In *Macrocystella*, *Ridersia*, and glyptocystitids there is a very pronounced difference between the proximal and distal parts of the stem. The same appears to be true of *Cambrocrinus* judging from published photographs. Where known, the proximal portion of the stem has an extremely large lumen and columnals are arranged alternately as an inner and outer series with synarthrial articulation.

19. *Cup plating organized into discrete circlets with BB, ILL, LL recognizable*.

20. *RR circlet of plates developed: anus lateral, lying between ILL, LL, and one radial plate*.

21. *Dichopores developed*.

22. *Dichopores disjunct*.

23. *Brachioliferous plates present*. In some genera the brachioles are attached to a single thecal plate which has the attachment facet, in others the brachioles are attached to two thecal plates and the attachment facet lies across a plate suture. The single brachioliferous plate is treated here as the derived condition. Ambulacral plating is not differentiated in either *Palaeosphaeronites* or *Sphaeronites*, the brachioles arising from facets on thecal plates.

24. *Theca flattened with well-developed marginal frame*. Traditionally *Lingulocystis* and *Rhipidocystis* have always been treated as closely related because of their similar body form, although their brachiole structure differs somewhat (see Ubaghs 1960; Bockelie 1981a).

25. *Stem reduced (A) or lost (B)*. In *Protocrinites* some species have a reduced stem, others have no stem (Bockelie 1984).
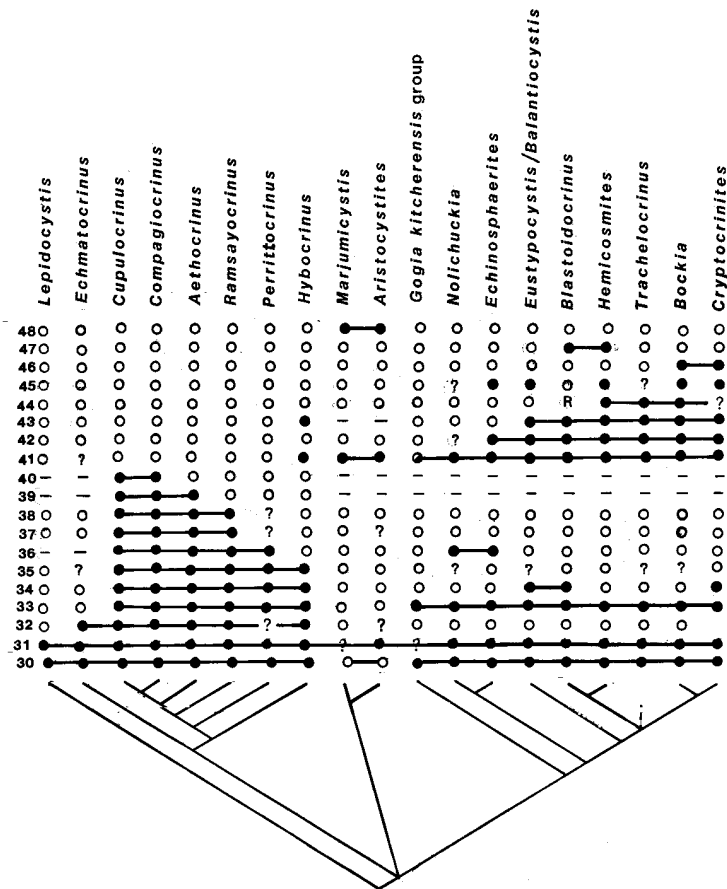
TEXT-FIG. 7. Cladogram of selected Cambrian to Lower Ordovician pelmatozoan groups. For a discussion of characters 30–48 see text.

26. *Respiratory pits formed:* (*A*) *internal pits* or (*B*) *diplopores which penetrate almost the entire plate thickness.* *Sphaeronites, Palaeosphaeronites,* and *Gylptosphaerites* all have diplopores that perforate the thecal wall. *Protocrinites* has sealed perforations (Bockelie 1984) probably formed by resorption from the interior. *Rhopalocystis* has sutural epispires but the interior of plates appears to be similarly covered in deep pits comparable to those in *Protocrinites.*

27. *Epithecal food grooves.* In many diploporite cystoids the brachioles are connected to the mouth by shallow epithecal grooves rather than discrete ambulacral grooves with recognizable ambulacra. This is treated as a derived state.

