

AUTECOLOGY AND THE FILLING OF ECOSPACE: KEY METAZOAN RADIATIONS

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Abstract: All possible combinations of six tiering positions in relation to the substratum/water interface, six motility levels and six feeding strategies define a complete theoretical ecospace of 216 potential modes of life for marine animals. The number of modes of life actually utilized specifies realized ecospace. Owing to constraints of effectiveness and efficiency the modern marine fauna utilizes only about half the potential number of modes of life, two-thirds of which (62 of 92) are utilized by animals with readily preserved, mineralized hard parts. Realized ecospace has increased markedly since the early evolution of animal ecosystems. The Ediacaran fauna utilized at most 12 modes of life, with just two practised by skeletal organisms. A total of 30 modes of life are recorded in the Early and Middle Cambrian, 19 of which were utilized by skeletal

organisms. The other 11 are documented from soft-bodied animals preserved in the Chengjiang and Burgess Shale Konservat-Lagerstätten. The number of modes of life utilized by skeletal organisms increased by more than 50 per cent during the Ordovician radiation to a Late Ordovician total of 30. Between the Late Ordovician and the Recent the number of utilized modes of life has doubled again. The autecological and taxonomic diversity histories of the marine metazoa appear to be broadly parallel, and future studies of theoretical ecospace utilization should provide more detailed tests of pattern and process in the ecological history of the metazoa.

Key words: theoretical ecospace, evolutionary constraint, mode of life, ecological complexity, tiering, motility, feeding.

ONE of the triumphs of the palaeobiological approach to palaeontology is the insight functional morphology has given us about the life activities of long dead organisms. Significant examples include: Trueman (1941) on the life orientation of ammonites; the explanation by Rudwick (1964) of the function of zigzag deflections in the commissure of brachiopods; Clarkson's work on vision in trilobites (Clarkson 1979); the work of Stanley (1970, 1972, 1975) on bivalve form and function; Fisher (1977) on the utility of the spines of the Carboniferous horseshoe crab *Euproops danae*; and Savarese's demonstration of the passive entrainment of flow in archaeocyathids (Savarese 1992). The methodology developed in such studies permits us to draw reasonable conclusions about the modes of life of fossil organisms with some confidence.

Valentine (1969, 1973) first forged the connection of palaeoecology to evolutionary palaeobiology. Since then Vermeij (1977, 1987, 2004) has written extensively about coevolutionary aspects of predation and its consequences as well as the general economic aspects of evolution; Thayer (1983) documented the role increasing bioturbation has had in affecting marine ecosystems; Bambach (1983, 1985, 1993) has argued that increasing ecological complexity has been fundamental in permitting increases

in diversity; and Bambach and Knoll (2000) have suggested that expanding ecological complexity marks a directionality in the history of life.

Curiously, despite the attention given to both ecological innovations and fluctuations in diversity over time, no one has *systematically* examined either the variety of autecologies present at different times or the sequence of ecospace filling. This paper is a preliminary effort at filling that gap. It applies a newly developed method of classifying autecological strategies to evaluate the occupation of ecospace on a global scale during four critical times in the history of marine metazoa. Specifically, we tabulate the number of autecological strategies (modes of life) in the marine metazoan faunas of the Ediacaran, Early–Middle Cambrian, Late Ordovician and Recent. Modes of life are defined here as the 216 categories formed by all possible combinations of six tiering categories with respect to the sediment–water interface, six motility levels and six feeding mechanisms.

The method of evaluating ecospace used here was developed as part of an ongoing project to examine and compare ecological structure within habitats in a rigorous and standardized fashion (Bush *et al.* in press, in prep.). One conclusion of that work is that average richness

within fossil assemblages (i.e. alpha diversity) doubled in terms of both number of genera and modes of life between the mid-Palaeozoic and the late Cainozoic (Bush and Bambach 2004a). As total taxonomic diversity (gamma diversity) also increased over that interval (Sepkoski 1981; Bambach 1999), these results raise the possibility that the number of modes of life increased as well, but the data on individual assemblages are not adequate to answer that larger question because they were compiled for only one general habitat setting so that comparisons across time could be made reliably. For the level-bottom marine ecosystem we examined, only 21 of the modes were filled in the Palaeozoic samples studied and only 25 were occupied in our Cainozoic samples. This implies that, for the level-bottom habitat, total (gamma) ecological diversity had changed only slightly whereas alpha ecological diversity had nearly doubled (Bush *et al.* in prep.). However, the sampling strategy emphasized large collections of skeletal fossils and was not designed to detect many modes of life that might be utilized by rare or infrequently preserved taxa. Thus, only 10–12 per cent of the possible modes of life were represented in our study of one ecosystem. These analyses left unexplored the key questions of how many of the modes of life unrepresented in this ecosystem were never filled by metazoans, how many were simply too rare to be sampled in our initial study, how many were filled by inhabitants of other ecosystems and how many were filled only by organisms that leave no regular fossil record.

Rather than sampling individual fossil assemblages, as done previously (Bush and Bambach 2004a), we have here sought to census all modes of life known to be present at several points in the history of metazoan life. This paper thus seeks to answer these unexplored questions, at least in a preliminary sense. How much ecospace (how many modes of life) is constrained to be empty because of functional difficulties or ecological inefficiency, thus making realizable ecospace different from potential ecospace? Did the full range of modern modes of life evolve early in the history of animal life, with further diversity increases accommodated by increased species packing within established modes of life, or has increased diversity on a global scale been accompanied by increased use of ecospace (the addition of modes of life)? Our studies of Palaeozoic and Cainozoic assemblages are too limited in scope to deal with either of these questions, hence this exploratory study.

We examine four critical times. Each includes or follows a major taxonomic radiation: the Ediacaran, the Early and Middle Cambrian, the Late Ordovician, and the Recent. The Recent fauna establishes the full range of occupied ecospace and, by comparing only taxa with a good fossil record with the total fauna, also allows us to estimate what proportion of occupied ecospace is likely to be represented

reliably in the fossil record. The Recent also follows the apparent rapid diversity rise of the Cainozoic and represents the time with the greatest known marine diversity. The Ediacaran represents the beginning of metazoan radiation and the Early and Middle Cambrian spans the Cambrian ‘explosion’ of skeletal organisms. If the range of modern modes of life was established in these earliest radiations, then the variety of modes of life represented in the earliest and latest Phanerozoic should be similar. If so, taxonomic diversification during the Phanerozoic occurred by packing more species into established modes of life or by subdivision of those modes. The Late Ordovician, the fourth interval tallied, occurred at the conclusion of the Ordovician radiation and the start of the Palaeozoic plateau, when taxonomic diversity appears to have fluctuated with no overall secular trend to either increase or decrease for 200 myr. If the Ediacaran and Early–Mid Cambrian radiations did not establish modern levels of ecological diversity, perhaps the Ordovician radiation, which established many new orders within the marine classes (Webby *et al.* 2004), was when the bulk of ecospace filling occurred. The Late Ordovician–Recent interval approximately equals the mid-Palaeozoic–late Cainozoic interval of our within-habitat comparisons of alpha diversity and ecospace use, which gives us a chance to compare changes at the alpha and gamma levels.

Although it is logical to assume that new modes of life have accumulated in each major radiation, no full evaluation of that idea using a standard method of analysis has been done before. As neontologists debate whether ecosystems are assembled by chance with little or no interactive determinism (Hubbell 2001), by interactions of organisms determining niche structure (Odling-Smee *et al.* 2003), or by some combination of the two, documenting the nature of the change from one time to another (if any) is of critical importance in addressing the question of whether organismic ecology or ecological interactions actually participate in determining diversity and other aspects of ecosystem structure.

This paper is primarily exploratory. Our goal was not to test one explanatory theory against another. It was to find out *if* change has taken place from one time to another. Because the data are global and, in most cases, taken from relatively long intervals of time, rather than representing local ecosystems on a temporal scale at which organisms interact, we cannot yet offer a detailed theoretical explanation of the changes observed. Because the data are drawn from intervals widely separated in time, the transitions from one ecological state to another are not documented. In the Ediacaran and Cambrian, the data are not parsed in temporal order and so ecological change that occurred within those intervals is not examined. However, these intervals were chosen to encompass the ecological forms produced during major taxonomic

radiations, so if there is a correspondence between taxonomic and ecological radiations, then we have captured the results of these events. Our goals are to sketch the rough outlines of an 'ecological diversity curve' and to indicate which time intervals should be studied further to fill in the details of this curve.

AUTECOLOGY, MODES OF LIFE AND ECOSPACE

Autecology, the relationship of animals as individuals to their biotic and abiotic environment, focuses on modes of life. We have developed a classification of general modes of life for marine organisms based on tiering position in relation to the substratum/water interface, motility level and feeding strategy, which we regard as fundamental ecological parameters (Bush *et al.* in press). Tiering is important because each location with respect to the sea bottom has particular physical characteristics that require adaptations to function efficiently. Motility level reflects the spectrum of activities an organism can achieve in response to disturbance and/or other external stimuli. Feeding strategy encompasses the means of acquiring the energy necessary to maintain life. In effect, these axes describe the basic autecology of an organism. The categories into which each axis was divided are listed in Table 1 and described fully by Bush *et al.* (in press).

This classification permits assignment of all marine animals to particular places in a three-axis grid. Those loca-

