

Trilobites

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The taxonomic diversity history of Ordovician trilobites has been explored on a broad global scale by Adrain et al. (1998), who provided an estimate based on a fourfold division of Ordovician time. Adrain and Westrop (2000) subsequently published a trilobite diversity curve based on nine Ordovician and five Early Silurian sampling intervals, and the pattern of trilobite alpha (within-habitat) diversity during the Ordovician has been documented by Westrop and Adrain (1998) and Adrain et al. (2000). The nature of the Ordovician radiation of trilobites is further characterized herein, through a new global analysis at finer resolution and by documenting geographic and environmental patterns in the data. Regional diversity curves are presented and discussed for Australasia, South America, Avalonia, Baltica, and South China, reflecting a spectrum of tectonic and paleogeographic settings through the Ordovician. Finally, the development of trilobite biofacies through the period is assessed in the context of the global and regional patterns of biodiversity change.

■ Global Patterns (JMA, SRW, RAF)

The Data Set

Data on the taxonomy and temporal and geographic distribution of Ordovician and Silurian trilobites have been compiled by J. M. Adrain beginning in 1997. In their assessment of post-Cambrian trilo-

bite diversity and evolutionary faunas, Adrain et al. (1998) used a database of 1,241 recorded genera, of which they accepted 945 as meaningful taxa—842 are Ordovician genera. At that stage, it was possible to present data only at a relatively coarse series-level resolution.

In order to achieve further insight, the resolution of the data set needed to be increased. Effectively, this required that (1) a workable set of intervals be developed that could be applied with a minimum of uncertainty to data from all parts of the world and (2) the data set be extended to species level in order to document genus ranges and geographic occurrence accurately through time. The sampling intervals chosen (see Adrain and Westrop 2000: note 30) were a necessary compromise between the high precision available from some paleocontinents (e.g., Laurentia, Baltica, Australasia, Avalonia, and parts of Gondwana) and the sometimes very coarse resolution in others (e.g., Siberia, the central Asian terranes, and much of South America). One alternative was to adopt a highly resolved scheme and then deal with less-resolved data according to an error distribution formula (the procedure used by Sepkoski 1986; see also Sepkoski and Koch 1996 as a result of dependence on secondary data sources). Although such a system is reasonable for a combined global diversity estimate, it does not allow effective comparison of geographic regions by time interval. We therefore

adopted a system in which data had a direct empirical assignment to a sampling bin, despite the limitations imposed by poorly sampled regions. The result is a ninefold division of Ordovician time, based on major correlative biohorizons identified by Webby (1995, 1998), corresponding approximately to the level of stage or subseries. In terms of the 19 time slices (*TS*) adopted for this book, our intervals are less well resolved but at least directly match particular time-slice boundaries. Relationship of the intervals is as follows: O1 = (*TS*.1a, 1b); O2 = (*TS*.1c, 1d); O3 = (*TS*.2a, 2b, 2c); O4 = (*TS*.3a, 3b); O5 = (*TS*.4a, 4b, 4c); O6 = (*TS*.5a); O7 = (*TS*.5b, 5c); O8 = (*TS*.5d); O9 = (*TS*.6a, 6b, 6c).

Compilation to the species level is now well advanced. Earliest and latest occurrences have been documented, and there is now considerable confidence in the genus ranges. Overall, the species compilation is sufficiently complete for preliminary analysis, and species data are used to document the latitudinal distribution of families later in this chapter. By 2000, the number of genera recorded had risen to 1383, with 994 accepted. Because about two-thirds of the added names were synonyms or *dubia* taken from more obscure primary literature, the effective database had increased in size by only 5.7 percent. This is the database analyzed in the present work. A small number of accepted new genera of Ordovician trilobites that were published in 2000 and 2001 are excluded from the present work in favor of concordance with the database used by Adrain and Westrop (2000).

Changes in the data set since 1998 include some taxonomic reassignment. Bathyrurids and bathyurelids were united in a family Bathyruridae in 1998 but are considered separate families for purposes of this analysis. A family Panderiidae was recognized in 1998, but the group is considered a subfamily of Bathyurellidae in the present data set.

The current global trilobite diversity curve based on these data is shown in figure 24.1. A listing of taxa, synonyms, and stratigraphic ranges of the genus data set is available on request from J. M. Adrain.

A New Global Analysis

The main conclusion of Adrain et al. (1998) was that a significant portion of post-Cambrian trilobites experienced rapid diversification during the Ordovi-

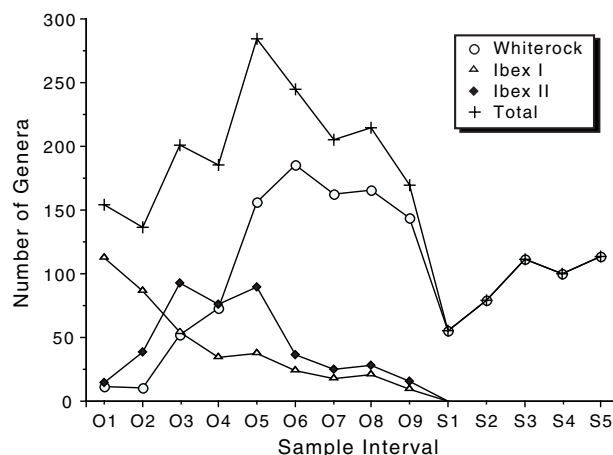


FIGURE 24.1. Ordovician and Early Silurian trilobite genus diversity. Whiterock, Ibex I, and Ibex II are evolutionary faunas defined by hierarchical cluster analysis (see figure 24.2). Sample intervals are as defined by Adrain and Westrop (2000:112, note 30). It should be noted that sample intervals O1–O3, O4–O5, and O6–O9 are equivalent to the tripartite Ordovician division, respectively, Lower (or Early), Middle (or Mid), and Upper (or Late) Ordovician, used in this volume. Intervals O1 and O5 also correlate with global Stages Tremadocian and Darriwilian, respectively.

cian Radiation in a fashion nearly identical to that of Sepkoski's (1981a) Paleozoic Evolutionary Fauna. The terms "Ibex Fauna" and "Whiterock Fauna" were introduced. The former comprised a cohort of families that peaked early, declined, and were eradicated before or during the end Ordovician mass extinction; the latter had low Early Ordovician diversity, diversified during the Ordovician Radiation, and contained all families that survived the end Ordovician mass extinction (a group termed the "Silurian Fauna").

Even though the fourfold division used by Adrain et al. (1998) clearly documented major unrecognized features of the trilobite record—Mid Ordovician diversification and its link to end Ordovician survival—a more stratigraphically resolved analysis of the current data set is desirable to test the cohesiveness of the new evolutionary faunas (essentially to see if they break down into discrete components) and better refine the timing of diversification events.

The analysis was carried out using the same protocols. Families were grouped according to similarity in their genus diversity through the Ordovician sampling intervals. Silurian data were not used in the analysis. At this increased level of resolution, the data

became subject to edge effects. In particular, there were eight families with single occurrences (in some cases of a single specimen) in the earliest part of O1. These taxa essentially have no Ordovician history but, when admitted to the analysis, cluster together with 100 percent similarity and exert undue influence on the pattern of similarity of the remaining (interesting) taxa that have a genuine Ordovician history. These “singleton” taxa (“Dokimokephalidae,” Idahoiidae, Lichakephalidae, Nepeidae, Norwoodiidae, Papyriaspidae, Plethopeltidae, and Solenopleuridae), restricted in occurrence to O1, were therefore excluded from the analysis.

The results of the cluster analysis are shown in figure 24.2. The main features are as follows:

1. The Ibex Fauna includes two distinct clusters with different diversity trajectories (see figure 24.1) during the O1–O3 intervals (lumped together as the Ibexian by Adrain et al. 1998). One group, termed “Ibex Fauna I,” had high O1 diversity but steadily declined afterward. The Olenidae and Ceratopygidae are typical of this fauna. A second group, termed “Ibex Fauna II,” had very low O1 diversity but radiated rapidly during O2, peaked during O3, and declined after O5. The Asaphidae and Bathyruridae are typical families of this fauna.

2. The Whiterock Fauna composition remains almost exactly as described in 1998, though there is a small amount of changed membership. The low-diversity families Dionididae and Bohemillidae, which had clustered with the Whiterock Fauna in the four-interval analysis, now move to Ibex Fauna II. Isocolidae, which had clustered with the Ibex Fauna, and Harpetidae, the sole unclustered family, both now move to the Whiterock Fauna. Twenty-two of 24 families are common to the 1998 and present versions of the Whiterock Fauna.

3. With increased stratigraphic resolution, it is evident that some Whiterock Fauna families began to radiate during the O3 interval (e.g., Trinucleidae, Raphiophoridae, Cyclopygidae), whereas others began to radiate during the early Whiterockian O4 (e.g., Illaenidae, Encrinuridae, Odontopleuridae). There is a strong geographic component to this distinction, which is discussed later in this chapter.

4. The two most surprising results in the analysis of Adrain et al. (1998) are confirmed. First, the

Whiterock Fauna—the majority of post-Cambrian trilobites—experienced an Ordovician radiation (figure 24.1) much like that of the Paleozoic Evolutionary Fauna. Second, Ordovician diversity history remains an extremely accurate predictor of end Ordovician fate. All families of both Ibex Fauna I and Ibex Fauna II became extinct either before or during the end Ordovician mass extinction, whereas 18 of 26 Whiterock Fauna families survived into the Silurian. There is a strong geographic component to this Whiterock Fauna survivorship, also discussed later herein.

Trilobite Radiation by Realm

Modern work on global Ordovician trilobite biogeography (using cladistic methods to search for common historical signals as opposed to phenetic methods to compare taxonomic lists) has not been attempted and is sorely needed. The best estimate of global pattern around the time of the radiation remains Whittington and Hughes’s (1972) classic quantitative study of taxic distribution, which used multidimensional scaling in the first comprehensive attempt to define major biogeographic areas in the Early Ordovician. Their analysis has largely been supported by subsequent work (Ross 1975; Fortey and Morris 1982; Cocks and Fortey 1982, 1988; Neuman 1984; Fortey and Cocks 1986, 1992; Fortey et al. 1989; Fortey and Mellish 1992), with the main additions being attention to the concept of biofacies and accounting for the effects of levels of endemism varying with environment. Current concepts of broad area relationships during the Early Ordovician have been summarized by Cocks and Fortey (1990). The level of precision in well-studied areas such as eastern Avalonia and western Baltica is now high, though data remain sparse in many other parts of the world. Nevertheless, it is clear that during the time of the radiation, trilobites occupied at least four distinct biogeographic realms (figure 24.3).

