

Diversity, disparity and distributional patterns amongst the orthide brachiopod groups

Diverzita, disparita a principy rozšíření mezi skupinami orthidních brachiopodů

(4 figs)

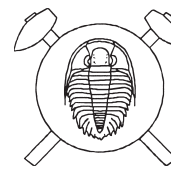
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The basic architecture of the deltidodont articulated brachiopod (strophomenates and early rhynchonellates) was established by the early Cambrian and diversified into a wide variety of morphologies during the early Ordovician radiation, prior to radiations amongst the more advanced cyrtomatodont types. The deltidodont division includes the pedunculate protorthides (early Cambrian–late Devonian), orthidines (mid Cambrian–mid Devonian) and dalmanellidines (early Ordovician–latest Permian). New classifications for the orthides, presented in the revised Treatise, are analysed using a number of tree metrics: The orthidine tree has a Stratigraphical Consistency Index (SCI), Relative Completeness Index (RCI) and a Gap Excess Ratio of 0.375, 78.79 %, 0.83 respectively whereas the dalmanellidine tree has SCI, RCI and GER values of 0.35, 48.47 %, and 0.395. The relatively low values of tree metrics for the punctate orthides partly reflect a less complete knowledge of dalmanellidine phylogeny. Many orthides originated and developed in shallow-water environments but radiated later into quieter, deeper-water niches or more specialised cryptic habitats. Radiations occurred as step-wise waves of diversification simulating ecological displacements by successive individual superfamilies within the Orthida and through the early Palaeozoic; peaks in diversity are matched by expansions in morphological disparity. The early to mid-Cambrian orthide radiation occurred at high latitudes; but by the early Ordovician most orthide families had widespread distributions. Few orthides occur in later Palaeozoic faunas. Macroevolutionary divergences presumably during the mid to late Cambrian, reflected at the family level, were apparently decoupled from later generic diversifications during the Ordovician together with abundance patterns of species and ecological events within superfamilial taxa.

Key words: Orthide brachiopods, Palaeozoic, diversity, disparity



Introduction

The basic architecture of the deltidodont articulated brachiopod (strophomenates and early rhynchonellates) was established by the early Cambrian and diversified into a wide variety of morphologies during the early Ordovician radiation, prior to radiations amongst the more advanced cyrtomatodont types (Williams et al. 1996). The deltidodont division includes, amongst others, the pedunculate protorthides (early Cambrian–late Devonian), orthidines (mid Cambrian–mid Devonian) and dalmanellidines (early Ordovician–latest Permian). This greater orthide group contains over 300 genera, with a record encompassing nearly 250 million years of earth history (Benton 1993). Schuchert – Cooper (1932) published an initial but authoritative analysis of the group prior to the first edition of the Treatise. Vladimír Havlíček (1977), however, in his detailed and beautifully illustrated revision of the Orthida of Czechoslovakia provided the most substantial compendium on the group predating publication of the revised Treatise (Williams et al. 2000). Orthide taxa were widespread geographically and occurred in a wide range of marine facies dominating the sessile benthos for much of the Palaeozoic. The recent phylogenetic revision of the group (Williams – Harper 2000a, b; Harper 2000) has permitted some analyses of the quality of the record and interpretations of the changing disparity, distribution and diversity of the orthide brachiopods through time.

Classifications

Two new cladistically-based classifications have been presented in the revised brachiopod Treatise (Williams et al. 2000) for the two suborders within the Orthida. The Orthida were defined and analysed with reference to over 40 sets of morphological characters (Williams – Harper 2000b, p. 720) and these formed the basis for the two classifications presented here (Figs 1, 2). The impunctate orthidines (Williams – Harper 2000b) were organized into two superfamilies, the Orthoidea (with 13 families) and Plectorthoidea (with 13 families) whereas the punctate dalmanellidines (Harper 2000) comprise the Dalmanelloidea (with 14 families) and the Enteletoidea (with 6 families).