28. *Mouth covered by a palate of oral plates.*

29. *Attached directly to the substratum.* In *Sphaeronites* and *Palaeosphaeronites* there is no stem and the base of the theca is moulded to fit the substratum.

30. *Aboral surface extended into a stalk* (as character 13).

31. *Arms extend free of the theca* (as character 10). In most cases it is clear that it is the ambulacra that extend extra-thecally to produce a filtration fan. It is not yet certain whether the subvective system in *Marjumicystis* is ambulacral, brachiolar, or a mixture. Similarly, the fact that in *Gogia kitchnerensis* there is a ?coelomic pore running through the biserial 'brachioles' (Sprinkle 1973) might suggest that these are ambulacral extensions not brachioles. However, the same structure has now been observed in *G. gondi* (Ubaghs 1987).

32. *Arms uniserial.*

33. *Cup composed of organized circlets of plates.*

34. *Stem clearly differentiated from the cup.*

35. *Arms attaching to a single brachial-bearing plate* (as character 23). In crinoids each arm is attached to a radial plate. The arms in some other groups are also attached to a single plate, not shared between adjacent flooring plates, and this is treated as a derived character.

36. *Stem ossicles meric.* The ossicles of the stem are unorganized in *Gogia* spp. but become organized into vertical rows of stout ossicles in primitive crinoids and in fistuliporite cystoids. *Nolichuckia* has a stem that appears to show semi-organized rows of stout, brick-like ossicles very similar to those of fistuliporite cystoids, judging from photographs in Sprinkle (1973, pl. 29, fig. 4).

37. *Free arms branch.* Primitively the free ambulacra appear to be unbranched, but in some crinoids the arms branch dichotomously at least once.

38. *Anal sac present.* Hybocrinids lack an anal sac, as does *Echmatocrinus*, but other primitive crinoids all have a well-developed anal sac.

39. *Cup composed of three or more organized circlets of plates.* Whether the monocyclic arrangement of plating, as seen in hybocrinids, or the dicyclic arrangement, as seen in *Cupulocrinus*, is the more primitive arrangement is unknown. *Aethocrinus* differs from *Cupulocrinus* and *Compagicrinus* in having a fourth circlet of cup plates while *Ramsayocrinus* appears to have either one or two circlets in its cup. This character separates *Aethocrinus*, *Compagicrinus*, and *Cupulocrinus* from *Ramsayocrinus* and *Hybocrinus*, but may turn out to be symplesiomorphic.

40. *Cup composed of infrabasals, basals, and radials.* *Aethocrinus* differs from the very similar *Compagicrinus* and *Cupulocrinus* in having a fourth circlet of plates incorporated into the cup. Jobson and Paul (1979) have argued that the condition seen in *Aethocrinus* is the more primitive.

41. *Epispires lost* (as character 16). The open structure of the anal sac in the crinoid tegmen is interpreted as homologous and derived from the condition of having sutural epispires scattered over the oral surface. If Lane (1984) is correct in interpreting the anal sac as housing the gonads then its sutural pores serve a comparable function.

42. *Oral area produced into a spout-like structure.* Here the adoralmost plates are modified into a spout-like structure from which the free arms extend. *Nolichuckia* probably has such a spout but the only known specimen does not show the structure of this area.

43. *Stem supported by holomeric columnals.* Unlike the holomeric columnals of *Akadocrinus* and glyptocystitid rhombiferans, these columnals are disc-like with only a small central lumen.