An equatorial Bathyrurid Realm (Bathyrurid Province of Whittington and Hughes 1972) includes Laurentia and Siberia/Kolyma and possibly parts of Kazakhstan (as far as is known; see Apollonov 1975 for summary) and North China (Zhou and Fortey 1986). Data adequate for quantitative analysis have been compiled only for Laurentia. The most characteristic pre-radiation faunal elements are the endemic bathyrurids

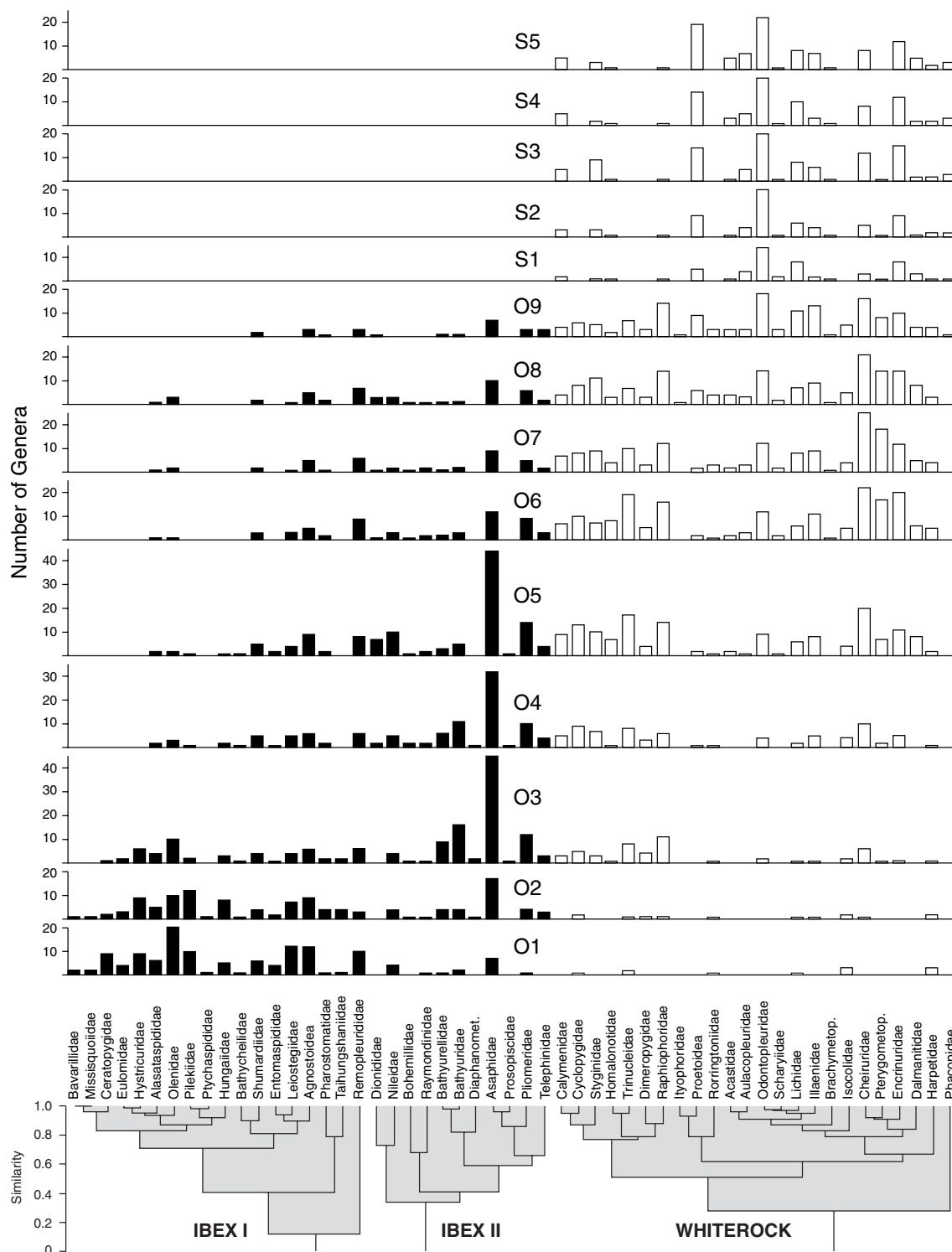


FIGURE 24.2. Cluster analysis of Ordovician trilobite families, with plots of their diversity through time. Clustering was based on Ordovician diversity only (intervals O1–O9). Taxa were clustered using as variables the number of genera in each of the nine Ordovician biostratigraphic intervals. The Pearson product-moment correlation coefficient was used as the index of similarity, and the clusters were formed using the average linkage method.

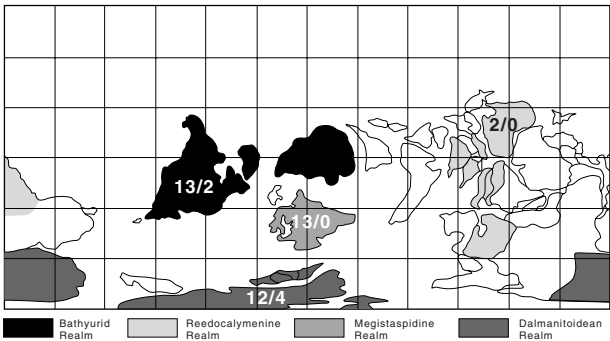


FIGURE 24.3. Four biogeographic realms during the time of the Ordovician Radiation, as defined by Whittington and Hughes (1972). Kazakhstan and North China are left unshaded because their affinities are not definite, but they may belong to the Bathyrurid Realm. Numbers indicate the number of Whiterock Fauna clades occurring in the realm at the time of the radiation and the number endemic to that realm (see table 24.1).

and cybelopsine pliomerids, though other taxa, such as dimeropygids and hystericurids, have their distributions concentrated in this realm (e.g., Ross 1951; Hintze 1953; Whittington 1963, 1965; Fortey 1979, 1980; Adrain and Fortey 1997). Thirteen major Whiterock Fauna clades were present in the Bathyrurid Realm (table 24.1) at the time of onset of the Ordovician Radiation, of which two were endemic.

A southern midlatitude Megistaspidine Realm occupies Baltica (Asaphid Province of Whittington and Hughes 1972) and is marked by a striking endemic

radiation of megistaspidine asaphids (Jaanusson 1953a, 1953b, 1956; Tjernvik 1956; Tjernvik and Johansson 1980; Nielsen 1995). Other elements of Baltic Arenig/Llanvirn faunas are shared with Laurentia (*Celmus*, *Nileus*, *Raymondaspis*, *Illaeus*), with which there are clearly the strongest faunal ties. Thirteen major Whiterock Fauna clades were present in the Megistaspidine Realm at the onset of radiation (table 24.1), but none were endemic to the realm.

A temperate southern Dalmanitoidean Realm (*Selenopeltis* Province of Whittington and Hughes 1972) includes Avalonia and parts of Gondwana (e.g., Armorica, Perunica, present-day North Africa). In keeping with its high-latitude position, this area has the fewest links with the other major realms and is dominated by cyclopygids, ogygiocarinine asaphids, trinucleids, reedocalymenine calymenids, and early dalmanitids (e.g., Hammann 1974, 1983; Fortey and Owens 1978, 1987; Henry 1980; Rabano 1990). Twelve major Whiterock Fauna clades were present in the Dalmanitoidean Realm at the onset of radiation (table 24.1), of which four were endemic.

A Reedocalymenine Realm also has tropical/equatorial distribution and comprises part of Gondwana, including South China, Australia, and much of South America (Asaphopsis Province of Whittington and Hughes 1972). The Hungaiidae (= Dikelocephalinidae; see Ludvigsen and Westrop in Ludvigsen et al. 1989 for discussion) is restricted to this

TABLE 24.1. Distribution by Faunal Realm of Whiterock Fauna Families and Subfamilies During the Onset of the Ordovician Radiation (intervals O3 and O4)

<i>Taxon</i>	<i>Bathyrurid</i>	<i>Megistaspidine</i>	<i>Dalmanitoidean</i>	<i>Reedocalymenine</i>
Calymenidae:				
Calymeninae	✓	✓	✓	
Colpocorpyinae			✓	
Reedocalymeninae			✓	
Cheiruridae	✓	✓	✓	
Cyclopygidae		✓	✓	
Dalmanitidae			✓	
Dimeropygidae	✓	✓		
Encrinuridae	✓	✓		
Homalonotidae			✓	
Illaeidae	✓	✓	✓	✓
Isocolidae	✓	✓	✓	
Lichidae	✓	✓		
Odontopleuridae:				
Ceratopcephalinae	✓			
Selenopeltinae	✓	✓	✓	
Proetoidea	✓			
Pterygomotopidae	✓	✓		
Raphiophoridae	✓	✓	✓	✓
Styginidae	✓	✓		
Trinucleidae		✓	✓	

realm during the Arenig. Benthic platform faunas are highly endemic (e.g., Harrington and Leanza 1957; Fortey and Shergold 1984; Jell and Stait 1985b; Laurie and Shergold 1996a, 1996b). Pelagic telephinids, however (Cocks and Fortey 1990: figure 3), are shared with equatorial Laurentia and may be difficult to distinguish between continents even at the species level (Fortey 1975b; McCormick and Fortey 1999). Strikingly, only two Whiterock Fauna families, Raphiophoridae and Illaenidae, were present in the Reedocalymenine Realm during the onset of radiation. These are also the only two Whiterock Fauna groups with a global, fully cosmopolitan distribution during this time.

There is therefore, for reasons thus far unknown, no evidence for a significant Ordovician radiation of trilobites in the Reedocalymenine Realm, and it was not until considerably after the radiation elsewhere (Edgecombe, Webby and Laurie, later in this chapter) that many Whiterock Fauna groups appeared in Australia. We therefore exclude this realm from consideration and concentrate on latitudinal patterns between the remaining three, which were positioned at low, intermediate, and high latitudes at the time of the radiation.

High- versus Low-Latitude Radiation and End Ordovician Extinction

Trilobites are an exemplar taxon for groups hard hit by the end Ordovician mass extinction. By all estimates, including our own (figure 24.1), trilobites lost around half of their global taxic diversity during the event. The question of selectivity at a major mass extinction is always of interest. Are extinguished groups related, and different from survivors, in some particular trait or pattern? Chatterton and Speyer (1989), for example, claimed that the larvae of some trilobites were benthic, whereas others were pelagic, and that groups with the latter suffered greater extinction. Adrain et al. (1998) related extinction propensity to clade size, showing that the end Ordovician event preferentially removed clades whose latest Ordovician genus diversity was low. Is there any geographic component to end Ordovician extinction patterns?

For Ordovician trilobites, geographic patterns are masked by a burst of cosmopolitanism during the

TABLE 24.2. Latitudinal Distribution of Whiterock Fauna Families and Subfamilies During the Time of the Radiation Contrasted with End Ordovician Fate

<i>Taxon</i>	<i>Early Distribution^a</i>			<i>End Ordovician</i>
	<i>Low</i>	<i>Middle</i>	<i>High</i>	
Calymenidae:				
Calymeninae	50	10	40	Survival
Colpocoryphinae	0	11	89	EXTINCT
Reedocalymeninae	6	29	65	EXTINCT
Cyclopygidae	4	13	83	EXTINCT
Styginidae	36	60	4	Survival
Homalonotidae	0	15	85	Survival
Trinucleidae	14	26	60	EXTINCT
Dimeropygidae	81	19	0	EXTINCT
Raphiophoridae	68	19	13	Survival
Proetoidae	60	0	40	Survival
Odontopleuridae	31	26	43	Survival
Lichidae	20	55	25	Survival
Illaeidae	49	32	19	Survival
Isocolidae	45	45	10	EXTINCT
Cheiruridae:				
Cheirurinae	63	26	11	
Survival				
Acanthoparyphinae	0	100	0	Survival
Cyrtometopinae	0	100	0	EXTINCT
Deiphoninae	75	25	0	Survival
Eccoptochilinae	0	26	74	EXTINCT
Sphaerexochinae	94	6	0	Survival
Pterygomotopidae	23	73	4	Survival
Encrinuridae	62	19	19	Survival
Dalmanitidae	0	0	100	Survival

^aThis early distribution is calculated as a percentage of total species present during intervals 03, 04, and 05, at low, middle, and high latitudes.

Ashgill in response to climatic cooling. During this time, many groups that had shown strong high-latitude endemism achieved wider, low-latitude distributions. For example, dalmanitids, chasmopine pterygomotopids, reedocalymenine calymenids, homalonotids, and cyclopygids, among others, became widespread just prior to the extinction.

Based on the summary presented here, Ordovician radiations of trilobites clearly occurred with a substantial latitudinal component (table 24.2). Some radiating groups were initially endemic or nearly endemic to high-latitude Gondwana and others to low-latitude Laurentia (and possibly Siberia/Kolyma, though data are very sparse).

This tabulation demonstrates that a strong majority (12 of 15) of clades that had their origin and early diversification centered in the Bathyrurid Realm or Megistaspidine Realm (i.e., had a majority or plurality of their species diversity occurring there) went on to survive the end Ordovician mass extinction and contribute to the Silurian Fauna. Further, of the 15 clades centered in either the Bathyrurid or Megistaspidine realm, 14 are next most common in the

other of these realms—that is, they have an extremely strong or exclusive intermediate and low-latitude distribution. The only exception is Encrinuridae, reflecting the high-latitude diversification of the dindymenines. In contrast, of eight clades that had their origin and early diversification centered in the Dalmanitoidean Realm, only three survived the end Ordovician mass extinction. The difference in survival between clades whose diversification occurred in low to intermediate latitudes and those with origins in high latitudes is statistically significant. A G-test with Williams's correction for small sample sizes (Sokal and Rohlf 1981) rejected the null hypothesis of independence of survival from latitudinal distribution at the .05 level.