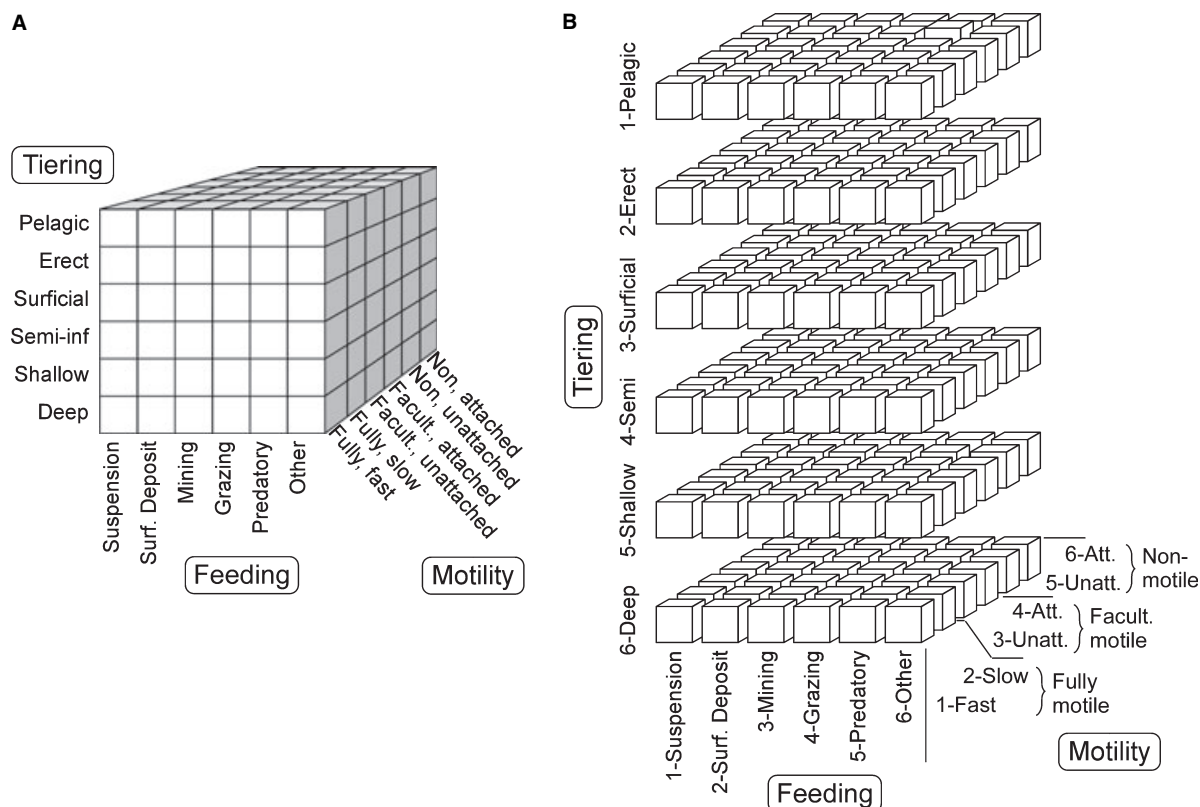
tions define general modes of life and the three-dimensional construct based on the three axes represents ecospace (ecological space) (Text-fig. 1A). The three axes form a complete theoretical ecospace. We have tried to define the six subdivisions of each axis so that all possible combinations of tiering, motility level and feeding mechanism are accounted for. The six subdivisions for each of the three axes designate 216 combinations, which we term modes of life (Text-fig. 1B).

ECOSPACE, NICHES AND GUILDS

Ecospace (location in a topographic setting, potential for motion or the maintenance of a fixed position, and method of acquiring food) is always present, whether animals are living in each tier or functioning in each possible way or not. The challenge for organisms is to construct the adaptations necessary to exploit ecospace. Thus, complex ecosystems develop as organisms acquire the behaviours and adaptations necessary to construct the ecological interactions that enable them to exploit un-utilized opportunities. In effect, the filling of ecospace over time conceptually parallels Valentine's 'tesserae' model of evolution, in which new taxa fill pre-existing empty 'niches', with small morphological changes (speciation) making small steps and large changes (the origin of higher taxa) making large, but rare, jumps (Valentine 1980, 1981; Walker and Valentine 1984).

TABLE 1. Basic ecological categories for tiering, motility level and feeding mechanism.

Category	Description
Tiering	
1. Pelagic	Living in the water column, free of the bottom
2. Erect	Benthic, extending into the water mass
3. Surficial	Benthic, not extending significantly upwards
4. Semi-infaunal	Partly infaunal, partly exposed to the water column
5. Shallow infaunal	Infaunal, living in the top c. 5 cm of the sediment
6. Deep infaunal	Infaunal, living more than c. 5 cm deep in the sediment
Motility level	
1. Freely, fast	Regularly moving, unencumbered (walking, swimming)
2. Freely, slow	Regularly moving, intimate contact maintained with substrate
3. Facultative, unattached	Moving only when necessary, free-lying
4. Facultative, attached	Moving only when necessary, attached
5. Non-motile, unattached	Not capable of self-propulsion, free-lying
6. Non-motile, attached	Not capable of self-propulsion, attached
Feeding mechanism	
1. Suspension	Capturing food particles from the water
2. Surface deposit	Capturing loose particles from a substrate
3. Mining	Recovering buried food
4. Grazing	Scraping or nibbling food from a substrate
5. Predatory	Capturing prey capable of resistance
6. Other	Varies, includes photo- or chemosymbiosis, parasitism



TEXT-FIG. 1. Ecospace as defined by the three axes of tiering, motility level and feeding strategy. A, the ecospace cube with categories on each axis labelled. B, the ecospace cube 'exploded', showing 216 'bins' or modes of life specified by the combination of the categories on each ecospace axis.

The ecospace concept should not be confused with niche concepts. From the very beginning, niche concepts have conveyed the idea, at least implicitly, of competitive exclusion leading to one niche per species (Johnson 1910; Grinnell 1914; see discussion in Hutchinson 1978, pp. 155–157). The ecospace concept refers to possible combinations of important ecological parameters without reference to limiting conditions, resources or competition among species. Although it has some resemblance to the Eltonian idea of 'roles' of species in the ecosystem (see discussion in Chase and Leibold 2003, pp. 7, 57), the ecospace concept describes which roles are utilized (or not utilized) and does not evaluate competition among modes of life or within modes. The general purpose of most niche theories is to define what makes individual species unique and how niche parameters control species and species interactions in ecosystems (Chase and Leibold 2003; Odling-Smee *et al.* 2003). The ecospace concept has a more general, descriptive goal: to evaluate how many of the potential modes of life that could exist were actually present in a particular regional or temporal framework. From this, we can look at how ecosystems have been structured at different times and scales, locally to globally.

This supplies a context in which theories about evolutionary interactions can be studied.

It would be possible to add axes to the basic ecospace 'cube' and specify factors such as temperature or salinity that can limit the survival or distribution of species. Likewise, it would be possible to add resource dimensions as well, assuming one can specify the resources that are critical in limiting particular species in the fossil record, and construct a Hutchinsonian 'n-dimensional hypervolume' that would describe a niche (Hutchinson 1965, 1978). But determining such limiting factors and critical resources for fossil organisms is speculative at best. Eventually this may be possible for some organisms or for some conditions, but now our goal is simply to discover how much of basic ecospace has been utilized at different times.

Similarly, although guilds can include multiple species, as can the various locations in ecospace, the ecospace concept is different from the guild concept (Root 1967; Bambach 1983). Guilds are properly defined as the taxa competing for some particular resource (thus grouping species that have niche overlap for that resource), but resources are not defined or specified in the fundamental ecospace concept.

REALIZED ECOSPACE IN THE MARINE REALM

Modes of life in the Recent marine fauna

All 216 modes of life are theoretically possible, but are they all utilized? For an initial answer to that question we surveyed a series of references on metazoan biology (Parker 1982; Nowak and Paradiso 1983; Carroll 1988; Long 1995; Kaufman 1996; Margulis and Schwartz 1998; Brusca and Brusca 2003; Cracraft and Donoghue 2004; Valentine 2004; plus numerous sites on the internet using *Google*). Using the list of 216 modes designated by the $6 \times 6 \times 6$ grid of the three-axis ecospace (Text-fig. 1; Table 1), we recorded the modes of life for all living marine metazoa (porifera through vertebrates, including microscopic and interstitial forms).

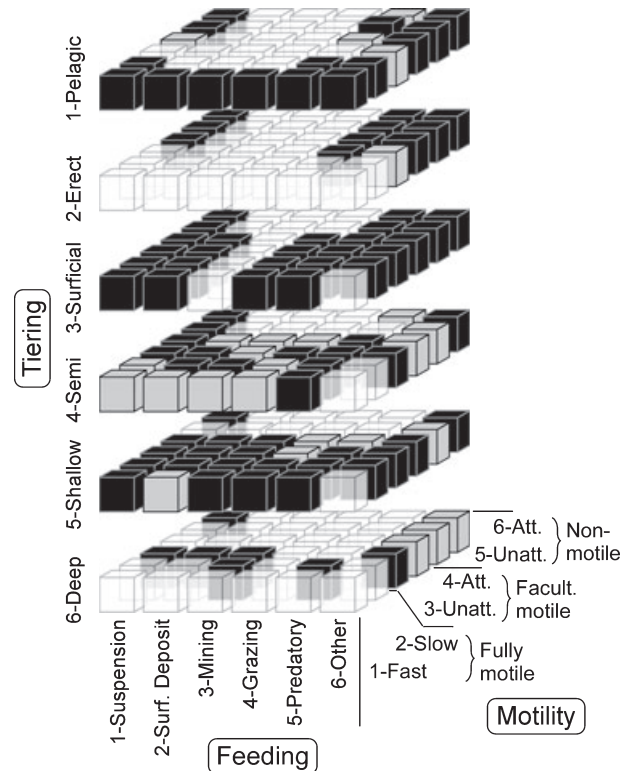
In our survey only 92 of the 216 theoretically possible modes of life were recorded as utilized (Text-fig. 2, black boxes). The list of taxa reviewed and the mode or modes of life used by each is available in part one of the online supplementary information (<http://www.palass.org>). Each mode of life has been assigned a three-digit number and the taxa recorded for that mode of life are listed accordingly. The supplementary data also have tabulations showing the number of groups recorded in our survey for each mode of life. The rationale for why some modes are not utilized is also given in the supplementary data.

What of the apparently un-utilized modes of life? If they are possible, why are they not used too? Is it that even after 600 myr of metazoan evolution there are untapped modes of life that evolutionary chance has yet to find? Or has evolution actually explored the full range of possibilities and some modes are unlikely because of constraints imposed by efficiency and effectiveness?

Constraint and missing modes of life

Because conditions vary along each of the three axes of ecospace, it is unlikely that all categories on one axis are equally likely to be effective or viable at each position along another. For instance, because some food types will be unavailable or rare in some tiers it is improbable that all feeding strategies will be equally likely for every tier, especially when coupled with different motility levels. Likewise, although it is conceivable that some organisms could evolve to practise every mode of life, various combinations of competition, danger and energetic limitations make some highly unlikely.

The processes that limit the number of modes utilized are types of externally imposed constraints (Gould 1989). The constraints that limit the number of modes of life



TEXT-FIG. 2. Modes of life utilized by Recent marine animals. Black boxes are modes of life documented in the survey reported in the text and listed in the online file of supplementary data. Grey boxes are modes of life that seem reasonably possible but were not noted in the survey for this paper. 'Ghost' boxes are theoretically possible modes of life that are unlikely to be utilized because of various constraints as noted in the text and supplementary data.

mostly parallel the idea of 'Class-1' constraints (Schwenk 1995), which are 'based on the idea that the path taken by an evolving lineage through phenotypic space is somehow bounded or limited' (Schwenck 1995, p. 253). These constraints are generally straightforward results of the combination of physical conditions favouring some activities over others in some environmental settings or are produced by differences in success among potential competitors. Functional and energetic requirements are imposed by each potential mode of life. Functional constraints relate to the way the mode of life works in a particular setting. Energetic constraints relate to the balance between energy intake and energy expenditure. Functional issues are issues of effectiveness; energetic issues are issues of efficiency. Most of the constraints are rooted in low likelihoods or improbability of success, rather than impossibility.