44. *Free arms bearing brachioles.* These are the so-called pinnate arms. *Eustypocystis* and *Balantiocystis* are so similar that I have treated them as synonymous. They have simple arms without brachioles. *Bockia* is almost identical to *Balantiocystis* in body form but differs in having brachioles developed on the free arms. *Trachelocrinus* also has 'pinnate' arms. The arms of *Hemicosmites* are unknown but Bockelie (1979*a*) assumed that they are pinnate from the occurrence of pinnate arms in the very closely related *Caryocrinites* (see Sprinkle 1975). The ambulacral structure in *Blastoidocrinus* is comparable to that of *Bockia* and more derived members of this clade (eublastoids), and parablastoids are interpreted here as having secondarily recumbent 'pinnate' arms.

45. *Anus positioned laterally, well outside the food gathering area.* In primitive crinoids and cystoids such as *Gogia*, the anus lies close to the mouth within the area of the subvective filtration fan. In some more derived cystoids, however, the anus has shifted to a lateral position well outside the oral area. The position of the periproct is unknown in *Blastoidocrinus*, but has been assumed to be near the apex of the test by comparison with the better known *Meristoschisma* (Sprinkle 1973).

46. *Theca with three basals.* These are not of equal size, there are two large and one small basal plates. *Trachelocrinus*, which is known from one specimen, shows three basals in profile and is thus likely to have either four or five basals. The number of basals in *Blastoidocrinus*, or for that matter in any parablastoid is unknown, but has been assumed to be five.

47. *Dichopore-type respiratory structures with internal thecal folds.* Hemicosmitids have traditionally been placed with glyptocystitid rhombiferans into the larger group Rhombifera, because of the similarity of their dichopore-type respiratory structures, which straddle plate sutures and form diamond-shaped regions of thecal folding for gaseous exchange (Paul 1968*c*). Thin-walled zones of thecal folds also occur in blastoids (where they also straddle plate sutures) and parablastoids (where they are confined to the deltoid plates: the so-called cataspires). However, major differences distinguish hemicosmitids (with their three-fold oral plating symmetry) and parablastoids (with their five-fold symmetry) and the presence of dichopore-type of respiratory structures of uncertain homology is not a strong character. Both hemicosmitids and parablastoids were left

unplaced in the analysis of Paul (1988) and are here tentatively placed as sister group to *Bockia*, *Cryptocrinites*, and their relatives, the eublastoids. These two taxa are the most difficult to place.

48. *Theca attached directly to the substratum by a rosette-like attachment disc.* Ubaghs and Robison (1985) described the attachment rosette of *Marjumicystis* and a similar structure is seen on aristocystitids. (Possibly the same as in sphaeronitid cystoids.)

49. *Aboral surface flat, composed of tesselate plating.* All of these echinoderms differ from pelmatozoans in lacking extensive development of the aboral surface into a holdfast. *Camptostroma* has a short aboral holdfast with spiral contraction zones and represents an intermediate condition.

50. *Stout ring of marginal ossicles between oral and aboral plated surfaces.*

51. *Aboral surface much reduced in area compared with the oral surface.*

TEXT-FIG. 8. Cladogram of primitive eleutherozoan groups. For a discussion of characters 49–63 see text.
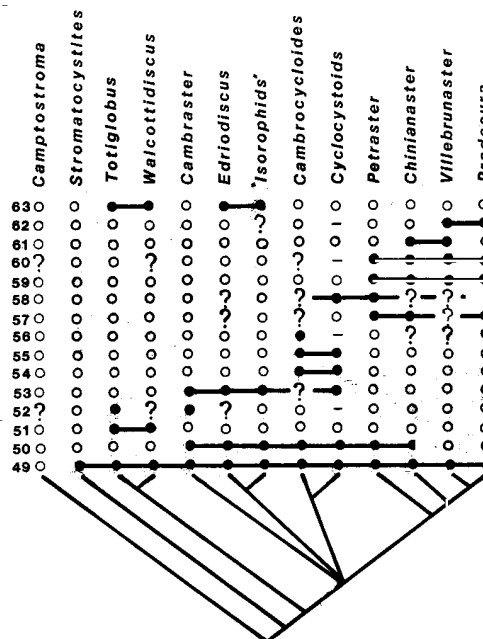
52. *Single large interradial ossicle forming the mouth frame.* These plates were interpreted by Smith (1986) as composed of fused ambulacral plates.