Hence, for whatever reason, a significant majority of clades that would survive the extinction and form the Silurian Fauna had their first occurrence and their radiation heavily concentrated in intermediate and low latitudes, and most were centered in the Bathyrurid Realm.

Development of the Whiterock Fauna in Laurentia

It is important to test for any environmental signal to the emergence of the Whiterock Fauna in all three realms in which a significant radiation of trilobites occurred. However, adequate data are currently limited to the low-latitude Bathyrurid Realm, which contributed more than half of the clades destined to form the Silurian Fauna. Here, the focus is on the environmental pattern of the radiation in Laurentia because this continent contributes the overwhelming amount of data for the Bathyrurid Realm and also has the best available environmental information.

Concern for Ordovician environmental distributions and their potential overprint on geographic patterns was pioneered by Fortey (1975a) in his qualitative analysis of Spitsbergen faunas. Ludvigsen (1978) applied quantitative techniques to biofacies analysis in the Middle Ordovician of northwestern Canada, and Q- and R-mode hierarchical cluster analysis of trilobite biofacies is now becoming routine (e.g., Ludvigsen and Westrop 1983; Westrop 1986; Ludvigsen et al. 1989; Westrop and Cuggy 1999). Fortey's biofacies scheme is intuitive and has been widely supported, but it has not been put on a formal analytical footing, a task that we attempt here.

Ideally, biofacies analysis should be undertaken with quantitative sampling data, so that relative abundance of taxa can participate in clustering. Such data are only occasionally available (summarized on a global scale by Westrop and Adrain [1998] and Adrain et al. [2000]) and are lacking for most well-described faunas from Laurentia at the time of onset of the Ordovician Radiation. As a result, simple presence/absence data were used, with the acknowledgment that information on relative abundance may in the future greatly enhance the analysis.

The results from analysis of 37 Laurentian collections from the O4 interval are shown in figure 24.4. Most taxa are genera, although occasionally subfamilies or even families are used where data were sparse. "Singleton" taxa restricted to a single collection were not scored. Analyses were performed with SPSS v.10.0 for the Macintosh computer (SPSS 2000). The analysis confirms the general applicability of Fortey's (1975a) scheme, yielding four progressively deeper-water biofacies labeled (following Fortey) Bathyrurid, Illaenid-Cheirurid, Nileid, and Olenid. The Bathyrurid biofacies includes collections from shallow subtidal environments (i.e., above-average storm wavebase) common on the craton interior. The Illaenid-Cheirurid biofacies occurs in deep subtidal and buildup collections, mostly derived from the craton margin. The Nileid and Olenid biofacies occur in progressively deeper-water, mostly marginal environments.

Does the Whiterock Fauna contribute more substantially to one or more of these biofacies? As demonstrated by figure 24.5, the majority of species occurring in the Illaenid-Cheirurid biofacies belong to Whiterock Fauna groups, whereas the Ibex faunas dominate in all other biofacies. The pattern is more striking still when only the Silurian Fauna (excluding the Raphiophoridae, as in Adrain et al. 1998) is plotted—groups that survived the end Ordovician were overwhelmingly concentrated in the Illaenid-Cheirurid biofacies. Hence, the trilobite radiation in Laurentia was initiated in marginal deep subtidal and buildup environments fringing the craton.

The pattern of origin and spread of the Whiterock Fauna in Laurentia is shown in figure 24.6. Early Ibexian faunas were completely dominated by elements of the Ibex faunas across the environmental spectrum. By the late Ibexian, the Whiterock Fauna had appeared in all environments but dominated

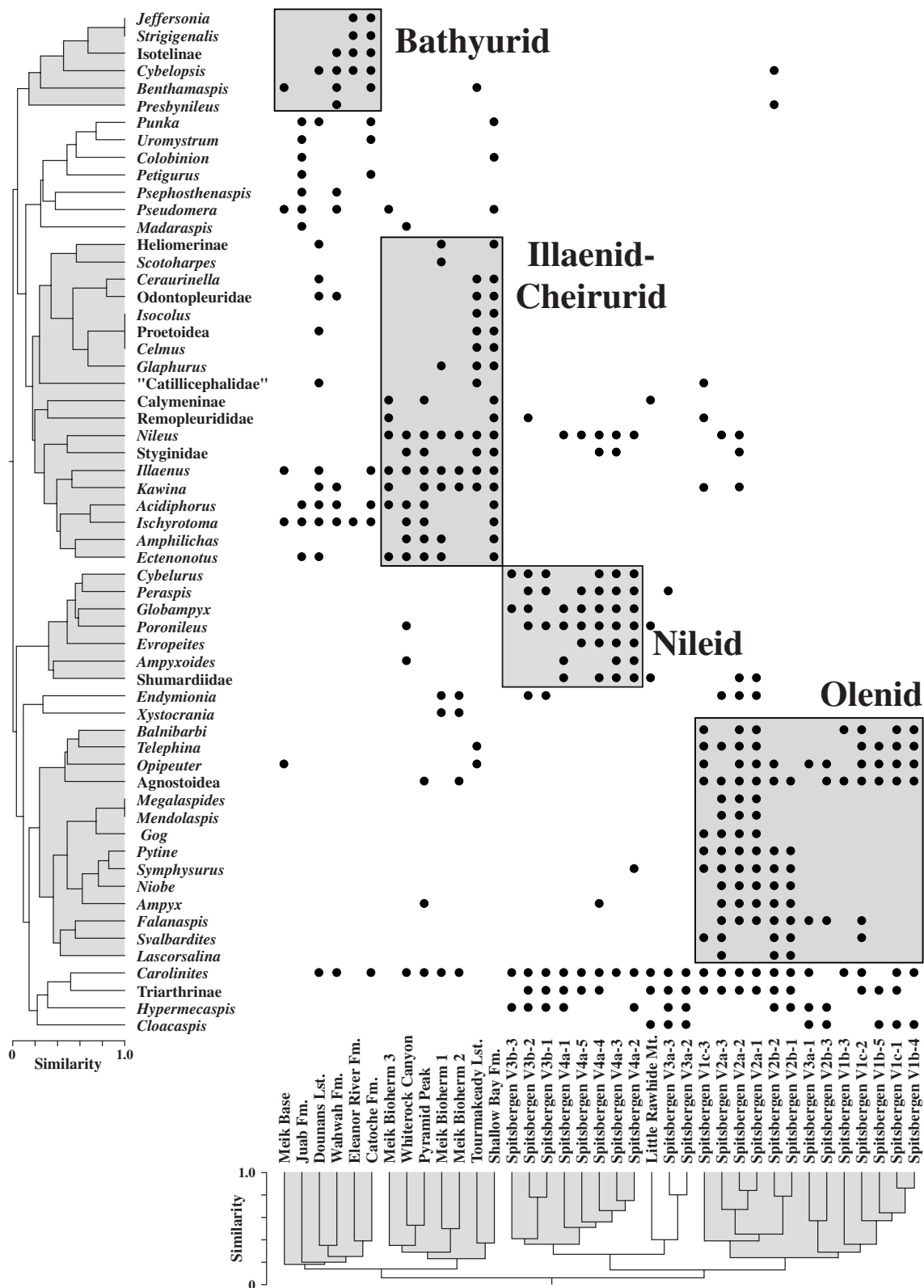


FIGURE 24.4. Definition of Laurentian trilobite biofacies during the onset of the Ordovician Radiation. Data matrix with horizons in Q-mode clustering order and taxa in R-mode clustering order. Data are presence/absence. Jaccard's coefficient was used as the index of similarity, and the clusters were formed using the average linkage method. Biofacies are defined using the intersection of Q- and R-mode clusters. Catoche Formation, western Newfoundland (late Ibxian); Dounans Limestone, Highland Border Complex, Scotland (late Ibxian); Eleanor River Formation, Ellesmere Island, Canadian Arctic (late Ibxian); Juab Formation, Ibex area, western Utah (early

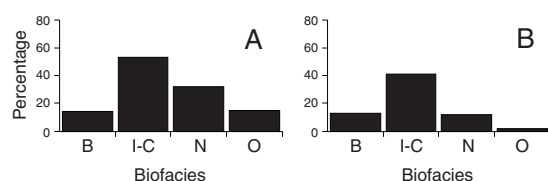


FIGURE 24.5. A, percentage of total species occurrence in each early Whiterockian Laurentian biofacies that is contributed by the Whiterock Fauna (B = Bathyrud Biofacies; I-C = Illaenid-Cheirurid Biofacies; N = Nileid Biofacies; O = Olenid Biofacies). B, percentage of total species occurrence contributed by the Silurian Fauna, excluding Raphiophoridae (see Adrain et al. 1998).

none. Transition to dominance by the Whiterock Fauna first occurred in deep subtidal and buildup environments during the early Whiterockian—at a time when the Ordovician Radiation of the Paleozoic Evolutionary Fauna was taking place. The Whiterock Fauna subsequently spread both on- and offshore, dominating all environments by the Late Ordovician and of course completely dominating Silurian environments with the extinction of all Ibex faunal elements by the end Ordovician.

Conclusions and Prospects from the Global Analysis

1. Ordovician trilobite families display one of three major diversification trajectories: earliest Ordovician success followed by steady and rapid decline and extinction prior to or at the end Ordovician (Ibex Fauna I); Early Ordovician radiation followed by Mid Ordovician decline and extinction prior to or at the end Ordovician (Ibex Fauna II); or Mid Ordovi-

cian radiation and Late Ordovician success, with substantial survivorship at the end Ordovician (Whiterock Fauna).

2. There was an Ordovician radiation of trilobites in all parts of the world except the tropical Gondwanan Reedocalymenine Realm. The radiation occurred at the same time as, and with dynamics similar to, that of the Paleozoic Evolutionary Fauna.

3. Whiterock Fauna clades that diversified at high latitudes were less likely to survive the end Ordovician mass extinction, whereas almost all of those that diversified at low latitudes survived.

4. In Laurentia, the Whiterock Fauna rose to dominance first in marginal deep subtidal and buildup environments and spread later to progressively dominate more on- and offshore environments.

Future research could be focused on improving all the analyses with more and better data and completely stepping the level of global resolution down to species level. Greater global stratigraphic resolution using trilobites seems unlikely in the foreseeable future owing to the limited study currently being undertaken in major areas. However, further progress could certainly be made in continents with good records. Particular questions requiring further investigation include the following:

1. What is the biofacies pattern of the transition in the Megistaspidine and Dalmanitoidean realms? Relative abundance data are even more sparse than for Laurentia (see Adrain et al. 2000), but it should be possible to collect presence/absence data.

2. What does the marginal Laurentian emergence of the Whiterock Fauna signify? Is there a major extrinsic cause for the trilobite radiation?

3. Are the radiations in the three realms one, two, or three events? The high-latitude radiation in the Dalmanitoidean Realm seems to precede that in the Bathyrud Realm (Owen and McCormick 2003). Did it have a different cause?