In Text-figure 2 the potential modes of life indicated as transparent 'ghost' boxes are those we feel are unlikely to have ever been utilized. Three general principles seem to

constrain the use of ecospace. (1) Either the animal or the food should be mobile. Animals must be able to move to their food or the food must be transported to the animal, otherwise they do not find each other. For example, non-motile animals do not graze, surface deposit feed or mine because there is a danger of exhausting the local food supply. (2) The animal and the food should occur in the same tier. For efficiency the food an animal eats is usually located in the tier in which the animal lives. This constraint does not apply to motile pelagic animals, which are free to swim down to the sediment (and in one case even mine), nor does it apply to infaunal suspension feeders that pump water for filtering. These exceptions are positive examples of constraint number one, motile animals going to food or food being transported to the animal. (3) Motility can be limited by the physical properties of the surrounding medium, making some motility levels incompatible with the physical conditions of some tiers. For example, the possibility of damage by being toppled or swept away by currents is a factor that generally precludes free motility for erect epifauna and penetrating through deep sediment precludes fast motion by deep infauna, although some may be able to move rapidly in pre-excavated burrows. A more detailed discussion of the constraints limiting the number of realized modes of life is provided in sections 3 and 4 of the online supplementary material (<http://www.palass.org>).

Life has explored most likely modes of life

Of the 124 potential modes of life not recorded as utilized, we feel 98 are unlikely to be used (the 'ghost' boxes in Text-fig. 2). The three different constraining factors just described account for 87 of those 98 unlikely modes of life and similar reasons can be cited for the other 11 (see supplementary data online). We interpret the other 26 modes of life unobserved in our tabulation (shaded on Text-fig. 2) as functionally reasonable, but either missed in our survey or not used in the Recent. In fact, we have assigned a few fossil forms to some of these reasonable but currently apparently un-utilized modes. These constraints and patterns of ecospace occupation suggest that marine animals have exploited most of the likely modes of life.

Realized ecospace

The idea of realized and fundamental ecospace parallels Hutchinson's terminology of realized and fundamental niches. The fundamental niche is determined by the range in values of niche parameters over which a species can survive in the absence of other species and the realized

niche is determined by the range of values of niche parameters the species commands even in competition with other species (Hutchinson 1978; Chase and Leibold 2003). The 92 utilized modes of life represent the realized ecospace animals have achieved in the marine realm in the Recent. The 92 utilized plus 26 other functionally possible but apparently unused modes together represent a minimum for fundamental ecospace, and the full ecospace cube, assuming all 216 modes could be functionally possible, would be the maximum fundamental ecospace. However, fundamental ecospace is almost certainly less than the complete set of 216 potential modes of life and may be considerably less. From our discussion above it seems probable that of the 98 potential, but un-utilized, modes of life that we suggest are unlikely some or all would not be practical, even without competitors. Uncertainty about which modes of life are absolutely forbidden makes exact determination of fundamental ecospace impossible, even though we can specify a complete theoretical ecospace. However, we can say that apparently realizable ecospace is represented by just 118 (the 92 documented and 26 seemingly possible modes of life) of the 216 total potential modes of life, only 55 per cent of theoretical ecospace. Values of realized ecospace as a proportion of total potential ecospace for the Recent and the time intervals to be discussed below are given in Table 2.

The three tiers (surficial, semi-infaunal and shallow infaunal) associated with the substratum/water interface have the greatest proportion of potential modes of life utilized. This probably reflects both the concentration of food sources at and near the sea-floor (Walker and Bambach 1974) and the opportunities the physical boundary

TABLE 2. Fundamental and realized ecospace. The number of utilized modes of life in compilations discussed in the text, along with the percentage of the potential total number represented by utilized modes.

Data set	Modes of life	
Theoretical ecospace (potential total)	216	
Recent Fauna		
Observed or reasonable	118	55%
Observed	92	43%
Taxa with a diverse fossil record	82	38%
Regularly preserved hard parts	62	29%
Ordovician		
Skeletal	30	14%
Early–Middle Cambrian		
Total	30	14%
Chengjiang Fauna	22	10%
Burgess Shale Fauna	18	8%
Skeletal Fauna	19	9%
Ediacaran		
Total	12	6%
Avalon Assemblage only	2	1%

between solid and liquid phases offer for different combinations of motility level and feeding strategy. Constraints imposed by physical conditions unique to each of the other tiers appear to limit the realized modes of life in those tiers.

THE POTENTIAL FOR EVALUATING ECOSPACE USE IN THE FOSSIL RECORD

Functional morphology and general taxonomic uniformitarianism should permit us to recognize most modes of life that fossil metazoans utilized. However, the fossil record is primarily that of mineralized hard parts with the exciting (but uncommon) preservation of organisms lacking hard parts in Konservat-Lagerstätten such as the Middle Cambrian Burgess Shale and the Late Jurassic Solnhofen Limestone. What proportion of Recent modes of life might end up being recorded by the fossil record? To consider this question, we culled the census of Recent modes of life in two ways: (1) modes of life present in groups that have an extensive and diverse fossil record and (2) modes of life present in a selected subset of the groups in the first set, in which members of the subset have readily and regularly preserved mineralized parts. The taxa included in each set are listed in Table 3.

The groups surveyed that have an extensive and diverse fossil record (see numbers in Table 3A) were those with a large number of genera with a fossil record as noted in the copy of Sepkoski's genus database held by Bambach (obtained from Sepkoski in 1996), which is quite close to the final version of early 1998 published posthumously in 2002 (Sepkoski 2002). About 29,000 fossil genera (about 81 per cent of the total in the Sepkoski compendium) occur in this set of taxa. Only half that number of fossil genera is present in the selected group of taxa with regularly preserved skeletal parts common in the fossil record (see numbers in Table 3B). The first set includes those taxa from the Recent that have a good enough fossil record that they are represented frequently in a global synoptic database, and the second set includes those that are robust enough to appear reliably in well-sampled fossil assemblages. The tabulation for groups with a diverse fossil record includes the full range of living organisms from those groups that are commonly encountered in the record, but not from groups with little or only rare representation in the record. The tabulation for groups with readily preserved hard parts represents those groups we expect to be noted in carefully compiled literature surveying the fossil record. The groups include ostracodes and the annelids with scolecodonts, so some 'microfossils' are included, but they have been studied in detail and are considered in the comprehensive reviews from which we

TABLE 3. Lists of living taxa with a significant fossil record.

A, living groups with a diverse fossil record (and the number of genera with a fossil record listed in the version of the Sepkoski genus database used in this paper).

Phylum Porifera	(1286 genera)
Phylum Cnidaria,	
Class Anthozoa	(2102 genera)
Phylum Arthropoda	
Class Chelicerata	
Subclass Merostomata	(112 genera)
Subphylum Crustacea	
Class Maxillopoda	
Infraclass Cirripedia	(92 genera)
Subclass Ostracoda	(1982 genera)
Class Malacostraca	(579 genera)
Phylum Mollusca	(11,127 genera)
Phylum Annelida	
Class Polychaeta	(251 genera)
Phylum Bryozoa	(1450 genera)
Phylum Brachiopoda	(4382 genera)
Phylum Echinodermata	(2546 genera)
Phylum Chordata	
Subphylum Craniata	(3006 genera)
These 12 groups incorporate 80.7 per cent of the genera listed in the Sepkoski database.	

B, living groups with regularly preserved skeletal parts common in the fossil record, and therefore available in many fossiliferous deposits, with the number of genera with a fossil record in the version of the Sepkoski genus database used in this paper.

Phylum Porifera	
Class Demospongia	
Order Lithistida	336 genera
Order Hadromerida	50 genera
Order Chaetetida	45 genera
Order Agelasida	121 genera
Order Verticellitida	96 genera
Class Calcarea	
Order Murrayanida	182 genera
Class Hexactinellida	
Subclass Hexasterophora	227 genera
Phylum Cnidaria	
Class Anthozoa	
Order Scleractinia	870 genera
Phylum Arthropoda	
Class Chelicerata	
Subclass Merostomata	112 genera
Subphylum Crustacea	
Class Maxillopoda	
Infraclass Cirripedia	92 genera
Subclass Ostracoda	1982 genera
Class Malacostraca	
Order Decapoda	
Infraclass Astacidea	
Infraclass Anomura	
Infraclass Brachyura	c. 400 genera

TABLE 3. Continued.

Phylum Mollusca	
Omitting Class Aplacophora	
Subclass Opisthobranchia	
Subclass Coleodea	10,552 genera
Phylum Annelida	
Class Polychaeta	
Order Eunicemorphia	70 genera
Order Serpulummorphia	75 genera
Phylum Bryozoa	1450 genera
Phylum Brachiopoda	4382 genera
Phylum Echinodermata	
Class Echinoidea	747 genera
Phylum Chordata	
Subphylum Craniata	
Class Chondrichthyes	381 genera
Class Reptilia	
Order Testudinata	53 genera
Class Mammalia	301 genera
These groups total about 40 per cent of the genera listed in the Sepkoski database.	

built our evaluations of modes of life from the Ediacaran and early Palaeozoic.

Text-figure 3 shows the modes of life in the living fauna recorded for the two groupings of taxa listed in Table 3. Eighty-two of the 92 modes of life documented for the entire living fauna are utilized by living members of the group of taxa with an extensive and diverse fossil record (Text-fig. 3A) and 62 of the 92 modes of life documented for the entire living fauna are utilized by living members of the group of taxa with regularly preserved skeletal parts common in the fossil record (Text-fig. 3B). Section two of the online supplementary material gives the number of taxa from our survey of the living fauna in each mode of life that fall in each of the three groupings discussed (total fauna, fauna with a diverse and extensive fossil record, fauna with preservable hard parts).

Modes of life not recorded in groups with an extensive and diverse fossil record or in groups with regularly preserved hard parts, but which are utilized by some Recent marine animals, are relatively evenly distributed by tier, so no marked bias against detecting modes of life for particular tiers should characterize the fossil record, at least in the Neogene. Neither is there an apparent bias against detecting modes of life for different motility levels for the groups with an extensive and diverse fossil record. However, more than half of the utilized modes of life for animals with facultative motility are not recorded by the groups with regularly preserved hard parts, reflecting some bias when studying only fossils of animals with regularly preserved hard parts. The only feeding category with a similar potential bias is the 'other' category, and then only for the selected set of groups with regularly preserved hard parts.

These results suggest that, unless there has been a major change in the proportion of the fauna with readily preservable hard parts, or in the variety of modes of life of animals without a significant fossil record, neither of which seems likely (see comments near end of paper), a careful examination of the fossil record should permit us to document about two-thirds of the modes of life that were utilized by the fauna at any time from hard part materials alone and as much as 90 per cent of all utilized modes of life if we survey a large amount of the record for most intervals of time, especially if the surveyed data include examples of unusually well-preserved material. Although some bias in finding particular modes characterized by facultative motility may limit detailed comparison of hard-part-only fossil faunas with the full Recent fauna, major changes in the number of modes of life utilized at different times should be apparent from the fossil record, despite taphonomic winnowing.