53. *Peripheral skirt of plates present outside marginal ring.*

54. *Aboral plates with a central perforation.*

55. *Marginal ossicles specialized with an inner crest and an outer cupule zone.*

56. *Arms extend free of the disc.* In *Cambraster* and an undescribed species from the Middle Cambrian of the Montaigne Noire, the arms extended slightly beyond the marginal ring (see Jell *et al.* 1985).

57. *Madreporite developed.* The hydropore is developed into a discrete calcified body.

58. *Loss of anus.* The presence of an anus is difficult to detect in some fossils, but does genuinely appear to be absent in primitive asteroids and ophiuroids.

59. *Stellate body form: vagile, living mouth downwards.* Precisely when an oral face downwards posture was adopted is impossible to say but it is here taken to coincide with the loss of the oral anus.

60. *Mouth angle plates articulated and no longer forming a fixed frame.*

61. *Virgalia developed.* Adjacent to ambulacra in somasteroids there are series of aligned interambulacral plates known as virgalia. These are only very feebly developed in *Archegonaster*.

62. *Radial water vessel internal.*

63. *Tesselate oral plating without epispires.*

DISCUSSION

1. *Apparent and real diversity patterns*

Taxonomic diversity is usually calculated by simply counting the number of taxa of equivalent rank present at each time interval. Using this method the pattern observed from the generic data compiled here (text-fig. 4), closely matches that obtained by using standard taxonomic data at family level (see text-fig. 2) and class level (text-fig. 1). All three sets of data show a rise in diversity which reaches a peak in the Middle Cambrian and a second, larger rise in the Lower Ordovician. The two peaks are separated by a distinct trough in the Upper Cambrian. Clearly then the pattern of taxonomic origination seen at family and class level provides a reasonable approximation to *sampled* species diversity (since the great majority of genera in the Cambrian are monospecific). However, this is not necessarily a real pattern, since we know that there is a very poor fossil record of echinoderms and carpoids in the Upper Cambrian. Using the cladistic analysis, it is possible to make some compensation for the vagaries of the fossil record. Missing taxa can be identified in two ways:

(i) *Where the primitive sister group predates and is separated by a stratigraphical gap from the derived sister group*, then at the very least there must have been one taxon that has not yet been found which existed between the last record of the primitive sister group and the first record of the derived sister group. This gap could be filled by extension of the range of the primitive sister group upwards, by extension of the range of the most primitive member of the derived sister group downwards, or by interpolation of one or more as yet unknown taxa that are intermediate in form. Furthermore, if the primitive sister group is not directly ancestral to the derived sister group (something that cannot be determined from the cladogram), then the range of the missing taxon may extend below the last appearance of the primitive sister group. Thus extension of the primitive sister group's range gives the absolute minimum interpolation of missing taxa.

(ii) *Where the earliest member of the derived sister group stratigraphically predates the earliest record of the primitive sister group*, then the range of the primitive sister group must extend down to the level at which the derived sister group first appears. Again this represents only the absolute minimum interpolation of taxa.

By using these two criteria, ranges of Cambrian to Arenig taxa known to have existed but which have not yet been discovered (i.e. Lazarus taxa) can be interpolated into the data set to compensate for the poor fossil record. In text-fig. 9 known occurrences of taxa are shown in solid lines, and minimum inferred missing taxa as dashed lines. Clearly the proportion of missing taxa increases greatly during the Upper Cambrian (text-fig. 4; Table 2) showing that this is indeed a period for which sampling is exceedingly poor in comparison with either the Middle Cambrian or the Arenig. A plot of estimated diversity (combining taxa both described and Lazarus taxa as yet undiscovered) still shows a small dip in the Upper Cambrian, though nowhere near as large as one based only on recorded diversity (text-fig. 4). Because only the absolute minimum number of taxa present can be determined, rate of origination at intervals where Lazarus taxa are known to be more numerous than sampled taxa is likely to be significantly underestimated. Generic diversity through the Cambrian has therefore been plotted using only those time periods which appear reasonably well sampled (text-fig. 10). This suggests that a more realistic interpretation of the data is of continuous exponential growth during the Cambrian and Lower Ordovician.