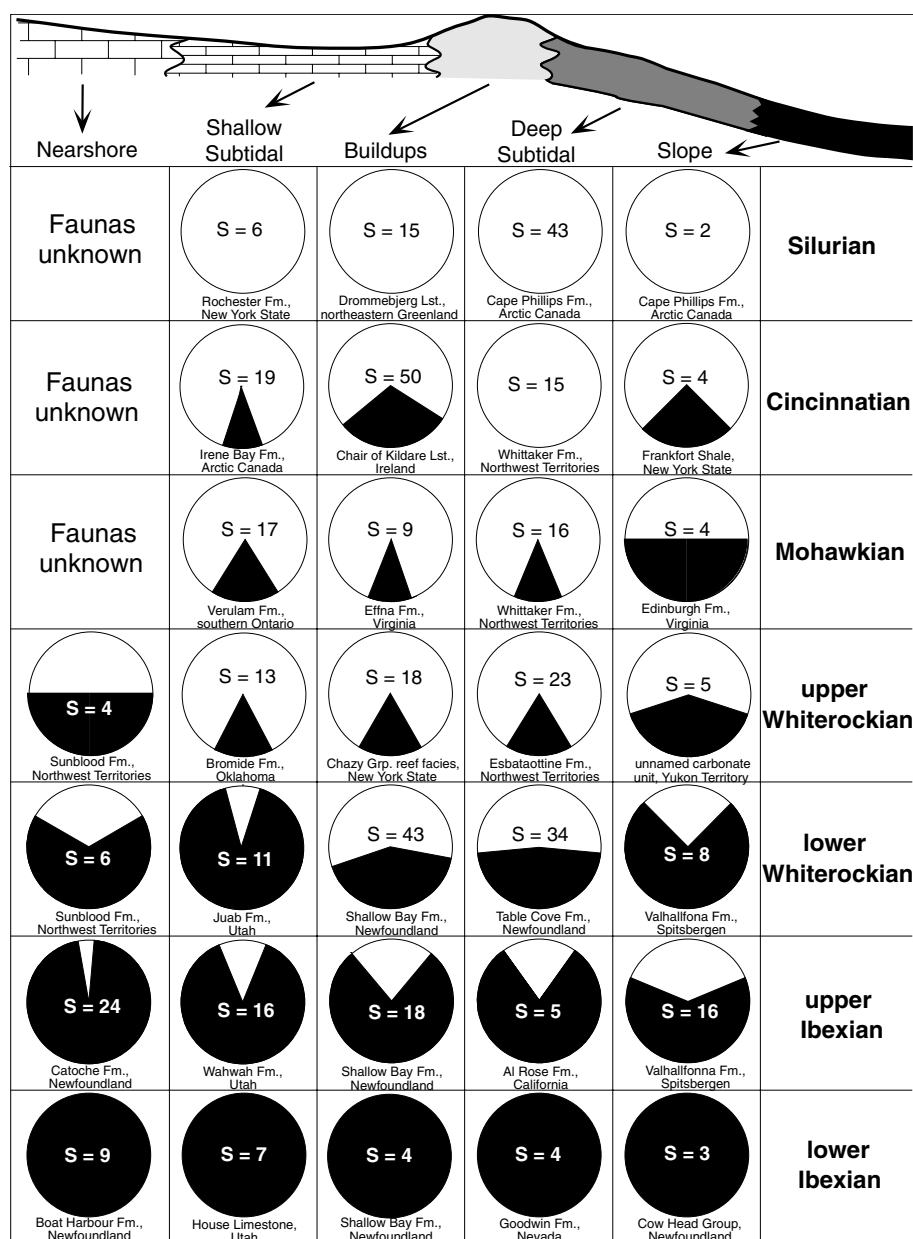
■ Regional Patterns in Australia and New Zealand (GDE, BDW, JRL)

Ordovician trilobite faunas of Australasia were reviewed by Webby and Edgecombe in Webby et al. (2000), with particular reference to their biogeographic affinities. Most of the data in that synthesis,

FIGURE 24.4. (Continued)

Whiterockian); Little Rawhide Mountain, Antelope Valley Limestone, central Nevada (late Ibexian); Meik Base = Meiklejohn Bioherm basal beds (early Whiterockian), southwestern Nevada; Meik Bioherm 1–3 = Meiklejohn Bioherm, separate collections from biohermal beds (early Whiterockian); Pyramid Peak, Death Valley, California (early Whiterockian); Shallow Bay Formation, western Newfoundland (early Whiterockian); Spitsbergen V1–V4, various stratigraphic levels in the Valhallfonna Formation, drawn from Fortey (1980: figure 1), ranging from late Ibexian to early Whiterockian; Tourmakeady Limestone, western Ireland (early Whiterockian); Wahwah Formation, Ibex area, western Utah (late Ibexian); Whiterock Canyon, Antelope Valley Limestone, east-central Nevada (early Whiterockian).

FIGURE 24.6. Representative Laurentian faunas through time and along an environmental gradient, showing the pattern of changeover from the Ibex faunas (black) to the Whiterock Fauna (white), with number of species recorded from each fauna.



as well as the present analysis, are from Australia (see Webby and Nicoll 1989: appendix 2 for a species list). New Zealand is represented only by Lower Ordovician faunas of the Patriarch Formation and Summit Limestone in the Takaka Terrane, South Island (Wright et al. 1994) and a few species from the Upper Ordovician Golden Bay Group of the adjacent Buller Terrane.

The trilobite record in Australia samples a broad range of biofacies. For example, Lancefieldian/Tremadocian assemblages include platform sediments representing the inner detrital belt (Shergold 1991) and peritidal carbonates (Shergold 1975), as well as an outer detrital biofacies sampled in western New

South Wales (Webby et al. 1988) and New Zealand (Wright et al. 1994). A succession of Ordovician faunas outlined by Webby et al. (2000) drew heavily on the biogeographic sensitivity of trilobites. The Lower Ordovician in Australasia was divided (in ascending order) into *Hysterolenus*, *Australoharpes*, *Koraipsis*, *Chosenia*, and *Encrinurella* faunas, all having affinities to North China and most having affinities to the Sibumasu Terrane. Relationships to China and Sibumasu are maintained through the Middle Ordovician *Railtonella* and *Prosopiscus* faunas, the latter also having links to Laurentia and the Precordillera of Argentina. A Gisbornian *Incaia* fauna in New Zealand

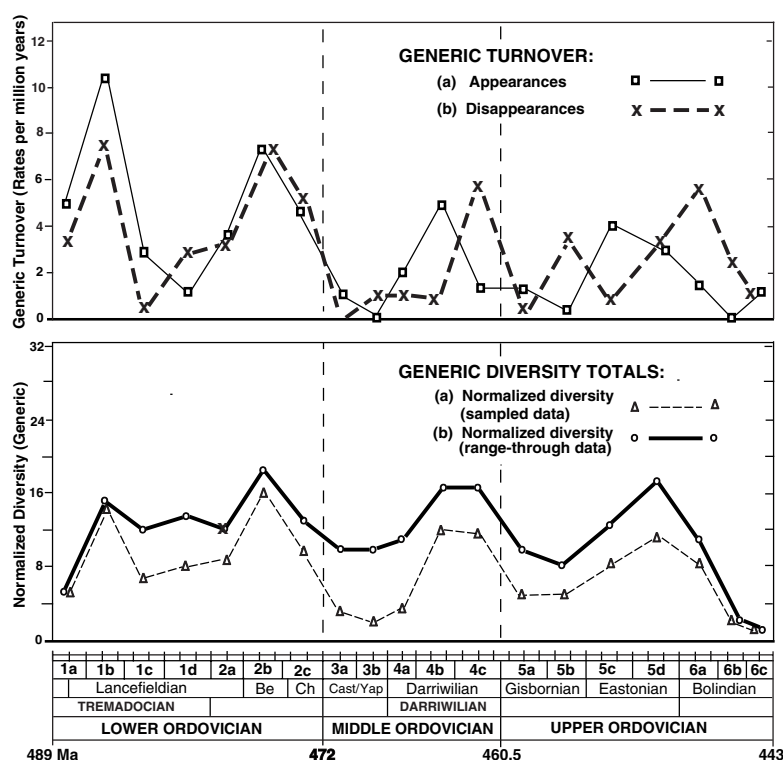


FIGURE 24.7. Generic turnover (appearance and disappearance rate per million years) and normalized generic diversity curves for Ordovician trilobites of Australia and New Zealand. Normalized diversity is plotted for sampled and range-through data. Be = Bendigonian; Ch = Chewtonian; Cast = Castlemanian; Yap = Yapeenian.

has South American affinities, whereas Eastonian-Bolindian trilobites of Australia (*Eokosovopeltis-Plimerina* fauna) display a clear association with Kazakhstan, North China, and terranes near the margin of Gondwana. Elements of the cosmopolitan *Hirnantia* Fauna (brachiopods and trilobites) have been recorded in Victoria and Tasmania.

Diversity data for Australia are affected by biases in geographic representation through the Ordovician. The Canning Basin in Western Australia (Legg 1976; Laurie and Shergold 1996a, 1996b) has a full record for the Early and Mid Ordovician but was a site of nonmarine and evaporite sedimentation in the Late Ordovician. Late Ordovician data are derived largely from the island-arc complexes of central-west New South Wales and platform carbonate sequence of Tasmania. Most known Ordovician faunas in Australasia have been described, and we have included unpublished data for the Amadeus Basin, Tasmania, and central-west New South Wales to eliminate bias.

The diversity curves in figure 24.7 have been compiled at the generic level, but because a majority of genera are represented by single species, discrepancies between generic and specific diversity are not a major issue. The relatively short temporal duration of many genera is reflected in a general correspondence be-

tween appearances and disappearances through most of the Ordovician, and longer-ranging genera appear to be randomly distributed through time. Intervals in which disappearances substantially exceed appearances are *TS.4c* (late Darriwilian) and *TS.6a* (early Bolindian). Qing et al. (1998), Shields and Veizer (chapter 6), and Barnes (chapter 8) have demonstrated a dramatic decline in strontium isotope ratios across the late Darriwilian to early Caradoc (*TS.4c–5a*) interval. Qing et al. (1998) and Barnes link this change to a possible global mantle plume event with associated orogenic quiescence and/or major flooding (the early Caradoc transgression of Cocks and Fortey 1988). Shields and Veizer attribute the cause to increased ocean-ridge spreading rates. In contrast, the *TS.6a* decline seems to have been related more to regional than to global factors, with the Benambran Orogeny causing major tectonic changes and volcanic activity, especially to eastern Australia (Webby and Percival in Webby et al. 2000:109).

Range-through and sampled diversity both show four maxima (listed in descending order using the range-through data) in the Bendigonian (*TS.2b*), Eastonian (*TS.5d*), Darriwilian (*TS.4b–4c*), and Lancefieldian (*TS.1b*). Range-through diversity particularly exceeds sampled diversity through two intervals of

the Ordovician, *TS.1c–2a* and *TS.3a–4a*. The latter (Castlemainian–early Darriwilian) is one of three marked minima in diversity by either measure, the others being in the Gisbornian (*TS.5a–b*) and in the globally depauperate late Bolindian (*TS.6b–c*). The diversity low through the *TS.3a–4a* interval may be at least in part an artifact of incomplete sampling, limited exposure, and/or restriction of favorable trilobite-bearing facies (Georgina Basin and Tasmania), and/or breaks (disconformities) that represent localized emergence through a part of this *TS.3a–4a* interval (Canning Basin).

Adrain et al. (earlier in this chapter) observed geographic variation in the expansion of their Whiterock Fauna (Adrain et al. 1998). Owen and McCormick (later in this chapter) noted an early (early Arenig) diversification of elements of this fauna in Avalonia, whereas it diversified relatively late in South America (Waisfeld, later in this chapter). Lower Ordovician faunas representing the inner detrital biofacies throughout Australia (e.g., Jell 1985; Jell and Stait 1985a, 1985b; Shergold 1991) are composed almost exclusively of members of the Ibex Fauna (e.g., asaphids, pilekiids, pliomerids, and hystricurids), like that of the diverse, highly endemic Bendigonian succession of the Canning Basin, where asaphids, pliomerids, and telephinids predominate (Laurie and Shergold 1996a, 1996b). In the Canning Basin, elements of the Whiterock Fauna such as illaenids and raphiophorids first rival the diversity of the Ibex Fauna in the Darriwilian (*TS.4b–c*; Legg 1976). Whiterock taxa, notably encrinurids, cheirurids, lichids, styginids, illaenids, and trinucleids, become dominant for the first time in the Eastonian faunas of New South Wales and Tasmania. Interval *TS.5c* (early Eastonian) is marked by generic appearances greatly exceeding disappearances, which appears to correspond to the expansion of the Whiterock Fauna.

Ibex elements (shumardiids, agnostids, telephinids) remain the sole or dominant component only in some Late Ordovician outer detrital biofacies (e.g., Shoemaker Beds in Tasmania: Burrett et al. 1983; Oakdale Formation in New South Wales: Webby 1974). This is, interestingly, opposite to the pattern for South America (Waisfeld, later in this chapter), where Ibex taxa preferentially survive in shallow-water settings. The near absence in the Australian record of particular shallow-water Ibex groups such as

bathyurids may figure in the difference between the South American and Australian patterns. The domination of the Whiterock Fauna in Australia is even later than in South America. Although the paucity of early Mid Ordovician (Castlemainian–early Darriwilian) trilobite faunas is a problem for understanding this transition, even later Darriwilian assemblages (e.g., Nora Formation in the Georgina Basin: Fortey and Shergold 1984) are composed almost exclusively of Ibex taxa such as asaphids, leiostegiids, dikelocephalinids, telephinids, and prosopiscids.