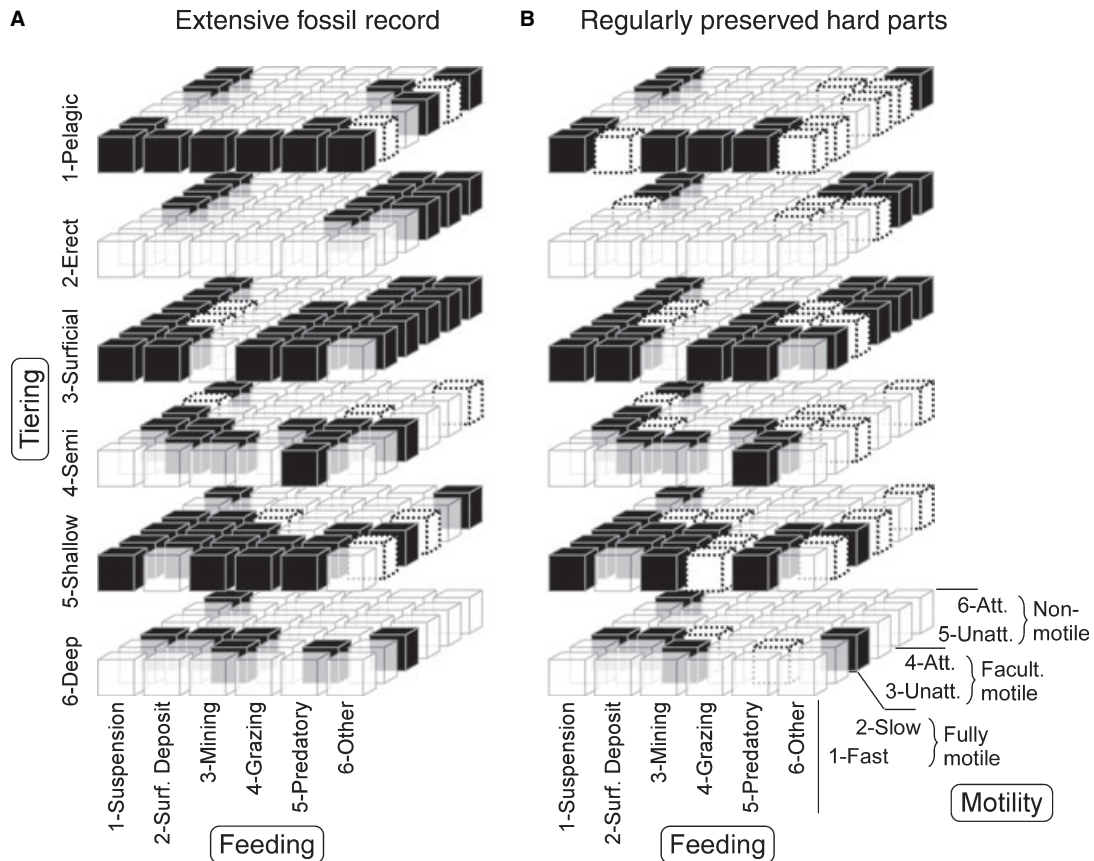
With data in hand for the Recent and the confidence that we should be able to see general patterns of use of ecospace from the organisms regularly preserved as fossils we can turn our attention to the questions raised in the introductory section of this paper.

BEGINNING OF METAZOAN FOSSIL RECORD AND INITIAL RECORD OF ANIMAL MODES OF LIFE

Interpreting modes of life of Ediacaran animals

Four recent developments have improved our ability to interpret the biology of the earliest animals: (1) discoveries about taphonomy in a world without bioturbation (Gehling 1999; Gehling *et al.* 2000; Jensen 2003; Jensen *et al.* 2005; Droser *et al.* 2006); (2) thinking about animals intermediate between the origin of multicellularity and fully established crown-group members as representing stem groups with some, but not all, characters of established crown groups (Gehling 1991; Budd 2003); (3) critical new discoveries about the morphology of early animals, such as the fractal modularity of the rangeomorphs (Narbonne 2004; Xiao *et al.* 2005) and the remarkable preservation of fossil embryos in the Duo-shantuo Formation (Xiao and Knoll 2000); and, finally (4) comparative developmental biology ('evo-devo'), which has revealed a rich source of information about highly conserved aspects of metazoan development and allowed insights into the nature of the earliest animals (Knoll and Carroll 1999; Valentine *et al.* 1999; Erwin and Davidson 2002; Davidson and Erwin 2006).

Although some have argued that Ediacaran fossils include representatives of more complex metazoans of



TEXT-FIG. 3. Modes of life utilized in the Recent by selected groups with a reasonable fossil record. Black boxes are modes of life utilized in the Recent by the selected taxa. Boxes with dotted margins and opaque white in colour are modes of life utilized in the Recent by taxa not included in the selected group. A, modes of life utilized in the Recent by the groups with an extensive and diverse fossil record listed in Table 3A. B, modes of life utilized in the Recent by the groups with regularly preserved mineralized tissues listed in Table 3B.

triploblastic grade, including arthropods, echinoderms and annelids (e.g. Glaessner 1984; Jenkins 1992), only *Kimberella* and a few unpreserved trace makers are convincingly bilaterians. A mouth, gut, anus and internal organs of mesodermal origin are synapomorphies of complex bilateria, and none occurs in most Ediacaran taxa. Undoubted complex Bilateria first appear in the fossil record at various times in the Cambrian and later, with many Early and even Middle Cambrian fossils better regarded as stem-group representatives rather than crown-group members. Bilateria must have existed prior to the evolution of extant clades. Lineages along the line between cnidarians and the last common bilaterian ancestor (LCBA), and between the LCBA and the crown groups of extant phyla, would not yet have all synapomorphies of the crown groups. The earliest forms might be difficult to distinguish from cnidaria because they were probably of a similar organizational level.

Because of the exotic nature of Ediacaran fossils, the autecology of these earliest macroscopic animals is less confidently interpreted than that for later faunas. There-

fore, we discuss their function and ecology in some detail in parts 5 and 6 of the online supplementary material and summarize that material below.

Ediacaran assemblages

The Ediacaran Period of the Neoproterozoic marks the first appearance of metazoan fossils. Three assemblages of metazoans of Ediacaran age have been recognized (Waggoner 2003; Narbonne 2005): (1) the Avalon assemblage, best known from south-east Newfoundland, but also reported from England and Russia; (2) the White Sea/Ediacara assemblage, the most diverse Precambrian assemblage, with extensive occurrences near the White Sea coast near Arkhangelsk, Russia, and in the Ediacara Member of the Rawnsley Quartzite in South Australia; and (3) the Nama assemblage, best known from the Nama Group, Namibia. A temporal sequence has been suggested for these assemblages because the earliest known Ediacaran fauna (between 575 and 560 Ma) is the

Avalonian assemblage from Mistaken Point on the Avalon Peninsula of Newfoundland and the youngest (549–542 Ma) is the Nama assemblage from strata just below the base of the Cambrian in Namibia. An alternative was proposed by Grazhdankin (2004), who argued that representatives of all three assemblages co-occurred between about 558 and 546 Ma in different environmental settings in the Arkhangelsk region of Russia, indicating that the three assemblages might represent faunas inhabiting different marine environments rather than different evolutionary phases. Avalon-type assemblages lived in deep-water settings, White Sea/Ediacara-type assemblages inhabited shallow shelf environments and Nama-type assemblages occurred in high sedimentation rate settings like distributary-mouth bars. Nonetheless, the best known Avalon assemblages occur up to 15 myr earlier than the other assemblages and no trace fossils or bilaterian-like body fossils occur in those earliest faunas, so some evolutionary significance may pertain to this earliest occurrence with its low diversity and lack of traces and bilaterian-like body fossils. Also, mineralized tissues, other than sponge spicules, only occur in the latest Neoproterozoic faunas.

Avalon assemblage. The Avalonian biota is characterized by rangeomorphs: bizarre frond-, spindle-, bush- or comb-shaped colonies composed of highly fractal modular elements. None of the taxa was skeletonized or capable of mobility (Narbonne 2005, p. 426). The same is true of the non-rangeomorphs that are also present. For several reasons related to their apparent lack of any differentiated internal anatomy (see part 5 of the online supplementary material) we list rangeomorphs as having ‘other’ as their feeding strategy (presumably absorptive) and list similar general forms of non-rangeomorphs as suspension feeders. The non-rangeomorphs would include otherwise unrecognized poriferans and cnidarians that were in fact suspension feeders. Although this is an arbitrary choice, it is conservative in that it covers the two possible feeding strategies for such morphologies. In fact, only one may have characterized all the animals in the Avalonian assemblage. The Avalon assemblage represents at most four modes of life (Text-fig. 4A), all appropriate for survival in deep, quiet water conditions.

White Sea/Ediacara assemblage. The classic White Sea fauna was summarized by Fedonkin (1992) and summaries of the fauna from the Ediacara Member of the Rawnsley Quartzite of South Australia are given by Gehling (1991), Jenkins (1992) and Droser *et al.* (2006), with reinterpretation of a number of discoid forms in Gehling *et al.* (2000). The existence of sponges in the Australian fauna has been corroborated by Gehling and Rigby (1996) and the presence of bilaterians is recorded by both the first trace fossils

(Jensen 2003; Jensen *et al.* 2005) and the body fossil *Kimberella* (Fedonkin and Waggoner 1997).

The diverse White Sea/Ediacara assemblage has representatives of ten modes of life, some of which are probably related to living in association with microbial mats. Surficial and erect, non-motile suspension feeders, including a variety of discoid forms, many originally interpreted as medusae that have been redesignated as holdfasts (Gehling *et al.* 2000), were common. Sponges were present, as well as several forms also seen in the Avalon assemblage interpreted as erect, non-motile attached, other (absorptive feeders). *Dickinsonia* was commonly associated with microbial mats. Its mode of life is interpreted to have been surficial, non-motile unattached, other (either chemosymbiotic or absorptive, possibly digesting the microbial mat it rested on). Bilaterally symmetrical forms with differentiated apparently anterior and posterior ends and a tapering, metameric body are present but none shows any convincing evidence of a gut or internal anatomy and none shows unequivocal evidence of motility. However, the apparent anterior–posterior orientation with bilateral general symmetry is almost universal among motile animals. If these forms were of low biomass and moved by ciliary traction they may not have left any trails, especially if they lived on cohesive microbial mats. They appear to have been surficial, facultatively motile, unattached and apparently were absorptive feeders and thus are put in the ‘other’ feeding category. *Kimberella* is regarded as the first bilaterian body fossil and may be a stem mollusc (Fedonkin and Waggoner 1997). If one accepts this interpretation it would have been a surficial, fully motile slow or facultatively motile unattached, grazer. Several types of trace fossils record evidence of other bilaterians. Unbranched, meandering trails and very shallow sinuous unbranched burrows occur in shallow-water facies beginning shortly after 560 Ma (Martin *et al.* 2000). Jensen (2003) interpreted the burrows as possible feeding/scavenging traces made within the sediment, but generally less than 10 mm from the sediment/water interface. Such burrowers would be shallow infauna, fully motile, slow and, because they were moving below the sediment/water interface, miners. Some surface trails are flat-bottomed with raised ridges of varied height on either side, indicating that the makers ploughed through surface sediments at different depths (Jensen 2003; Jensen *et al.* 2005). These creeping organisms were surficial to semi-infaunal, fully motile, slow, surface deposit feeders. Most other reported Neoproterozoic trace fossils are now interpreted as tubes, not trace fossils, or features formed in ways other than by animal locomotion (Jensen 2003; Jensen *et al.* 2005).