The number of extinctions identified from non-cladistic taxonomic data differs significantly from the number calculated from the data presented here. This is because a taxon may disappear from the record because of: (i) biological extinction or (ii) pseudoextinction. Traditional (non-cladistic) taxonomic data bases have not distinguished between these two very different events (extinction and morphological divergence) whereas a cladistic data base can provide a minimum estimate of genuine extinctions, as follows.

A branch of the cladogram with two or more species (i.e. united by an autopomorphy) that disappears from the stratigraphical record can be assumed to be an extinction event. A branch
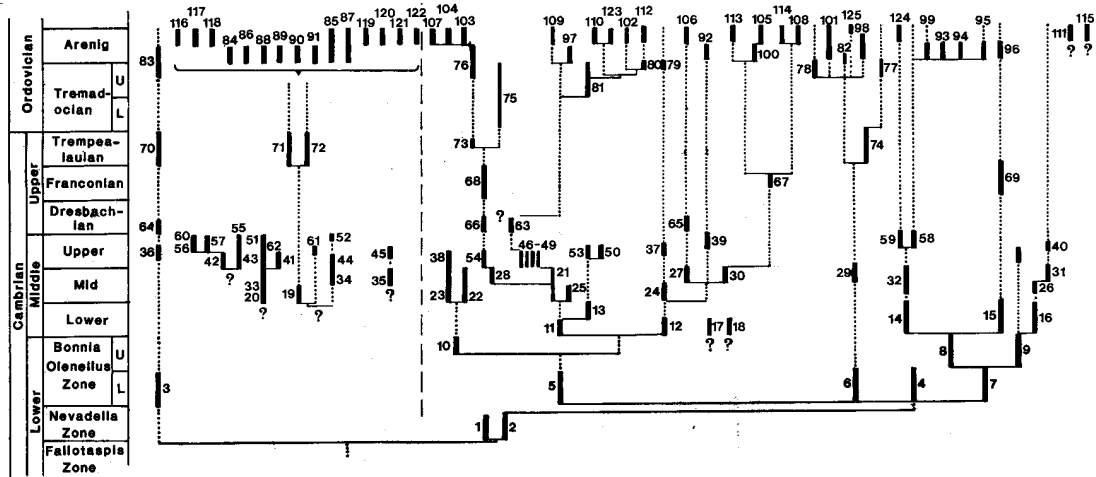
TEXT-FIG. 9. Stratigraphical distribution of all published Cambrian to Arenig (Lower Ordovician) echinoderms. Known ranges are shown as heavy black lines; interpolated ranges as dotted lines; phylogenetic relationships, derived from the character analysis presented here are indicated by fine lines. Table 3 lists all occurrences plotted here and provides the key to species, which are numbered 1–125 on this diagram. Broken vertical line separates 'carpoids' from radiate echinoderms.