■ Regional Patterns in South America (BGW)

Trilobite records in the Ordovician of South America are derived from three different geodynamic and environmental settings: pericratonic platforms developed along the southwestern edge of Gondwana (Andean belt), volcanic island-arc settings parautochthonous to the Gondwanan margin (Famatina Range and western Puna), and an allochthonous Laurentian-derived terrane (Argentine Precordillera).

The Andean belt records deposition in shallow marine siliciclastic shelves. In northern South America, Ordovician deposits are poorly known, and trilobite records are sparse. In contrast, better-known and trilobite-rich successions, mostly early Tremadocian to mid Arenig in age, crop out in the Central Andean basin (Cordillera Oriental of Peru, Bolivia, and northwestern Argentina). Trilobite species diversity is high in the early Tremadocian to mid Arenig (figure 24.8). Tremadocian successions are composed of transgressive deposits that frequently represent dysaerobic environments, punctuated by regressive episodes (cf. Moya 1988) represented by intertidal and shallow subtidal settings. The greatest number of species occurs in the early Tremadocian, associated with the global rise in sea level and the development of mud-dominated platforms, dominated by relatively widespread olenids and several families of agnostoids.

High diversity was maintained in the late Tremadocian to the early and mid Arenig, with a remarkable radiation of endemic asaphids in the early Arenig (*T. approximatus* to *B. deflexus* graptolite zones) associated with dysaerobic facies in distal parts of the inner shelf (Waisfeld et al. 1999). In the mid Arenig (uppermost *B. deflexus* and *D. bifidus* graptolite zones),

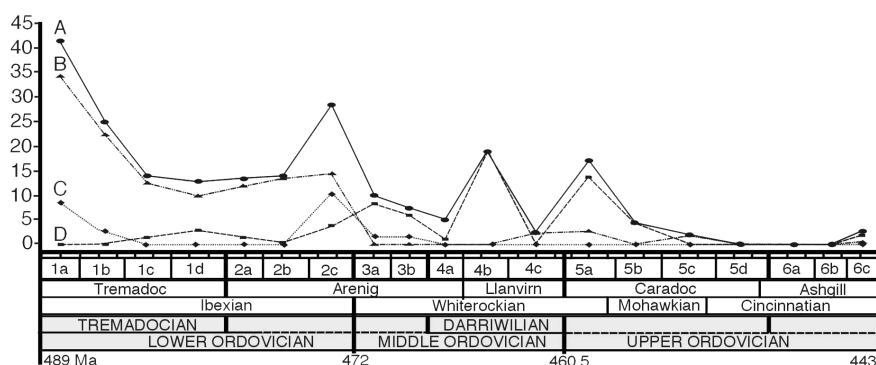


FIGURE 24.8. Normalized diversity of trilobite species in South America. A, aggregate diversity curve for all the basins. B, diversity curve for the Andean belt. C, diversity curve for Famatina Ranges and Western Puna. D, diversity curve for Argentine Precordillera.

in shallower and more aerobic waters of the inner shelf, there was a radiation of endemic trinucleids, raphiophorids, pliomerids, nileids, and asaphids. Diversity increase is also related to the occurrence of a few immigrants from northwestern Gondwana (Waisfeld 1995). Post-Arenig trilobite records in the Andean belt are sparse and restricted to isolated outcrops and, except in Argentina, mostly lack accurate chronological constraints. A few asaphids, along with calymenids, homalonotids, and trinucleids, are recorded in Llanvirn to Caradoc strata.

In Argentina there is evidence for active vulcanism during the mid Arenig in the Famatina Range and during the early Tremadocian and the mid Arenig in the western Puna region (Astini and Benedetto 1996; Kouharsky et al. 1996; Mángano and Buatois 1996). Trilobite information is still preliminary, particularly in the latter region. In the Famatina Range, trilobites exhibit the highest diversity in siliciclastic and volcanoclastic deposits of the proximal- to middle-shelf environment, associated with an increase in volcanic activity (conodont-based *O. evae* Zone). No particular radiation of endemic forms is recognized in this basin, but immigrants from West Gondwana coexist with East Gondwanan and Baltic forms (Vaccari 1995; Waisfeld and Vaccari 1996).

The Argentine Precordillera terrane rifted from Laurentia in the Early Cambrian and drifted from low to high latitudes during the Ordovician (Astini et al. 1995). From the latest Tremadocian, open marine carbonates prevailed, yielding a relatively complete record of the benthic fauna. Late Tremadocian to early Llanvirn carbonate sedimentation is represented by inner- and middle-ramp settings (Cañas 1999). Trilobite diversity is relatively low and composed largely of representatives of the Ibex Fauna.

The base of the Whiterockian is within this carbonate succession, but it is not marked by particular expansion of families belonging to the Whiterock Fauna. Endemic genera are restricted to a single pliomerid in the mid Arenig and a single scutellinid in the early Llanvirn (Vaccari 2003) both from the middle ramp. Both are associated with immigrants from the low- and intermediate-latitude Bathyrurid Province of East Gondwana and Baltica (cf. Vaccari 1995).

A change from the middle to distal ramp and a shift in facies from exclusively carbonate to mixed carbonate-siliciclastic sedimentation took place diachronously from late in the mid Arenig to the early Llanvirn. This facies change is linked to a tectonic shift associated with the generation of subsiding depocenters and with global sea level rise in the early Llanvirn (mid Darriwilian) (Astini 1999a; Cañas 1999). This shift was critical in the expansion of trilobites. The earliest records (conodont-based *B. navis* to *M. parva* zones) of trilobites in the distal ramp environment comprise relatively widespread elements (nileids, olenids, raphiophorids, etc.), but in the early Llanvirn (conodont-based *E. suecicus* Zone) these are associated with a radiation of new genera, particularly Raphiophoridae, and also Trinucleidae and Toernquistiidae. Families belonging to the Whiterock Fauna account for 40 percent of the fauna.

Caradoc and younger deposits show a strong facies differentiation in the Precordillera. Trilobites are particularly restricted to carbonate remnants that persisted locally after carbonate sedimentation was drowned in most parts of the basin. Their occurrence and diversification appear to be strongly controlled by environmental constraints imposed by the regional topography and local tectonics. An early Caradoc (graptolite-based *N. gracilis* and *C. bicornis* zones) peak in trilobite

diversity is coincident with one of these carbonate remnants. Trilobites occur in slope-apron deposits in either autochthonous deep-water limestones (hemipelagites) or slightly shallower water resedimented carbonates (cf. Astini 1995). New species of earlier endemic raphiophorids and toernquistiids occur, together with endemic encrinurids and a remarkable radiation of trinucleids. The latitudinal position of the Precordillera during the Caradoc is still debated, with mixed biogeographic affinities of the fauna indicating proximity to the Gondwanan margin and a possible location at intermediate latitude (Benedetto 1998; Benedetto et al. 1999). Trilobite records in the late Caradoc to Ashgill of the Precordillera are scarce, with only a few homalonotids and dalmanitids associated with the *Hirnantia* Fauna.

Biodiversification of trilobites in South America shows a strong biogeographic and environmental overprint. In the Andean belt, local radiation of forms is remarkable in the early and mid Arenig among the representatives of the Ibex Fauna. The Whiterock Fauna is well developed in the Precordillera, in contrast to the Andean belt, where Middle and Upper Ordovician records are limited. The Whiterock Fauna diversified diachronously from late in the mid Arenig to the early Llanvirn, tracking the progressive development of distal ramp settings in the basin, while trilobite families of coeval shallower settings are still dominated by representatives of the Ibex Fauna. This pattern is similar to that reported by Adrain et al. (1998) in Laurentia. However, the initial development of the Whiterock Fauna appeared to take place slightly later. This could be a result of the appropriate distal facies being developed slightly later in the basin.

■ Regional Patterns in the Anglo-Welsh Sector of Avalonia (AWO, TMcC)

The Anglo-Welsh area contains the most complete Ordovician successions from Avalonia. They record the history of that microcontinental terrane from its Early Ordovician location on the intermediate to high-latitude Gondwanan margin, probably close to West Africa (McNamara et al. 2001), through its early Mid Ordovician rifting and northward drift leading to its collision with Baltica in the Late Ordovician and the Laurentian margin in the Early Silurian (Cocks et

al. 1997; van Staal et al. 1998; Cocks 2000). The Anglo-Welsh Ordovician trilobite faunas are well documented, and their temporal and spatial diversity patterns have been investigated using a literature-based relational database in which the occurrences of species at localities are linked to an array of taxonomic, geographic, and stratigraphic data (Owen and McCormick 1999; McCormick and Owen 2001).

We have described elsewhere the patterns of trilobite diversity change in the Ordovician of the Welsh basin at genus and species level (McCormick and Owen 2001) and the whole Anglo-Welsh area at genus level (Owen and McCormick 2003). In doing so, we have demonstrated that members of the Whiterock Fauna became the dominant component of the Avalonian trilobite fauna earlier (early Arenig) than its rise to dominance in global terms and that they were fairly evenly distributed through the whole spectrum of shelf to upper-slope environments. These analyses were undertaken using the stages recognized in what is the historical type area for the Ordovician (Fortey et al. 1995, 2000) as the “time slices” and utilizing a simple measure of diversity that counted as unity the occurrence of a taxon within a given stage or inferred (in the case of “range-through” analyses) to have been present in that stage because of its presence in the preceding and succeeding intervals.

We present here species- and genus-level curves (figure 24.9) using the normalized diversity measure recommended for the IGCP 410 clade analyses and equating the Anglo-Welsh stratigraphy as closely as possible to the time slices recommended for the international project (chapter 2). Few of the boundaries between the latter divisions match exactly the chronostratigraphic or biostratigraphic boundaries defining the units within which the data were compiled, and the equivalencies used are shown in the caption to figure 24.9. The normalized diversity measure per time slice counts the number of taxa occurring within the slice and also found above and below it, plus half the number of those taxa that either originated or became extinct during that interval plus half the number of taxa restricted to the slice.

Two sets of curves have been computed, one based on recorded occurrences within each slice and one that infers the existence of taxa within an interval on the basis of the “range-through” principle (see earlier in this chapter). The stratigraphic age of some of

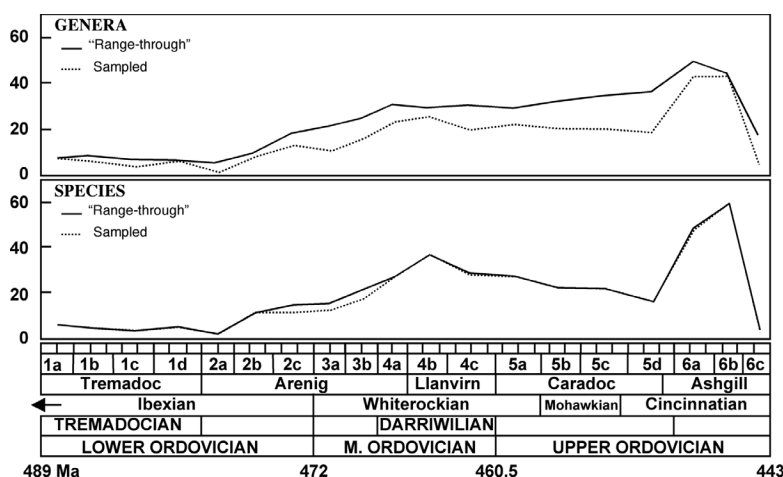


FIGURE 24.9. Sampled and range-through trilobite normalized biodiversity curves for the Anglo-Welsh sector of Avalonia. Note that the boundaries between many of the time slices recommended by Webby et al. (chapter 2) cannot be recognized in the Anglo-Welsh area or that the shelly faunal data could not be compiled relative to them. The time slices as used here have the following equivalencies in the Anglo-Welsh chronostratigraphy: *TS.1a* = Cressagian; *TS.1b* = early Migneintian; *TS.1c* = mid Migneintian; *TS.1d* = late Migneintian; *TS.2a* = early Moridunian; *TS.2b* = late Moridunian; *TS.2c* = Whitlandian; *TS.3a* = early Fennian; *TS.3b* = mid Fennian; *TS.4a* = late Fennian; *TS.4b* = early Aberdeiddian (= graptolite-based *D. artus* Zone); *TS.4c* = late Aberdeiddian + Llandeilian; *TS.5a* = Aurelucian; *TS.5b* = Burrellian; *TS.5c* = Cheney + Streffordian; *TS.5d* = Pusgillian; *TS.6a* = Cautleyan; *TS.6b* = Rawtheyan; *TS.6c* = Hirnantian.

the records in the database is known only to two or (rarely) more stages, in which case the taxa are counted as 0.25 in any resultant time slice above or below the unequivocal range of the taxa concerned and, in the case of the “sampled” data, 0.5 where the uncertain record fills in part of the known range of the taxon. The difference between the sampled and range-through curves is particularly marked in intervals where the rock succession, and therefore the sample coverage, includes only a limited set of biofacies. Moreover, because many species are confined to a single stage (e.g., Thomas et al. 1984) whereas most genera have a much longer range, the lower weighting placed on taxa restricted to a time slice in the diversity index produces the apparently anomalous situation of there seeming to be more genera than species in many time slices.