Nama assemblage. The Nama assemblage is of lower diversity than the White Sea/Ediacara assemblage (Droser *et al.* 2006), possibly because it inhabited more stressful

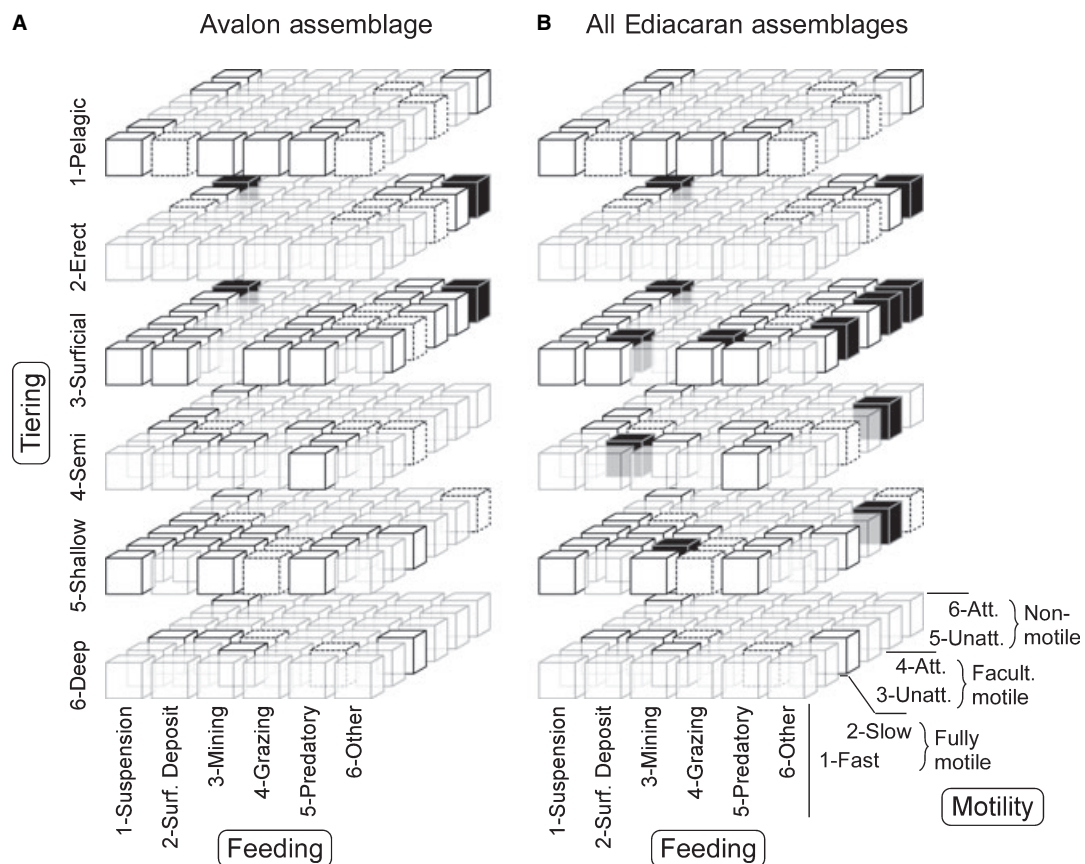
settings where the fauna had to cope with greater sedimentation rates and potential disturbance. The Nama assemblage is characterized by two unusual groups of organisms, each common in different shoal-water facies: (1) siliceous sandstones contain a suite of ‘vendobiont’-style animals (Petalonamae) and (2) thrombolite-stromatolite biohermal carbonates contain the first calcified metazoans. The ‘vendobionts’ have been interpreted as infaunal, semi-infaunal and erect. We interpret all as having other feeding (absorptive feeding). The calcified taxa include surficial and erect forms; all were non-motile, and are interpreted as suspension feeders.

General observations on realized ecospace in the Ediacaran Period

The Avalon assemblage had only four modes of life represented (Text-fig. 4A). Ten are found in the White

Sea/Ediacara assemblage, including all four Avalon modes. The Nama assemblage has five modes represented in this analysis, three of which are also represented in the White Sea/Ediacara assemblage. Overall, 12 modes of life are represented by Ediacaran-age animal remains (Text-fig. 4B). No utilized modes are pelagic and none is deep infauna. Only five modes included motility and only four represent animals that moved regularly to find food. The other eight are all suspension feeding or ‘other’ (probably absorptive) feeders. Two of the modes of life [semi-infaunal, non-motile unattached, other (absorptive feeding) and shallow infaunal, non-motile unattached, other (absorptive feeding)] suggested for Ediacaran animals were not recorded in our survey of Recent marine animals, although the possibility of their existence seemed reasonable.

Students of Neoproterozoic animals have often emphasized apparent similarities of Neoproterozoic ecosystem structure to the Recent, as if it is somewhat surprising,



TEXT-FIG. 4. Modes of life utilized in the late Neoproterozoic Ediacaran Period. Black boxes are modes of life utilized by the designated fauna. Boxes opaque white in colour and with solid black margins are modes of life not documented in the Ediacaran Period but utilized in the Recent by the taxa with readily preserved hard parts listed in Table 3B; boxes opaque white in colour and with dotted margins are modes of life not documented in the Ediacaran Period but utilized in the Recent by the taxa with a diverse fossil record listed in Table 3A. A, modes of life utilized by the Avalon assemblage. B, modes of life utilized by all taxa reported from the Ediacaran Period.

creating a sense that life had achieved 'modernity' at this early date. However, if the Ediacaran organisms were animals it is not surprising that ecological patterns similar to the Recent are detectable in even the earliest communities (Clapham *et al.* 2003). What is ecologically interesting is that Ediacaran ecosystems were so 'bare bones' simple (compare Text-figs 2 and 4). Individual Ediacaran bedding surfaces display a *maximum* of 12 taxa (Droser *et al.* 2006) whereas single bed collections of shelly fossils alone in the mid Palaeozoic have a *median* genus richness of 12.4 genera at 200 specimens, without correcting for taphonomic losses, and temperate Neogene shelly collections have twice that genus richness, with tropical single bed collections double that or more (Bush and Bambach 2004b). There are only 12 modes of animal life recorded for the entire 30-Myr interval of the fossiliferous part of the Ediacaran (Text-fig. 4). This contrasts with the 92 recorded in the Recent, 82 of which are utilized by taxa with an extensive fossil record and 62 of which are utilized by taxa with easily preserved hard parts (Text-figs 2–3). If anything, the number of modes of life noted for the Ediacaran fauna is somewhat inflated because we have included all reasonably likely modes of life one can interpret from the morphologies of Ediacaran fossils; if we have made incorrect assignments it would more likely have increased, rather than limited, the number of modes of life recorded. The simplicity of Neoproterozoic animal ecosystem structure is not surprising for communities with a limited range of morphological (and functional) complexity. The Neoproterozoic was not like modern or any later fossil ecosystems. It was ecologically very simple in structure.

ECOSPACE UTILIZATION GENERATED BY THE RADIATIONS OF THE EARLY PALAEOZOIC

There were two phases to global diversity increase in the early Palaeozoic (Sepkoski 1979, 1981). The first radiation was confined to the Early Cambrian, after which diversity fluctuated without any overall change through the rest of the Cambrian, an interval of about 25 Myr. Then, over the first 30 Myr of the Ordovician, family diversity tripled and genus diversity nearly quadrupled. The Early Cambrian evolutionary explosion brought a variety of taxa with mineralized hard parts onto the scene. Trace fossil diversity also increased, and the two great Cambrian Konservat-Lagerstätten (the Chengjiang fauna from the Early Cambrian of China and the Middle Cambrian Burgess Shale from Canada) let us see the variety of taxa that lacked mineralized hard parts. The Ordovician is characterized by diversification within many skeletonized clades, although it lacks spectacular Konservat-Lagerstätten that

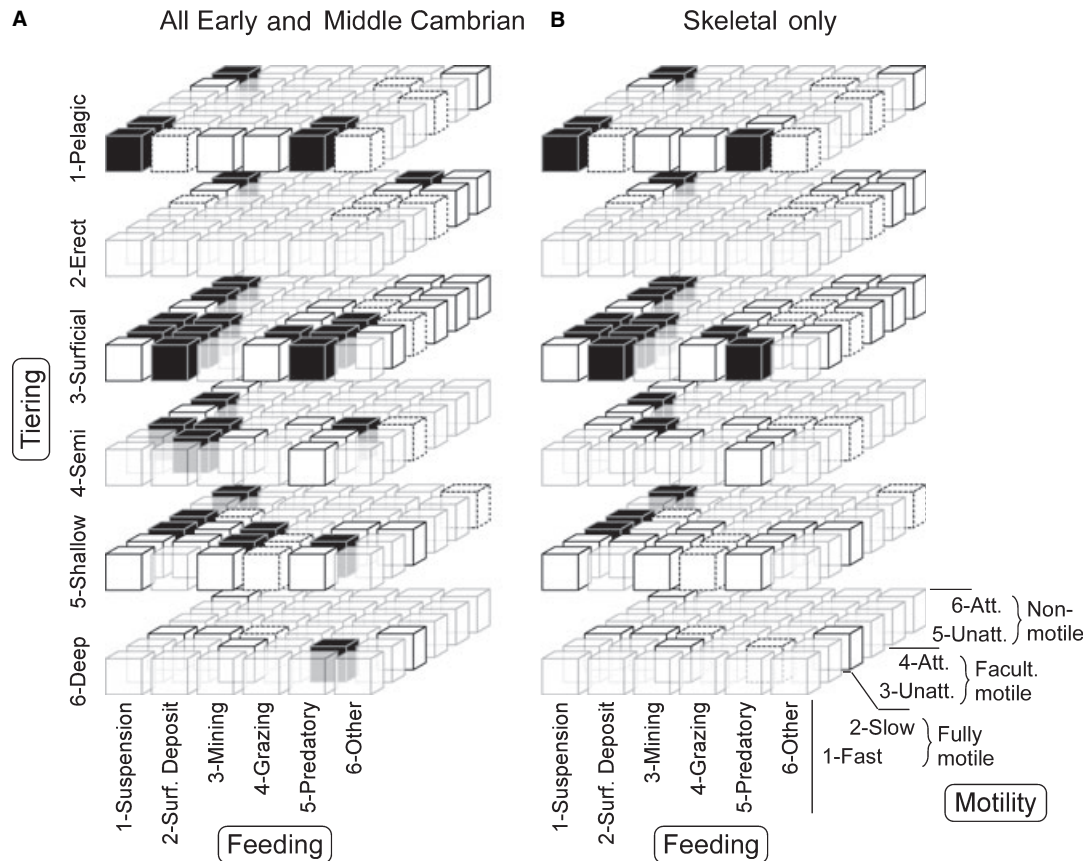
document the presumed parallel radiation of the soft-bodied fauna. Combined, the two early Palaeozoic biodiversification events produced a faunal mix that, at the class level, persisted for 200 Myr (Sepkoski 1981).