TEXT-FIG. 10. Plot of generic diversity for each time interval. Only those intervals in which estimated number of Lazarus taxa forms less than 50 % of the total data (solid dots) are used to construct the diversity curve. Open circles represent known diversity in time periods where Lazarus taxa form more than 50 % of the calculated total diversity and which are likely to underestimate real diversity considerably due to poor sampling.
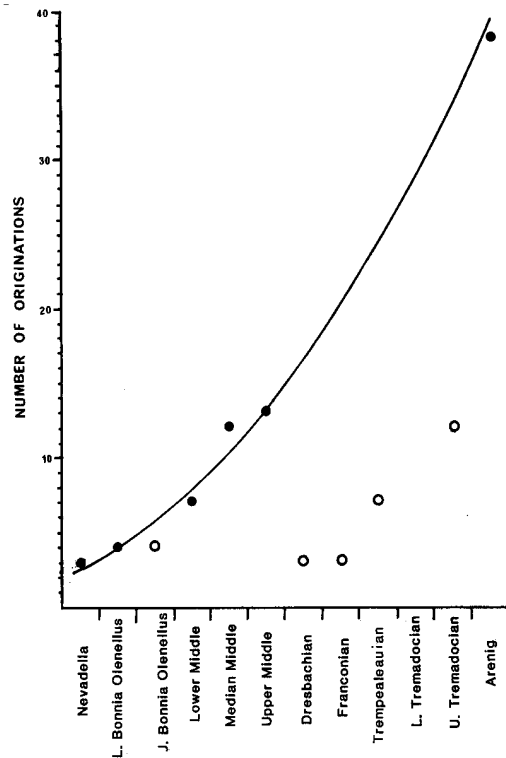
with only a single species may be produced by having a taxon that is ancestral to its derived sister group or a taxon that forms an evolutionary side branch but which shares a common ancestor with its derived sister group. Thus single species branches cannot be assumed to have gone extinct unless they are demonstrably derived themselves or post-date the derived sister group. In practice, a genuine extinction event is accepted where it affects a multitaxon branch on the cladogram or where it affects a single taxon with a unique autapomorphy or where a plesiomorphic sister species is stratigraphically younger than its derived sister group. This will provide a minimum estimate of genuine lineage terminations.

Whereas Sepkoski's family-level compendium (1982, plus supplements) recognizes thirty extinction events during this period, mostly concentrated at the end of the Middle Cambrian, the generic-level analysis here suggests that genuine extinctions are relatively rare events. For echinoderms, there is one obvious extinction of the *G. spiralis* group at the end of the Middle Cambrian and a possible second of the *G. kitchnerensis* group at about the same time. Helicoplacoids, which were apparently quite diverse during the Lower Cambrian probably represent another extinction. Without a cladistic analysis for all carpoids, it is impossible to state how many extinction events there have been in the early history of this group. However, it seems likely that there were at least two, one terminating the ctenocystoid clade and another terminating the cinctan clade (or a branch within the group if it is paraphyletic).

Thus genuine extinctions are rather few during the Cambrian diversification of echinoderms. Although the limited extinctions seem to be restricted to the median or upper Middle Cambrian, it is not certain that this pattern is correct, because of the poor fossil record from the Upper Cambrian. In summary, the evidence presented here shows that for echinoderms the Cambrian was a period of exponential increase in taxonomic diversity and low extinction rate. The very different picture that emerges from analysing taxonomic categories at family and/or class level is largely artefact.

2. *Multiphase models of taxonomic diversification*

Sepkoski (1979, 1981*b*), on the basis of his compilation of non-cladistic taxa at family level, proposed that marine metazoan diversification during the Palaeozoic occurred in two phases. An initial phase of diversification took place in the Cambrian to produce the 'Cambrian fauna', followed by a second phase of diversification during the Ordovician to produce the 'Palaeozoic fauna'. A third phase was later postulated to produce the 'modern fauna'.

As demonstrated above, the apparent peak in taxon origination in the Middle Cambrian, the decline in the Upper Cambrian, and the second peak of origination in the Lower Ordovician are purely artificial for echinoderms and reflect a poor Upper Cambrian record. Whether sampling is also the cause of this pattern in other taxonomic groups remains to be tested.

Furthermore, a number of the groups Sepkoski included within his 'Cambrian fauna' are paraphyletic. Sepkoski described the fauna as being dominated by trilobites, hyolithids, eocrinoids, inarticulate brachiopods, and monoplacophoran molluscs. The last three of these are demonstrably paraphyletic (though including a number of good clades) and, as shown here for eocrinoids, must contain a number of lineages that are ancestral to later, more derived groups. The relationships of Ordovician trilobite families, most of them true clades, to the Cambrian trilobite families is a matter of contention. Many Ordovician families appear *de novo* above the Ordovician boundary but their Cambrian sister taxa have not yet been identified (R. A. Fortey, pers. comm.). The implication is that some of the Upper Cambrian families are paraphyletic—hence even trilobite extinction at the Cambro-Ordovician boundary is partially a taxonomic artefact. This is borne out by the recent analysis of trilobite family extinctions at this boundary (Briggs *et al.* 1987), where more than 50 % of family disappearances are attributed to pseudoextinction.