Compared with our earlier, genus-level analysis (Owen and McCormick 2003), the twofold division of the Moridunian stage produces a curve showing a more even rise in diversity through the Arenig, and the combining of the graptolite-based *murchisoni* Zone and Llandeilian stage and the Cheney and Streffordian stages to comprise *TS.4c* and *TS.5c*, respectively, produces smoother “sampled” diversity curves. Otherwise, patterns emerge from the analysis

that are similar to those obtained earlier, testifying to the robustness of the signals. Bootstrap tests (multiple random resampling of the data in each time interval—see Gilinsky and Bambach 1986 for other examples) of the sample data in our earlier analyses show that (1) the number of samples or the range of biofacies preserved within a time unit can have a strong influence on the sampled diversity and (2) the range-through curves are probably a closer reflection of the true picture (McCormick and Owen 2001; Owen and McCormick 2003).

The range-through diversity curves presented herein (figure 24.9) show a rise through the Arenig to a late Arenig–early Caradoc (*TS.4a–5a*) plateau at genus level but a slight early Llanvirn (*TS.4b*) peak at species level. McCormick and Owen (2001) suggested that elevated levels of species richness of genera in the late Arenig–early Llanvirn in the Welsh basin may be linked to the rifting of Avalonia from Gondwana at that time (Cocks et al. 1997). Species-level diversity apparently fell during the Caradoc to earliest Ashgill (*TS.5a–d*), but this is to some extent an artifact of a combination of the restriction in range of preserved shelf biofacies as the basin deepened and the absence of the very deepest water trilobite biofacies from the Anglo-Welsh area. The latter, the

cyclopygid-atheoptic association, was composed largely of long-ranging genera that reappeared in the Ashgill, and hence the range-through genus-level data show a trend contrary to the species data. The mid Ashgill (Cautleyan-Rawtheyan) peak in diversity in the Anglo-Welsh area contrasts markedly with the global curves (Adrain et al., earlier in this chapter), which show a maximum in the late Arenig and Llanvirn and a considerable decline thereafter. The Cautleyan-Rawtheyan peak in both genus and species diversity and the high species-to-genus ratio reflect the extreme heterogeneity of the environment and hence the wide spectrum of trilobite biofacies preserved in the Anglo-Welsh area prior to the extinctions that led to the Hirnantian diversity crash (Owen and McCormick 2003).

■ Regional Patterns in Baltica (ØH)

Baltoscandia provides the most complete record for the biodiversity history of Baltica during the Ordovician. It is believed that the region as a whole preserves a fairly complete stratigraphic sequence, although formations can be condensed, in particular in the Baltic countries.

The genus- and species-level diversity curves presented here (figure 24.10) have been derived from a larger database (openly available on the Internet at <http://asaphus.uio.no>), covering all major fossil groups from the Ordovician of Baltoscandia (Hammer in press). Owing to the nature of the literature, especially the older publications, it has not been possible to collect sufficient data about individual

samples. The basic unit of the database is therefore first and last occurrences of a species at one locality, according to one publication. As far as possible, the “first-appearance datums” (FADs) and “last-appearance datums” (LADs) are then converted to apparent, calibrated ages according to the timescale used in this volume and correlations with local zones according to recent literature. In cases in which only the formation is known, the approximate ages of the lower and upper formation boundaries are used as the FAD and LAD, potentially overestimating real ranges and also by necessity disregarding diachronous lithological boundaries. The diversity estimates within each time slice (chapter 2) are then made using the range-through assumption and the normalized diversity count, whereby taxa having their FAD and/or LAD within a time slice count as only one-half of a unit within that slice. An alternative estimate involves counting taxa restricted to a time slice as one-third of a unit. There is no correction for the different durations of the time slices. Even though sample data have not been collected, it is to some degree possible to estimate sampling coverage by constructing “artificial samples” each consisting of taxa registered within a fixed time duration (e.g., one million years) at one locality. These quasi samples can then be subjected to bootstrap tests and other randomization methods (Hammer in press).

At the time of writing, the database consists of 10,340 stratigraphic ranges at localities, taken from 141 publications. Some 962 species and 259 genera of trilobites are included, with a total of 2,691 range entries. The trilobite taxonomy has been revised ac-

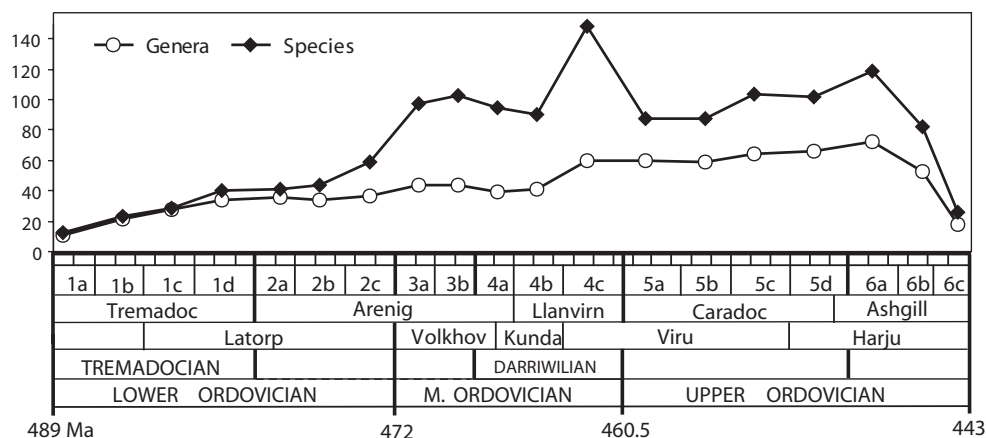


FIGURE 24.10. Range-through, normalized trilobite diversity curves for Baltoscandia, representing Baltica.

cording to Bruton et al. (1997), but the taxonomic uncertainties in the material are still rather extensive. It can only be hoped that the taxonomic problems are relatively unsystematic and will therefore deteriorate the signals, rather than producing false ones (Benton 1999).

The main feature of the curves is a more or less even, substantial increase in trilobite biodiversity throughout the period. In addition to global evolutionary trends, such a pattern may also have been influenced by local factors. Baltica drifted from a mid- to high-latitude position in the Southern Hemisphere in the Early Ordovician to low latitudes by the end of the Ordovician (Torsvik et al. 1992). In the context of the present-day latitudinal diversity gradient (Rosenzweig 1995), this movement may have contributed to the increase in diversity that is observed in all Balto-scandian fossil groups through the Ordovician. However, for trilobites, the diversity increase is less clear when the data are subjected to randomization tests (Hammer in press).

At the specific level, a steep increase in trilobite diversity is observed in *TS.3a* (mid Arenig) and is strongly supported by the randomization tests. This diversification event close to the Ibexian-Whiterockian boundary is contemporaneous with the beginning of a probably quite protracted regression in the area (Nielsen 1995:61).

A diversity peak in the species curve in the upper Llanvirn (*TS.4c*) is mainly due to Estonian data (in particular, those of Rõõmusoks 1970) and is not observed in the curves for Norway or Sweden. Trilobite diversity reached its all-time high in the early Ashgill (*TS.6a*) before dropping significantly during the late Ashgill. Even taking into account the artifacts produced by not counting Lazarus taxa, this end Ordovician decrease in diversity seems as dramatic as elsewhere in the world.

■ Regional Patterns in South China (ZYZ)

The South China Block exhibits extensive exposures of Ordovician deposits, with the most complete sequences and occurrences of fossil groups in China. The strata are well documented and the stratigraphic units highly resolved, with many selected as stratotypes for classifying and correlating the Ordovician of China. As reviewed by Cocks (2001), the South

China Block was situated in low-latitude zones along the western margin of Gondwana during the Ordovician. Cocks and Torsvik (chapter 5) further considered the South China Block as a peri-Gondwanan terrane that, like the Sibumasu Terrane, drifted from intermediate to low latitudes outboard of various Himalayan fragments close to the Indian part of Gondwana.

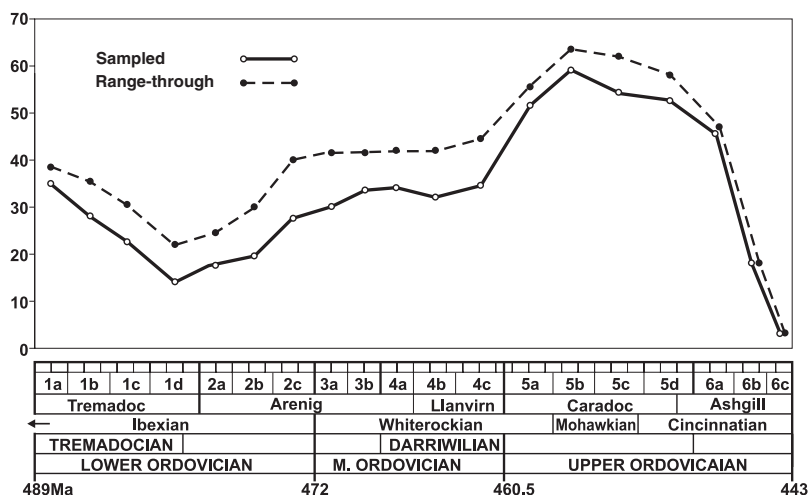
Ordovician trilobites are well recorded (e.g., Lu 1975), and faunas display a progressive on-shelf to off-shelf transition in composition and diversity from present-day west either to the southeast or to the north and northeast of the block, with benthic forms most diversified in the shallower outer shelf and mesopelagic cyclopygids mainly distributed in the deeper outer-shelf and off-shelf slope (see Zhou et al. 1999, 2001, 2003; Yuan et al. 2000). Trilobite faunas exhibit close relationships to those of Australasia, Kazakhstan, the North China and Tarim blocks, and the Sibumasu Terrane on the one hand and to the Middle East, southern, central and western Europe, and the Indochina Terrane on the other (Zhou and Dean 1989; Zhou et al. 1998a, 1998b), providing evidence of links between the different Ordovician Gondwanan and peri-Gondwanan faunas of higher to lower latitudinal zones.

In the absence of an existing database of the geologic and geographic distributions of the Ordovician trilobites in the South China Block, the genus diversity curves (figure 24.11) presented here are derived from a genus-range chart that will be described more fully in a future paper. The chart was compiled on the basis of data from the literature and collections made recently by Zhiyi Zhou, Zhiqiang Zhou, and Wenwei Yuan from 36 measured Ordovician sections along a bathymetric gradient in South China. The basic data comprise 220 taxonomically valid trilobite genera. Of these the Asaphida are the predominate group, represented by up to 41.6 percent of the entire South Chinese Ordovician trilobite generic component.

The diversity data are presented using the unified Ordovician timescale with subdivisions into 19 time slices and correlations to equivalent Chinese chronostratigraphic intervals as outlined by Webby et al. (chapter 2). The data were calculated using normalized diversity measures, as recommended by Cooper (chapter 4).