How was use of ecospace altered by these diversification events? To assess this for the Cambrian explosion, we examined the Early and Middle Cambrian marine fauna using the comprehensive review of Cambrian ecology edited by Zhuravlev and Riding (2001), supplemented by the complete descriptions of the Chengjiang and Burgess Shale faunas (Briggs *et al.* 1994; Hou *et al.* 2004) and major reviews of the Early Cambrian shelly fauna of South Australia (Bengston *et al.* 1990) and the Middle Cambrian shelly fauna of Antarctica (Wolfart 1994). We used the recent comprehensive review of the Ordovician radiation edited by Webby and others (Webby *et al.* 2004) to evaluate the range of modes of life represented in the skeletal fauna in the Late Ordovician. Because many of the groups represented in the fossil record in Cambrian and later rocks are widely familiar, we will not discuss the criteria used for assigning modes of life for most of the taxa in these faunas. Assignment of modes of life for well-understood taxa, such as brachiopods, is generally common knowledge and most other of our interpretations are drawn from discussions by the authorities who compiled the references cited and are available in those works. Lists of our assignments are given in the online file of supplementary data for this paper.

Ecospace use in the wake of the Cambrian Explosion

In aggregate, 30 different modes of life are recognized from the Early and Middle Cambrian combined (Text-fig. 5A), two and a half times the 12 documented in the Neoproterozoic, but only one-third of the 92 recorded from the Recent. Nineteen of the modes of life recorded for Early and Middle Cambrian marine animals are represented by fossils with preservable mineralized parts (Text-fig. 5B) and 11 (37 per cent) are recorded by non-mineralized animals preserved only in Konservat-Lagerstätten.

The Konservat-Lagerstätten had markedly higher numbers of modes of life preserved than either of the individual shelly faunas surveyed; 22 of the 30 Cambrian modes of life are represented in the Chengjiang fauna (Text-fig. 6A) and 18 are represented in the Burgess Shale (Text-fig. 6B). Skeletal fossils account for only seven of the 22 modes of life recorded in the Chengjiang fauna. However, seven modes of life that are represented only by animals without hard parts in the Chengjiang fauna were represented by taxa with mineralized tissues at other localities in the Early and Middle Cambrian (such as surficial fully motile slow grazers, represented only by lobopods in the Chengjiang fauna, but known from



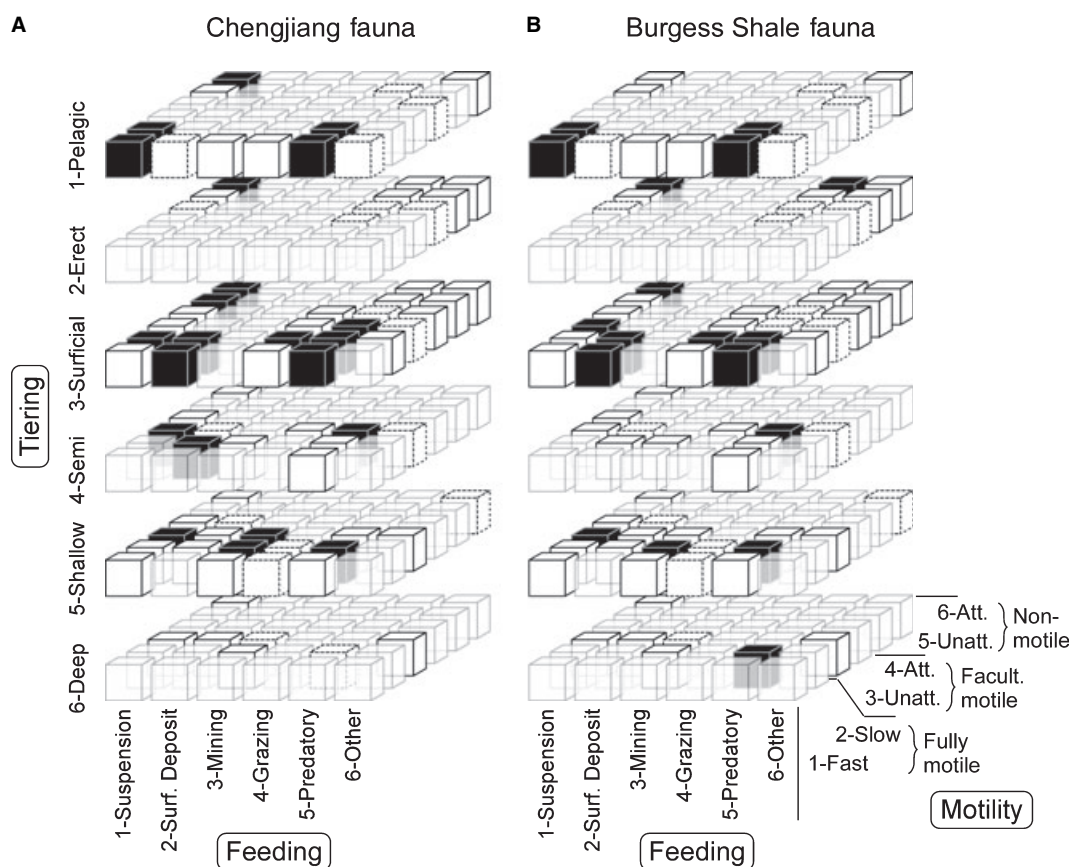
TEXT-FIG. 5. Modes of life utilized in the Early and Middle Cambrian. Black boxes are modes of life utilized by the designated fauna. Boxes opaque white in colour and with solid black margins are modes of life not documented in the Early and Middle Cambrian but utilized in the Recent by the taxa with readily preserved hard parts listed in Table 3B; boxes opaque white in colour and with dotted margins are modes of life not documented in the Early and Middle Cambrian but utilized in the Recent by the taxa with a diverse fossil record listed in Table 3A. A, all modes of life recorded for fossils in the Early and Middle Cambrian. B, modes of life recorded only for skeletal fossils in the Early and Middle Cambrian.

monoplacophorans and gastropods elsewhere). For the Burgess Shale, nine of the 18 modes of life represented are displayed by animals with skeletal parts and three modes represented only by non-skeletal organisms in the Burgess Shale are known in skeletonized organisms elsewhere. Six modes of life in the Burgess Shale fauna are only known from non-skeletonized animals and four of these modes are also recorded in the Chengjiang fauna. Taxon lists and our mode of life assessments are listed in the online file of supplementary data.

The South Australian Early Cambrian is rich in 'small shelly' fossils and 13 modes of life are recorded in that skeletonized fauna. One of the interesting things about our method for evaluating use of ecospace is that general morphological data can strongly constrain the possible modes of life of organisms with uncertain phylogenetic affinities. For example, body fossils of chancellorids in the Burgess Shale and the remarkable complete halkieriids from Greenland (Conway Morris and Peel 1995) give us

enough information to suggest reasonably that chancellorids were erect, non-motile attached, suspension feeders and halkieriids were surficial, fully motile, slow, deposit feeders or grazers. Likewise, cap-shaped shells are very likely to have been associated with surficial, fully motile, slow, surface deposit feeders or suspension feeders and the inhabitants of tubular fossils were almost necessarily either surficial or erect (depending on observable orientation), non-motile attached, suspension feeders. In this way we can gain some understanding of the modes of life of the diverse 'small shelly' fossils of the Early Cambrian without knowledge of the phylogenetic relationships of these extinct exotic forms. Many of the other Early and Middle Cambrian fossils were plesions, but often belonged to stem groups of classes rather than phyla (Budd 2003), so assessing their general modes of life is relatively straightforward.

As noted above, none of the Ediacaran fauna was pelagic or deep burrowing and few were motile. In the



TEXT-FIG. 6. Modes of life represented in Cambrian Konservat-Lagerstätten. Black boxes are modes of life utilized by the designated fauna. Boxes opaque white in colour and with solid black margins are modes of life not documented in the Early and Middle Cambrian but utilized in the Recent by the taxa with readily preserved hard parts listed in Table 3B; boxes opaque white in colour and with dotted margins are modes of life not documented in the Early and Middle Cambrian but utilized in the Recent by the taxa with a diverse fossil record listed in Table 3A. A, Chengjiang fauna. B, Burgess Shale fauna.

Cambrian some taxa occupied every tier, with deep burrowers the least represented (only one form, the priapulid *Louisella*, in the Burgess Shale). The paucity of deep burrowing in the early Palaeozoic has been observed before (Thayer 1983; Sepkoski *et al.* 1991; Orr 2001). All motility levels were now utilized, with non-motile unattached and facultatively motile attached categories the least frequently recorded motility levels. All feeding strategies were utilized, with grazing the least frequent, although the 'other' category is not directly documented in the data reviewed. This is a common problem with interpreting fossils, because parasites are seldom preserved and chemo- and photo-symbionts also seldom have definitive characteristics, although there are cases where those strategies can be inferred (e.g. Cowen 1983).

Although the Cambrian explosion produced representatives in each major ecospace category, the Cambrian ecosystem was still simple compared with the Recent. There were five, not 15, modes utilized in the pelagic tier; two, not ten, utilized in the erect tier; 11, not 25, utilized in

the surficial tier; five, not 14, utilized in the semi-infaunal tier; six, not 21, utilized in the shallow infaunal tier; and one, not seven, utilized in the deep infaunal tier. On balance, about one-third of the modes of life used in the Recent were occupied during the Early and Middle Cambrian. These differences hold up well even if the modes of life in the Recent for the 'other' feeding mechanism are omitted and only the remaining modes of life for taxa with readily preserved hard parts are tallied. Then the numbers are four, not eight, for the pelagic tier; one, not four, for the erect tier; nine, not 16, for the surficial tier, two, not eight, for the semi-infaunal tier; three, not 13, for the shallow infaunal tier; and none, not four, for the deep infaunal tier as compared with the Recent; with just 19, not 53, modes of life utilized overall, still about one-third (36 per cent) of those used in the Recent.

The ratios of Cambrian to Recent modes of life may be underestimates because of greater sampling intensity in the Recent, but we doubt this is the determining factor producing such large differences. This is particularly true

for skeletal faunas, for which global Cambrian sample sizes are, in fact, quite large. It may be somewhat of a factor for the soft-bodied faunas, for which only two Cambrian biotas are available. However, these biotas are quite diverse, well preserved and have been extensively investigated. Evidence from sedimentary fabric analyses, cited above, also indicates that infaunal ecospace occupation was much reduced in the early Palaeozoic. The parallel trends between the skeletal and total faunas also suggest that we are not missing a large number of modes of life.