It is hardly surprising that paraphyletic groups such as eocrinoids 'go into decline' after the Cambrian, since taxonomists have pruned off all the successful post-Cambrian lineages originating from these groups and placed them into other taxa. The decline of these elements of the 'Cambrian fauna' is thus no more than taxonomic artefact.

Sepkoski (1979) searched for a biological reason for this apparent two-phase pattern of diversification, and suggested that the Cambrian radiation favoured the appearance of generalist forms, whereas the Ordovician radiation produced more specialized forms that outcompeted the Cambrian fauna. However, an alternative explanation is that it is the product of taxonomists creating paraphyletic Cambrian groupings which are terminated (at arbitrary points) by the abstraction of monophyletic groups.

3. Rank, morphological distance, and macroevolution

Several workers (Paul 1979; Valentine 1980; Sprinkle 1983; Campbell and Marshall 1986) have put forward the idea that there was something rather different going on in evolutionary terms during the Cambrian with the appearance of so many high level taxa (phyla, classes). Valentine (1980) explained this in terms of vacant ecological space availability, suggesting that it is easier to make 'phylum-level or class-level jumps' during the early radiation of metazoans while ecological space was relatively empty. Clearly, these workers believe that morphological innovation was proceeding much faster and by many fewer steps than later in the Phanerozoic. Hence Paul (1979, p. 417) was able to claim that 'virtually all echinoderm evolution was over by the end of the Ordovician'.

The evidence for rates of evolution in the production of marine invertebrate phyla is difficult to study because much of the morphological diversification must have gone on prior to the evolution of skeletal systems and we thus have no fossil record. In echinoderms, however, we do have a fossil record with which to assess morphological distance in the origination of 'classes'. Evidence provided in this paper for the first 60–90 million years of echinoderm diversification does not support claims of major macroevolutionary jumps in the creation of 'classes'. Were echinoderms to have gone extinct at the end of the Arenig, it is doubtful whether many of the classes recognized today by traditional taxonomists would have been created. The same conclusion has been reached by Runnegar (1986) for early Palaeozoic molluscs. Furthermore, the nested pattern of character distribution identified in cladograms such as text-fig. 6 suggests that diversification was more gradual and stepwise than has previously been recognized.

The arbitrariness with which 'classes' have been recognized in the past has been discussed above. Echinoderm taxonomists have been inconsistent when it comes to designating rank. To mention just a couple of examples, the evolution of uniserial arms is seen as the primary character that separates *Echmatocrinus* from blastozoans and places it in the subphylum Crinozoa (Sprinkle 1973, 1976b). Yet some gomphocystitid cystoids have also evolved uniserial ambulacra (Bockelie 1979b), and *Rhipidocystis*, which is not even separated at family level (Sprinkle 1973), has uniserial 'pinnules'. The class Coronoidea was erected for a group of cystoids (Blastozoa) with erect, pinnate arms (Brett et al. 1983) yet both *Bockia* and *Trachelocrinus* with almost identical pinnate arms are left as genera within the Eocrinoidea. Taxonomic rank in non-cladistic data has been applied for such non-commensurate reasons that it seems unlikely that any biologically meaningful results can come from analysis that uses such data purporting to measure morphological distance.

Note added in proof. The Upper Arenig Al Rose Formation of California has been omitted from the list of echinoderm Lagerstätten in error. Ausich (1986) has described two crinoids from there, *Proexenocrinus inyoensis* Strimple and McGinnis and *Inyocrinus strimplei* Ausich.

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