Range-through diversity maintains a relationship roughly similar to the sampled diversity through the

FIGURE 24.11. Sampled and range-through normalized generic biodiversity curves for Ordovician trilobites of the South China Block.



Early to Mid Ordovician (figure 24.11), but then the differences between the two sets of values become less marked during the Caradoc and eventually more or less coincide through the Ashgill (*TS.6a–c* interval). The overall diversity trend shows an initial sharp rise in *TS.1a* and then a decline to a low in *TS.1d*. This is followed by a rise to a broadly flattened to slightly elevated peak during the Mid Ordovician centered on *TS.4a*. Then a more intense radiation occurred during the Caradoc–early Ashgill (*TS.5a–6a* interval) with peak diversification in *TS.5b*, followed by a dramatic decline through the middle Ashgill to *TS.6c*. Although the limited *TS.1a* diversity increase in the early Tremadocian seems comparable to that of the South American, particularly the Andean Belt, plot (figure 26.8), the sharp diversity decrease in the Hirnantian is synchronous worldwide. The more or less steady rise in diversity shown here from the Arenig to early Ashgill is also revealed in Avalonia (figure 24.9) and Baltica (figure 24.10), especially the latter, where a similar Caradoc–early Ashgill diversity plateau also occurs. However, as a whole, the Ordovician trilobite biodiversity curves displayed in the different regions do not match one another very closely.

In summary, the diversity plot of South China shows peaks in the earliest Tremadocian, early Darriwilian, and Caradoc and two minima at the end of the Tremadocian and in the Hirnantian. The mid Ashgill diversity maximum illustrated by Owen and McCormick using Avalonian data (figure 24.9) is not depicted in South China, probably because there is a paucity of trilobite-rich rocks through this interval. Mechanisms that triggered the Ordovician bio-

diversity alternation may have involved a range of geologic, geographic, climatic, and oceanographic factors (Webby 2000). With the exception of the end Ordovician glaciation that caused the extinction of Ibex Fauna I and II and the decrease in diversity of the Whiterock Fauna (Adrain, Westrop, and Fortey, earlier in this chapter), the trilobite diversity changes exhibited in South China seem related generally to the sea level fluctuations delineated by Fortey (1984) and Ross and Ross (1992). High diversities seem to be associated with transgressive phases, and low diversities coincide with regressive intervals. The Caradoc diversity maximum may, for example, be connected with the Ordovician climax of transgression that took place in China (Zhou et al. 1989, 1992), as it did elsewhere in the world (Fortey 1984). It remains to be determined whether the correspondence between sea level and diversity change represents cause and effect or whether the diversity curve includes sample biases linked to sea level change (e.g., see Smith 2001).

In the South China Block, taxa of Ibex Fauna I had high diversity in *TS.1a*, and most of them belong to the *Hysterolesus* fauna of latest Cambrian–earliest Tremadocian, including mainly agnostids, dikelokephalinids, ceratopygids, kainellids, and olenids. The diversity of Ibex Fauna I declined steeply to *TS.1d*, and from that point on the related forms never became diversified again (figure 24.12B). The Ibex Fauna II (chiefly Asaphidae and Nileidae) peaked in *TS.2b*, but otherwise its diversity was uniformly low through the Ordovician (figure 24.12B); members of it were only proportionally higher in *TS.1d–3a*

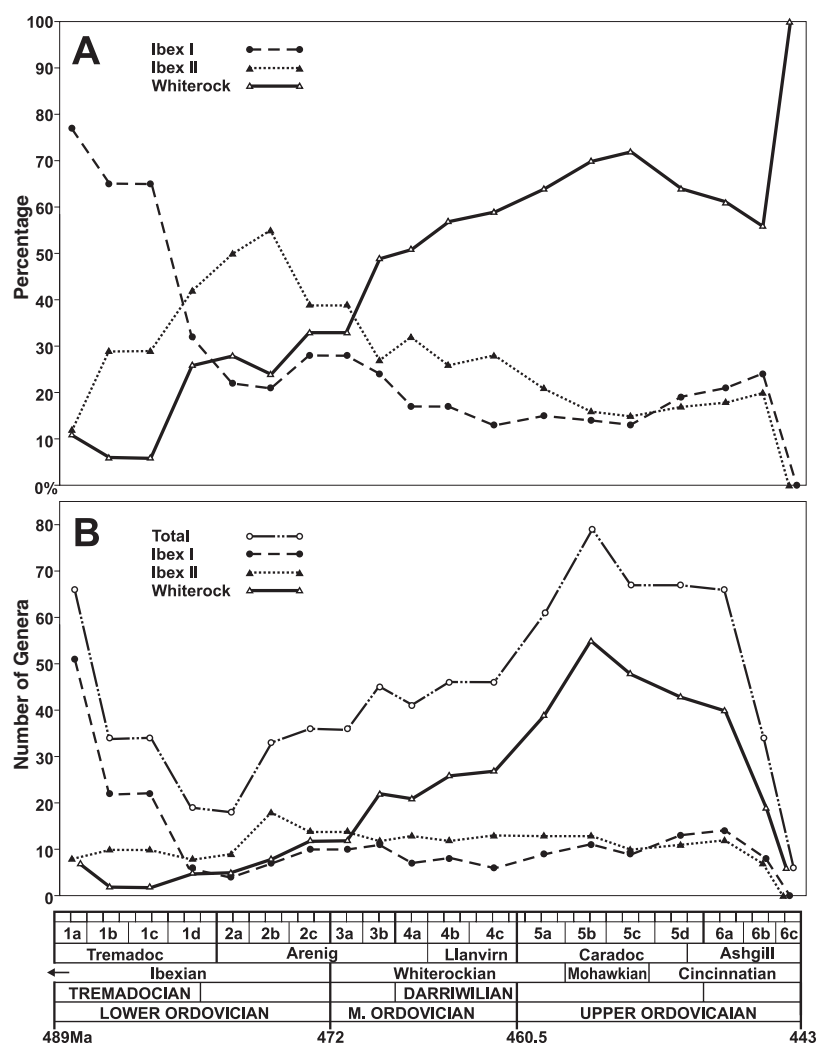


FIGURE 24.12. Proportion (A) and diversity (B) of Ordovician trilobite genera belonging respectively to the Ibex I, Ibex II, and White-rock faunas (Adrain, Fortey, and Westrop, this chapter) in each of 19 sampled intervals of the South China Block.

(figure 24.12A), suggesting that this fauna had once radiated here during the latest Tremadocian to early late Arenig. Both Ibex I and II faunas became extinct just prior to the end Ordovician mass extinction.

The main radiation of the Whiterock Fauna is recorded from the Mid Ordovician onward, with the peak of diversification attained during *TS.5b* (figure 24.12B). A slight decline in diversity followed through to *TS.6a*, and then there was a rapid decrease to the Hirnantian (figure 24.12B). The fauna was proportionally dominant over that of either the Ibex Fauna I or II from *TS.3b* (49 percent of total fauna) to *TS.6c* (100 percent) (figure 24.12A), consisting of mainly cyclopygids, cheirurids, raphiophorids, trinucleids, illaenids, calymenids, and isocolids. Most of the members were outer-shelf dwellers. The Whiterock Fauna survived the two-phase end Ordovician mass extinction and, after a short period of recovery,

reappeared in South China as the Silurian Fauna with representatives of up to 11 of its families during the mid Llandovery (mid to late Aeronian). In South China the main diversification of the Whiterock Fauna seems to have commenced during *TS.3b*, that is, early in the Mid Ordovician (just prior to the Darriwilian), when elements of the fauna occupied most environmental niches for the first time. This included the diversification of the mesopelagic cyclopygids as the Cyclopygid biofacies (see Fortey, later in this chapter) became established in South China during *TS.3b*.

■ Adaptive Deployment (RAF)

Biofacies profiles with their accompanying suites of trilobite faunas have now been recognized in the Ordovician for all the major paleocontinents. Although these follow a broadly shallow- to deep-water

trajectory, the factors controlling their distribution may be only secondarily related to depth per se—for example, the level of oxygenation present at the sediment surface may be the prime influence on which organisms are present in any given location, and characteristic trilobites adapted to deoxygenated habitats may have a depth spread. The range of niches occupied by the trilobites is an important part of the Ordovician Radiation. The taxonomic constitution and guild distribution of trilobite “communities” during the Ordovician are considered here along with the ways in which they differed from those in the Cambrian and Silurian. In so doing, assumptions must be made about life habits, which are by no means universally agreed. Fortey and Owens (1990a) identified a series of typical morphologies (“morphotypes”) repeatedly adopted by trilobites that subsequently (Fortey and Owens 1999) was extended to recognize feeding habits and habitat type. According to their criteria, the Ordovician was a time when more disparate trilobite taxa adopted a wider variety of morphotypes than at any other time, before or after (see also Foote 1991). This model is adopted here as the basis for discussion, although it would be surprising indeed if there were no modifications to this scenario in the future; nonetheless, it provides an explicit basis for this summary.

Pelagic Biofacies

Ordovician pelagic trilobites, mostly bearing enlarged (“hypertrophied”) eyes, were polyphyletically derived. The pelagic biotope was more richly populated in the Ordovician than in the Late Cambrian and was never reestablished in the Silurian or later, and thus it is a characteristic component of the Ordovician Radiation. The taxa involved belong to the Ibex Fauna and Whiterock Fauna of Adrain et al. (1998). Pelagic trilobites included both epipelagic and mesopelagic species (McCormick and Fortey 1998). The former included some of the most widespread of all trilobites across biofacies; the latter were particularly characteristic of sites marginal to Ordovician paleocontinents, to which they were confined until late in the Ordovician.

The mesopelagic community was preserved in the Cyclopygid biofacies and was remarkable for its stability. The earliest record is in the Tremadocian of

Argentina. The early history of the biofacies is entirely peri-Gondwanan. From the Arenig (Fortey and Owens 1987) to the Ashgill (Apollonov 1974) the Cyclopygid biofacies is taxonomically conservative, with the eponymous family dominating the trilobites. Fewer than 10 genera are present, and 6 (*Cyclopyge*, *Microparia*, *Degamella*, *Sagavia*, *Ellipsotaphrus*, and a pricyclopogyne) are to be found in virtually all these faunas. The fact that rarer, but distinctive, genera such as *Gastropolus* Whittard also have Arenig-Ashgill ranges indicates that the whole biotope may eventually be known virtually throughout the Ordovician. These genera are so conservative in morphology that it can be difficult to discriminate an Ashgill from an Arenig species. Cyclopygids are accompanied by the bizarre pelagic bohemillids—now considered aberrant remopleuridioids—and by the enigmatic *Cremastoglottos*; the latter having as long a stratigraphic range as any cyclopygid. The mesopelagic habitat therefore persisted without a temporal break virtually throughout the Ordovician. The Cyclopygid biofacies did not survive into the Silurian, another line of evidence proving an oceanic crisis at the end of the Ashgill. It had no successor, and so it is absolutely diagnostic of the Ordovician Radiation. Pre-Ashgill Ordovician occurrences were in Avalonia, South America, central Europe, China, and Kazakhstan; in the Ashgill, typical Cyclopygid biofacies are known from Girvan, Scotland, and from Quebec, proving that it had crossed the Iapetus remnant into tropical paleolatitudes by then. *Symphysops* is known from “mound” faunas at that time (Dean 1974), and it is conceivable that the cyclopygids had extended their bathymetric range toward the end of their history. Although very occasional cyclopygids can be found in shallower biofacies in the early Ordovician, they are mostly “stragglers.”

The epipelagic biotope is typified by Telephinae (*Carolinites*, *Oopsites*, *Opipeuter*, *Telephina*, and *Phorocephala*). The first three named did not survive the Mid Ordovician (Whiterockian) and were pan-tropical. One species (*Carolinites genacinaca*) has been described from North America, Siberia, China, and Australia (McCormick and Fortey 1999). *Telephina* and *Phorocephala* have early Laurentian records but apparently extended their ranges into high paleolatitudes by the Late Ordovician. No epipelagic type survived into the Silurian.