Ecospace utilization by the shelly fauna in the wake of the Ordovician Radiation

Because there are no Konservat-Lagerstätten in the Ordovician comparable with the Chengjiang or Burgess Shale in the Cambrian, our survey of Ordovician modes of life is restricted to organisms with mineralized parts. The lack of soft-part preservation may relate in part to chance, but increased oceanic oxygenation and changes in ocean circulation, plus sediment disturbance in hypoxic settings from the diversification of burrowing organisms in Ordovician sediments (Orr 2001; Mángano and Droser 2004) probably also closed a taphonomic window, limiting the likelihood of forming such deposits. Thus, comparisons of the Ordovician with the Cambrian and the Recent are made only with respect to the skeletal portion of those faunas.

In the Late Ordovician, skeletal organisms utilized 30 different modes of life (Text-fig. 7A). Only three modes of life utilized by skeletal animals in the Early and Middle Cambrian are not recorded from the Late Ordovician. In one case (pelagic, non-motile attached, suspension feeding), a Cambrian brachiopod was identified specifically as having an epiplanktic mode of life, but that claim was not found for any animal in the resources surveyed for the Ordovician. Such forms may well have existed in the Late Ordovician. Similar interpretive choices may also be involved with the other two 'missing' Cambrian modes. However, the 14 modes seen in Late Ordovician fossils not recorded by skeletal forms in the Early and Middle Cambrian illustrate the sharp increase in ecological complexity brought about by the Ordovician Radiation. In effect, the skeletal Late Ordovician fauna displays more than half again the diversity of modes of life seen in the Early and Middle Cambrian skeletal fauna. Although there are four modes of life of soft-bodied Early and Middle Cambrian taxa not recorded by skeletal Late Ordovician forms, eight of the 14 modes of life added in the Ordovician for the skeletal portion of the fauna are not represented by soft-bodied Cambrian forms, further supporting the point that increased ecological complexity had accumulated by the end of the Ordovician radiation.

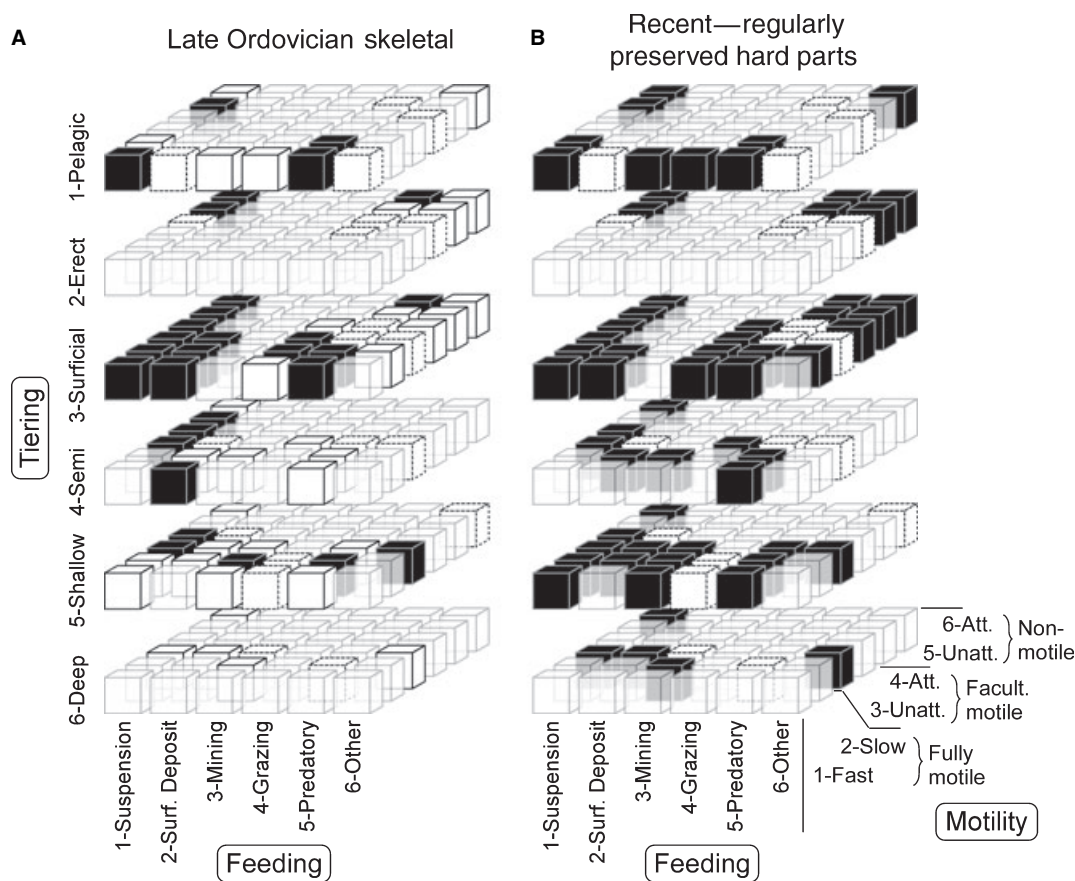
The increase between the Middle Cambrian and Late Ordovician from 19 to 30 (or possibly a few more) modes of life represented by skeletal marine animals is not the end of the story. Evolution from the end of the Ordovician to the late Cainozoic again doubled the number of modes of life utilized by the marine fauna. Sixty-two modes of life are distributed among the living marine fauna characterized by readily preserved hard parts and 82 are recorded for the group of living taxa that have a rich and diverse fossil record (Text-figs 3, 7B).

RADIATIONS AND THE FILLING OF MARINE ECOSPACE

Text-figure 8 summarizes the secular trends in ecospace filling documented in this paper. The number of utilized modes of life approximately triples between the late Ediacaran and the Early–Middle Cambrian when one looks at all modes (12–30) and the increase is more dramatic for modes represented by animals with hard parts (2–19). Between the Cambrian and the Recent the number of modes of life triples again, whether one looks at all modes (30–92, or 82 for just the groups with an extensive fossil record) or only those modes utilized by animals with easily preserved hard parts (19–62).

We remind the reader that these data are the sum of all modes of life recorded during particular intervals. In the case of the Ediacaran, ecological diversity undoubtedly increased during the interval, but available data do not permit us to track the path of change through time in detail. However, the likely increase is suggested by the presence of only four modes of life in the earliest preserved assemblages and a total of 12 for the Ediacaran as a whole, when younger faunas are included. Likewise, our data for the Early and Middle Cambrian sum all noted modes of life recorded from that 40-myr interval. Many studies have documented the increase in diversity of skeletal taxa from the start of the Nemakit-Daldynian to the Botomian in the Early Cambrian and further evolutionary diversification and turnover occurs during the Middle Cambrian as well. Therefore, our data do not follow the temporal course of evolution of new modes of life as the marine fauna evolved but account for the total number of modes produced during the 'Cambrian explosion'. Similarly, we have not followed the course of change from the late Ediacaran into the Cambrian. What we show is that three times the number of modes of life present in the entire Ediacaran had accumulated during the Cambrian radiation.

In a similar vein, the Late Ordovician data illustrate the degree of ecospace filling after the 40-myr-long Early and Middle Ordovician radiation. Our data do not follow the course of change from the structure of the Middle



TEXT-FIG. 7. Modes of life utilized by skeletal fossils in the Late Ordovician contrasted with those utilized in the Recent by taxa with regularly preserved mineralized hard parts. A, modes of life represented in the Late Ordovician. Black boxes are modes of life utilized by the designated fauna. Boxes opaque white in colour and with solid black margins are modes of life not documented in the Late Ordovician but utilized in the Recent by the taxa with readily preserved hard parts listed in Table 3B; boxes opaque white in colour and with dotted margins are modes of life not documented in the Late Ordovician but utilized in the Recent by the taxa with a diverse fossil record listed in Table 3A. B, modes of life utilized in the Recent by the groups with regularly preserved mineralized tissues listed in Table 2. Symbols as in Text-figure 3B.

Cambrian fauna to the Late Ordovician; they just demonstrate that the number of modes of life of the skeletal fauna had increased by approximately 50 per cent by the end of the Ordovician radiation. Similarly, we do not follow the course of ecospace change during the rest of the Palaeozoic, the Mesozoic or the Cainozoic, but document that by the Recent the number of modes of life had doubled yet again.

The data indicate that the increase in ecospace use was driven by expansions in both the skeletal and the non-skeletal faunas. If the increase in the number of modes of life had resulted predominantly from the addition of skeletal forms to formerly non-skeletal groups or just from the evolution of new skeletal forms, the proportion of modes of life represented by skeletal taxa compared with all modes should have increased markedly. However, the proportion of modes represented by skeletal taxa does not change (63 per cent in the Early and Middle Cambrian,

62 per cent in the Recent), although the number of modes of life triples. Changes in the depth and rate of bioturbation through the Phanerozoic (Thayer 1983; Sepkoski *et al.* 1991; Orr 2001) also suggest considerable change in the soft-bodied infauna over time. Increases in diversity of less readily preserved taxa, such as arthropods and fish, also support the contention that the increase in modes of life seen in the fauna with readily preserved hard parts is occurring in the fauna as a whole.

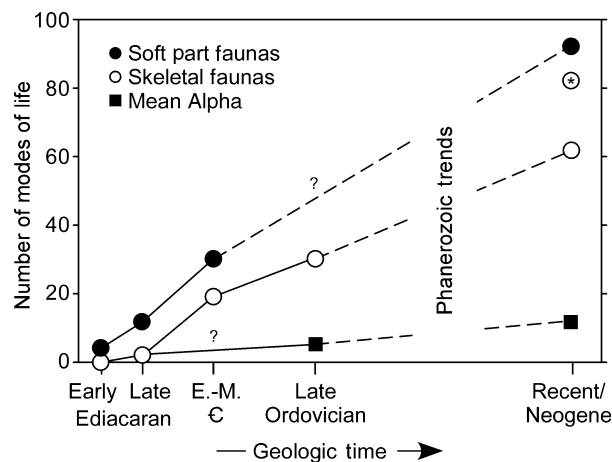
As demonstrated in the work that inspired us to attempt this global study, the number of modes of life represented in individual local fossil assemblages also increased between the middle Palaeozoic (Late Ordovician–Middle Devonian) and the Neogene (Text-fig. 8, lower curve) (Bush and Bambach 2004a; Bush 2005; Bush *et al.* in prep.). In a major application of the ecospace concept, Bush (2005) and Bush and others (Bush and Bambach 2004a; Bush *et al.* in prep.) link this increase to

an observed increase in alpha diversity, echoing the arguments of Bambach (1983) based on guild analysis.