Olenid Biofacies

The olenid biofacies is typified by sulfide-rich, laminated black shale/dark limestone lithologies that accumulated under critically low oxygen conditions and included a restricted fauna adapted to these (Henningsmoen 1957), possibly including specialists capable of living symbiotically with sulfur bacteria (Fortey 2000). The biofacies continues uninterrupted through the Cambrian-Ordovician boundary and is thus composed of Cambrian-style taxa. Olenidae, often with many segments, low convexity, and wide thoraces, constitute the eponymous family. It is controversial whether the agnostoids that may co-occur with them were co-benthic. Other taxa were recruited into the Olenid biofacies through the Ordovician and at the same time assumed olenimorph morphological features, including alsataspidids (*Seleneceme*), Dionididae (*Aethedionide*), and remopleuridids (*Robertgia*). Multiplication of segments in some of these forms is spectacular. All are of Ibex Fauna type. It has been recognized that some members of this biofacies (e.g., *Bienvillia*, *Parabolinella*, *Hypermeccaspis*) were more or less independent of paleogeography. The Olenid biofacies typically is low gamma diversity/high individuals of species.

The terminal Ordovician crisis that extirpated the Cyclopygidae also eliminated the Olenid biofacies. Deep-sea oxygenated water entrained in oceanic overturn may have been the crucial factor in eliminating the appropriate environment. However, before the end of the Llandovery, olenimorphs (e.g., *Aulacopleura*) had reappeared, and so this trilobite habitat and biofacies is not uniquely Cambro-Ordovician.

Filter-Feeding Trilobites

Generally small trilobites having a vaulted cephalic chamber flanked by genal prolongations, thorax suspended above the sediment surface, weak axial musculature, "elevated" hypostome, and (usually) reduced eyes have been interpreted as having lived by filtering edible particles from suspension in a feeding chamber. Fortey and Owens (1990a) termed this the "trinucleimorph" design, and indeed this distinctive morphology is exemplified by the Trinucleidae, a diagnostically Ordovician family. However, it did not

first appear in trinucleids, and more than one Cambrian family likely to be only remotely related to Trinucleidae also included genera that showed trinucleimorph design. In the Ordovician, Raphiophoridae, Harpetidae, and Dionididae also typically adopted this morphology. Of these, the first two named are known to be present in the Tremadocian and have plausible Cambrian relatives; trinucleids and dionidids are known from Arenig and younger strata. Rarely, similar morphologies were adopted from other families; for example, the bathyurid *Madaraspis* was a Laurentian endemic found in strata otherwise lacking species with trinucleimorph design.

The early Trinucleidae were overwhelmingly Gondwanan in distribution, achieving more global distribution by the later Llanvirn (late Whiterockian). Raphiophoridae, Harpetidae, and Dionididae seem to be pandemic from the first, and certain genera belonging to these families (e.g., *Ampyx*, *Dionide*) are as widely distributed. Among harpetids some genera (*Eoharpes*) are confined broadly to high paleolatitudes, others (*Hibbertia*) to low ones. By contrast, trinucleids tend to endemism. Avalonia, for example, has at least 12 endemic genera (admittedly they may be "oversplit"); other endemic trinucleids are present on the Precordillera terrane of Argentina, which likewise enjoyed an independent history as a microplate. Some raphiophorids are as local: peculiar few-segmented forms such as *Taklamakania* and the distinctive *Bulbaspis* are confined to eastern Gondwana and common only in Tarim and Kazakh terranes. Elevated total diversity curves for these trilobites at times of terrane separation will be influenced by the addition of such local taxa. However, high endemism sits ill with the premise that the asaphoid larvae of trinucleimorphs were planktonic in habit (Chatterton and Speyer 1989), unless this planktonic phase was exceptionally short lived.

Suspension-feeding trilobites were not confined to one biofacies but are commonest in outer, or at least quieter, shelf environments, which is to be expected given their substrate preferences. They are typical of the Raphiophorid biofacies around Gondwana (Wales: Fortey and Owens 1978; Argentina: Waisfeld 1995) and Nileid biofacies or equivalent in Laurentia, South China, and Baltica. Although they have reduced eyes or are blind, they may be found associated with other trilobites bearing normal eyes. They may be abundant:

Ampyxina is commonly dominant on shaley limestones of Mid Ordovician age in Virginia, and the present author has observed black limestones of slightly younger age largely composed of *Taklamakanina* in northeastern Kazakhstan and Tarim (see also Zhou et al. 1994).

The great majority of Ordovician suspension feeders were members of the Ibex Fauna (Adrain et al. 1998; Adrain, Westrop, and Fortey, earlier in this chapter). Only one trinucleoid genus, *Raphiophorus*, survived the end Ordovician extinction, persisting until the Ludlow. Apart from the long-ranging harpetids, no other candidate for this life habit is known from the Llandovery, but later proetide-derived genera such as *Cordania* probably adopted it, and so it is not peculiarly Ordovician. However, it is true to say that these kinds of trilobites never again achieved the numerical abundance that they did during the Ordovician biodiversification event.

Particle Feeders

Small to middle-sized trilobites with natant hypostomes have been identified as sediment ingesters or particle feeders or both. They are abundant in the Cambrian among the paraphyletic “ptychoparioids.” During that time they may be found in any water depth. In the earlier Ordovician (Ibexian) the habit is represented mostly among Cambrian-style “survivors,” and in Laurentia, Siberia, North China, and Australia it is exemplified by trilobites traditionally assigned to the Hystricurinae. These are mostly found in rather shallow water deposits and may be associated with carbonate muds and silts. Some of the related Dimeropygidae may have had similar habits. In the Tremadocian of Gondwana, in fine-grained clastic deposits for the most part, some olenids that extended beyond the Olenid biofacies, and the eulomatids, were probably the ecologic equivalents of the Laurentian particle feeders. However, after the early Arenig there is a dearth of such forms in Gondwana, the reason for which is unclear. An important change occurs at the base of the Middle Ordovician, when Proetoidea and Aulacopleuroidea (Whiterock Fauna) appear with this morphology and remain almost its sole exemplars until the extinction of the Trilobita. It is clear that these trilobites must have had Cambrian ancestors, but the appearance, radiation, and spread

of these small trilobites through the Mid and Late Ordovician faunas remains a striking phenomenon. They were little affected by the end Ordovician extinction event and are familiar components of Silurian faunas. They also appear to have been tolerant of a variety of biofacies but are most varied and numerous in carbonate “mound” biofacies such as the Boda Limestone (Ashgill) in Sweden.

Predators/Scavengers

Trilobites with large, rigidly attached, often buttressed hypostomes with modified posterior borders (forks, burrs, and the like) are attributed to this life mode. There is clearly a variety of specializations within this general category of which we have as yet only speculative ideas. Phacopoids, with specialized visual systems, are considered together with highly distinctive odontopleurids, and it is likely that there were subdivisions with regard to nocturnal or diurnal habits, prey type, and so on, about which we know nothing. However, it is clear that the largest trilobites are of this type. Asaphids, in particular, include very large and robust trilobites, consistent with a position near the top of the food chain, and these are joined by Lichida in the later Ordovician, both groups having pronounced hypostomal forks. The largest trilobites in the Ordovician trilobite faunas of Bohemia (*Nobiliasaphus*), Avalonia (*Basilicus*), Iberia (*Uralichas*), North China (*Eoisotelus*), and Laurentia (*Isotelus*) conform to this type.

Trilobites of this giant kind are apparently found in inshore habitats, but predator/scavenger morphology can be found in any biofacies except the typical Olenid biofacies. The Early to Mid Ordovician inshore *Neseuretus* biofacies of Gondwana (and its temporal successors) is dominated by trilobites with conterminant hypostomes having calymenoid, dalmatoid, and asaphoid affinities. Hammann (1985) suggested that some trilobites with elevated eyes such as homalonotids may have been capable of burrowing. In deeper-shelf biofacies these groups are accompanied by trilobites with other feeding modes, continuing downslope to the atheloptic biofacies, in which the exemplars are often blind or have much reduced eyes. In Early Ordovician Laurentia, cheirurids (Pliomeridae, Cheiruridae) accompany asaphids in the shallower environments and are joined by caly-

menoids, Phacopina, Encrinuridae, Odontopleurida, and Lichida in younger strata. Asaphids are particularly varied in the shelf limestones of the Baltic paleocontinent.

Asaphida are part of the Ibex Fauna, which diminished progressively in importance through the Ordovician. However, asaphids (*Isotelus*) remain conspicuous in shelf limestones in the Cincinnati of North America. None survived the end Ordovician extinction event, and the proliferation of this group across Ordovician shelf seas can be regarded as a characteristic part of the “great biodiversification.” However, it is striking that the components of the Whiterock Fauna of Adrain et al. (1998) that survived the Ordovician-Silurian event included an array of suborders/families with predator/scavenger morphology that were among the most important components of post-Ordovician faunas: dalmanitids, phacopids, cheirurids, encrinurids, styginids, Lichida, and Odontopleurida among them (figure 24.2). Hence trilobites with attached hypostomes—with the addition of the natant Proetida—survived the Ordovician to provide the basis for subsequent trilobite evolution.

Atheloptic Trilobites

Fortey and Owens (1987) coined this term for a “community” of deep-water trilobites that were blind or with eyes much reduced, the majority of which also had close relatives with normal eyes inhabiting more shoreward paleoenvironments. In the Ordovician they were often accompanied by such trilobites as shumardiids and raphiophorids, which lacked eyes in the whole clade. Shumardiids were the last of the miniaturized (at about a millimeter in length) benthic trilobites, which were more diverse in the Cambrian and underwent a modest Ordovician radiation; they may have been particle feeders. They did not survive the Ordovician. The earliest atheloptic assemblage is Tremadocian from northern England (Rushton 1988). Examples are known from all the “series”: Arenig of South Wales, Llanvirn of Bohemia, Caradoc of Kazakhstan, and Ashgill of North Wales. A blind dalmanitoid, *Songxites*, is known from the Hirnantian of Dob’s Linn, Scotland, and Ireland (Siveter et al. 1980).

The atheloptic assemblage of genera typically includes a mixture of Ibex Fauna clades (e.g., nileids such as *Illaenopsis*, shumardiids) and Whiterock ones

(dindymenines, cheirurines, dalmanitoids). This biofacies, however, was apparently erased at the end of the Ordovician for a period lasting at least through the earlier half of the Silurian. Atheloptic biofacies are well developed again in the Devonian, but none of the proetides or phacopides occupying it then is closely related to the Ordovician examples.

■ Summary (JMA, GDE, RAF, ØH, JRL, TMcC, AWO, BGW, BDW, SRW, ZYZ)

Cluster analysis of all Ordovician trilobite families using nine biostratigraphic intervals shows that groups followed one of three diversity trajectories. Ibex Fauna I was successful during the Tremadocian and then rapidly declined; Ibex Fauna II radiated during the Arenig and then declined rapidly; the Whiterock Fauna radiated during the Ordovician diversification and was successful through the Ordovician. All the families that survived the end Ordovician mass extinction were members of the Whiterock Fauna. An Ordovician radiation of trilobites occurred globally, except for the tropics of Gondwana, and there was a strong geographic pattern to the radiation. Groups centered in high-latitude Gondwana began to radiate early in the Arenig, and the majority did not survive the end Ordovician. Tropical Laurentian (and Siberian) groups radiated during the late Arenig/early Whiterockian, and almost all survived the extinction. The Whiterock Fauna first dominated craton-margin environments in Laurentia and then spread onshore and offshore during the rest of the Ordovician. Regional diversity curves for Australasia, South America, Avalonia, Baltica, and South China reflect some of the paleogeographic subtleties of the biodiversity change of Ordovician trilobites across a spectrum of tectonic and latitudinal settings.

Ordovician trilobites occupied a variety of benthic niches in shallow to deep-water habitats and colonized the open seas. The pelagic habitat was remarkably persistent but did not survive the end Ordovician extinction event. The Olenid biofacies and atheloptic habitat were similarly affected, but their ecologic equivalents are known (with unrelated taxa) from younger strata. Among shelf faunas, the Ordovician was characterized by a proliferation of suspension-feeding genera; proetides were the principal deposit feeders from the Whiterockian onward. Members of

the Ibex Fauna dominated the pelagic and Olenid biofacies and included also some of the largest predatory/scavenger taxa. The majority of trilobites of the Whiterock Fauna that survived the end Ordovician extinction had attached hypostomes.

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