We can now say that the full range of modes of life did not evolve early in the history of life, with subsequent diversity increases accommodated by species packing within established modes of life. Instead, on a global scale, increased diversity has been accompanied by the increased use of ecospace (addition of modes of life). In fact, new modes of life have accumulated throughout the Phanerozoic in parallel to the apparent increase in global marine diversity. Ecosystem structure has changed between or during each of our temporal bins. In Hutchinson's terms, the evolutionary play keeps modifying the ecological theatre.

Beyond counting: shifts in the ecological importance of modes of life

In this paper, we have restricted ourselves to an analysis of the number of modes of life present at different stages of metazoan evolution. The coarseness of the data, both temporally and spatially, do not permit us to reach detailed conclusions about the causes of change or the temporal sequence in which they occurred, but some general patterns may already hint at potential explanations. For example, much of the promise of this method for palaeobiological theory lies in documenting shifts in the abundance or relative abundance of ecological types, rather than just a change in their presence. For example,



TEXT-FIG. 8. Change through time in realized ecospace. Top line represents all recorded modes of life, middle line represents modes of life of skeletal fauna only; bottom line records mean number of modes of life for single assemblages (from Bush *et al.* in prep.). For the Recent, the open circle represents those recent taxa with readily preserved hard parts, and the open circle containing an asterisk represents those taxa with a diverse fossil record.

in an initial demonstration using middle Palaeozoic and Neogene fossil assemblages, Bush *et al.* (in press) documented drastic shifts in importance of various modes of life within palaeocommunities, as evaluated by the relative abundance of specimens in fossil assemblages. Motility, infaunalization and predation all increased in relative abundance within palaeocommunities between the Palaeozoic and Neogene. Madin *et al.* (2006) also reported similar trends on a global basis.

Stanley (1974, 1977) pioneered the argument for the ecological impact of predators in macroevolution and Vermeij (1977) focused attention on the 'Mesozoic Marine Revolution' by documenting increases in shell robustness, increased evidence of predatory attack (shell drilling and the like), increased infaunalization, and a decrease in diversity of sessile animals incapable of reattaching when disturbed, paralleling many of Stanley's points. Aberhan *et al.* (2006) traced the development of similar patterns during the Jurassic. Stanley and Vermeij both suggested that these changes were coevolutionary responses to increased predation pressure and Vermeij later generalized these ideas in his theory of escalation (Vermeij 1987). Kowalewski *et al.* (1998) have further documented the increase in frequency of shell drilling predation in the Mesozoic and Cainozoic.

However, the potential effect of predators on the marine fauna was not restricted to the Mesozoic–Cainozoic. Predators have increased in diversity and/or abundance in the marine fauna five separate times during the Phanerozoic (Bambach 1999, 2002): in (1) the Cambrian 'explosion', (2) the Ordovician Radiation, (3) the Devonian turnover in dominant marine taxa, (4) the Triassic and (5) the Late Cretaceous and early Cainozoic. Prior to the Cambrian radiation there is no unambiguous evidence of animal predation; the few apparent boreholes in *Clouidina* cannot be demonstrated to have occurred while the tube was occupied. By contrast, predatory trilobites and a variety of unambiguously predatory stem arthropods, such as *Anomalocaris*, appeared by the Middle Cambrian. Cephalopods, which first appeared in the Late Cambrian, starfish and eurypterids are among the predatory groups that diversified in the Ordovician radiation, even as predatory trilobites persisted. During the Devonian, jawed fish and ammonoids joined the ranks of predators. In the Triassic, marine reptiles appeared, and the proportion of global diversity represented by predators increased from the Palaeozoic average of 15 per cent to an average of 24 per cent for the rest of the Mesozoic (Bambach *et al.* 2002). In the Cretaceous, shell drilling increased and caenogastropods, brachyuran crabs and teleost fish began to diversify. During the Palaeogene recovery from the end-Cretaceous mass extinction, the average proportion of predators increased from its Mesozoic average of 24 per cent to 36 per cent of global diversity, where it remained

during the Neogene (Bambach 2002; Bambach *et al.* 2002).

This pattern of increase in predators is supported by observed changes in global ecospace utilization. We find no predatory modes of life recorded in the Ediacaran, nine occur in the Early and Middle Cambrian, and there are 21 in the Recent, with 20 recorded for taxa with a diverse and extensive fossil record (Text-figs 2, 3A). For skeletal taxa only two predatory modes have been recorded for the Early and Middle Cambrian, seven are present in the Late Ordovician and 13 predatory modes of life are utilized in the modern skeletal fauna. Clearly, predators have expanded their ecological range over time.

A conclusion of Bush *et al.* (in press) is that the increase in predation may have been a passive (undriven) trend, but that the increases in motility and infaunalization of suspension feeders appear to have been driven, possibly in large part, by increased predation pressure. If the source of the driven trends for motility and infaunalization was predation pressure, then a link between timing of changes in predatory disturbance and ecospace use should exist.

Increased infaunalization has also influenced the way organisms function in benthic settings. The depth and intensity of bioturbation have increased over time (Thayer 1983; Sepkoski *et al.* 1991) and this has forced benthic forms to adjust to increased levels of disturbance. Transitions seem to have occurred in (1) the Early Cambrian, with the expansion of diversity of trace fossils (Jensen 2003); (2) the Late Cambrian–Late Ordovician, with a further expansion of trace fossil activity and diversity (Orr 2003; Mángano and Droser 2004); (3) during the Devonian, extending into the Carboniferous (Bambach 1985, 1999; Bottjer and Ausich 1986); and (4) from the Jurassic through the Cenozoic, illustrated by the diversification of siphonate bivalves (Stanley 1968) and irregular echinoids (Smith 1984). The intensity of disturbance in the Recent from burrowers is suggested by the experiment of Clifton (1971) in which uniformly orientated sets of valves of bivalves placed on the sea-floor and undisturbed by currents become randomly orientated with up to half the shells buried in a 40-day period. Labarbara (1981) has noted that disturbance from crabs is sufficiently intense in the Recent that unattached reclining oysters, such as *Gryphaea* and *Exogyra*, which were common in the Mesozoic, probably could not survive on the modern sea-floor.

CONCLUSIONS

At the global scale, both the skeletal fauna and the total fauna occupied progressively more modes of life in each of the four intervals examined that span the Ediacaran and Phanerozoic (Text-fig. 8). Ecological variety and

complexity emerged during the Phanerozoic as specialized morphologies and functions evolved. On average, the total and skeletal faunas approximately tripled in ecospace use between the Late Ediacaran and end of the Early–Middle Cambrian and between the Early–Middle Cambrian and Recent (Text-fig. 8).

Ecosystems became more complex over time as the number of modes of life (in effect the number of major autecological categories) increased. This is true globally, as noted above, and it is also true at the community level (Text-fig. 8, lower curve; Bush *et al.* in prep). Knowing that the realized use of ecospace has increased over time and that the importance of different modes of life has changed as well (Bush *et al.* in press), two major questions in evolutionary palaeoecology arise: when did these transitions in ecospace utilization occur, and why? Detailed analyses of carefully collected and quantitatively evaluated assemblages are still needed if we are to establish the trajectory of the change in ecospace use at the local (community) level. Regional patterns also need to be documented, as it is known that patterns of diversification vary from place to place during events such as the Ordovician Radiation (Miller and Mao 1998). Thus, it also seems likely that ecosystem change was not globally uniform.

However, simply knowing that changes in realized ecospace occurred between the Ediacaran, Early–Middle Cambrian, Late Ordovician and Recent, with the additional knowledge cited in the previous section, we would predict that gradients of reorganization of ecospace use in marine communities occurred (1) during the Ediacaran, (2) in the Early Cambrian (Nemakit–Daldynian–Botomian) and (3) from the start of the Late Cambrian through the Early Caradoc in the Late Ordovician. For the rest of the Phanerozoic, we know that (4) the Middle Devonian–Early Carboniferous also saw major change in dominant taxa, (5) recovery from the end-Permian extinction during the Triassic and through the Mesozoic saw the diversification of many new groups such as siphonate bivalves, caenogastropods, brachyurans, infaunal echinoids and teleost fish, and (6) diversification of the modern fauna took place during the Cenozoic. It would be interesting to know if there is a shift in basic use of ecospace accompanying these transitions (as suggested for the Devonian by Signor and Brett 1984 and for the Devonian and Mesozoic–Cenozoic by Bambach 1999). It is also an open question whether ecosystem structure changed during times of taxonomic stability. Was there much change during the Middle Cambrian when taxonomic turnover was very high but little change occurred in the standing diversity of dominant groups? How does Late Ordovician ecospace use compare with that in the Early Devonian? Was there much change from the middle of the Early Carboniferous to the Middle Permian as climates changed from greenhouse to icehouse and back again? How similar (or

different) were the Middle Jurassic and Early Cretaceous? The work of Aberhan *et al.* (2006) indicates that they should be different. And, finally, did the Pliocene differ from the Eocene?

These questions need to be examined quantitatively as well as qualitatively. We need to evaluate large samples with abundance data so that we can determine whether the importance of modes of life changed, possibly even when the variety of modes of life did not. Reef ecosystems, abyssal ecosystems and terrestrial ecosystems may have had different times of structural change and need to be examined in detail as well.

All modes of life are not equal. Some are apparently excluded because of physical difficulties or problems of efficiency. Others may be exploited only in a limited number of ways, or provide only limited access to critical resources and are utilized by few taxa. But because modes of life are not defined on the basis of resources, no *a priori* competitive exclusion is involved and taxon packing can and did occur within some modes of life as taxonomic diversity increased. However, incentives to invade new modes of life could forge links between taxonomic diversity and ecospace use. Unused resources (or increasing availability of resources) in an unoccupied mode of life would enhance the success of early pioneers in that mode. In addition, increasing taxonomic diversity would provide more chances for the adaptations needed for the invasion of unoccupied ecospace to arise (a style of increase in ecospace use by passive diffusion). Likewise, no mode of life provides unlimited access to all critical resources. As packing within a mode of life increased the benefit for cost ratio for invading less crowded ecospace would become more favourable (a style of driven change). In similar fashion, some modes of life would provide opportunities to avoid dangers that might arise in others. For example, the rise of predation, mentioned above, would have been a driving force to invade infaunal or motile modes. Therefore, a correlation between taxonomic diversity and ecospace use is expected.

We have described the end points of change in utilization of ecospace and a few critical points at different spatial scales along the way. Now we need to compile the data to reveal the detailed narrative of change in use of ecospace over time. Ultimately, however, we are interested in the processes that underlie these changing patterns of ecospace utilization. Ecology and evolution are often thought of as separate fields of study. However, all evolution occurs in some ecological context and, as we have shown, much of the critical evolutionary history of the metazoa occurred in ecological contexts different (and simpler) from those of today. The evolutionary play is not only staged in the ecological theatre (Hutchinson 1965); the ecological theatre itself evolves. Ecospace, as defined in this paper, gives us a theoretical construct in which to track

ecosystem change and attempt to answer not just what changed and when, but, how, why and to what effect.

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