Tree analyses

Three tree metrics were generated to assess and explore the efficacy and reality of these classifications. The Stratigraphic Consistency Index (SCI) measures the proportion of nodes on a tree that are stratigraphically consistent (Huelsenbeck 1994). The sequential appearance of nodes indicated by the cladogram is compared with the stratigraphical order of appearance of the fossil material. A particular node is considered to be consistent if the node below it is either stratigraphically older or of the same age according to data from the fossil record (Benton – Hitchin 1996). Values of the metric range from 0 to 1; a

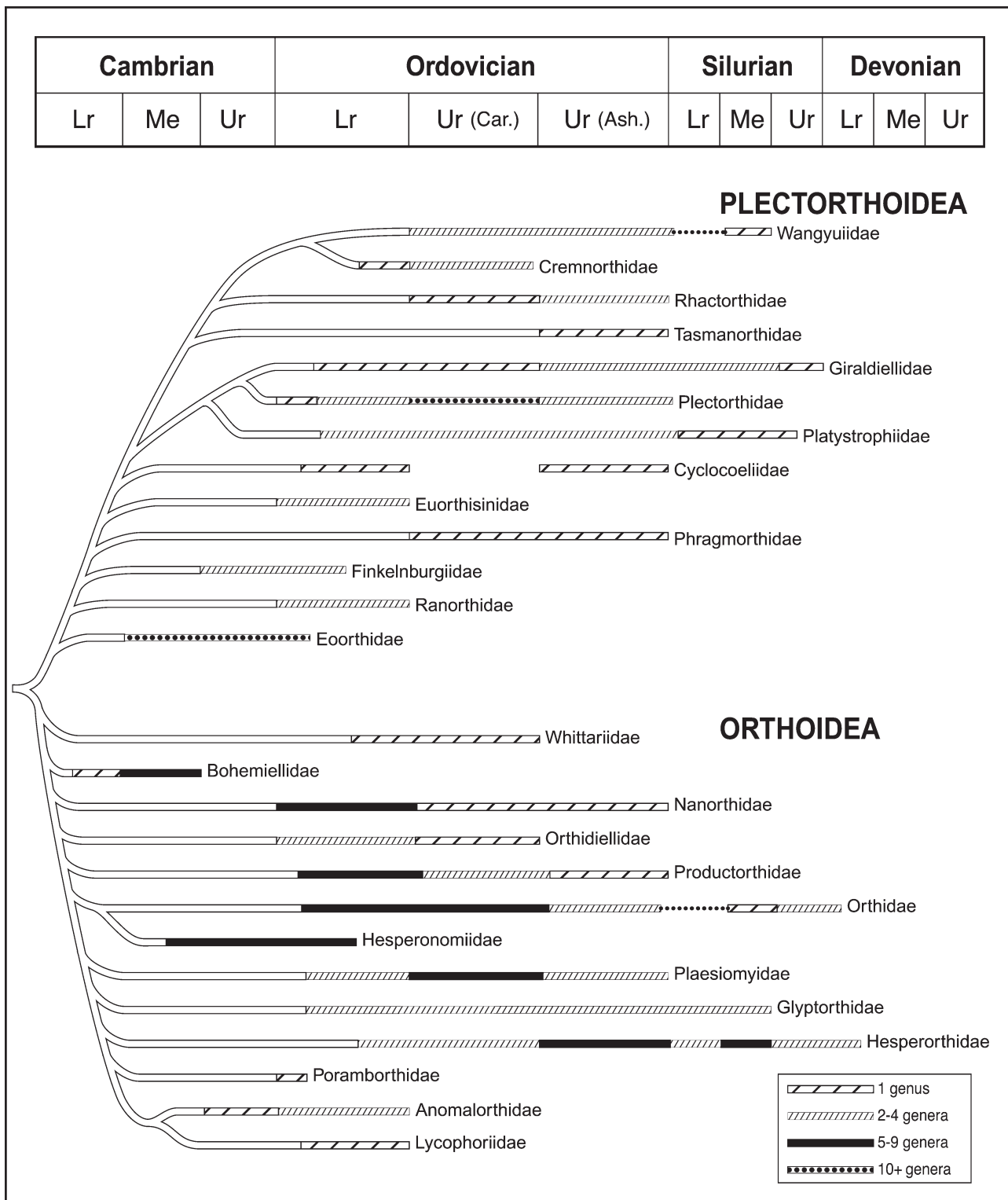


Fig. 1 Classification of the Orthidina: Phylogenetic tree for the orthidine brachiopods superimposed on a stratigraphical framework. The tree was developed from the published character set in the revised Treatise (Williams – Harper 2000b) and the tree together with its diversity data forms the basis for the analysis presented here.

value of 1 is recorded when all the nodes are consistent and 0 when all are inconsistent.

The Relative Completeness Index (RCI) is a measure of the amount of stratigraphical gap indicated by a comparison between the respective cladogram and strati-

graphical range chart for a group of related fossils (Benton – Storrs 1994). The proportion of the reported range, or standard range length, is compared with the minimum implied gap, or ghost range; the results are expressed as percentages.

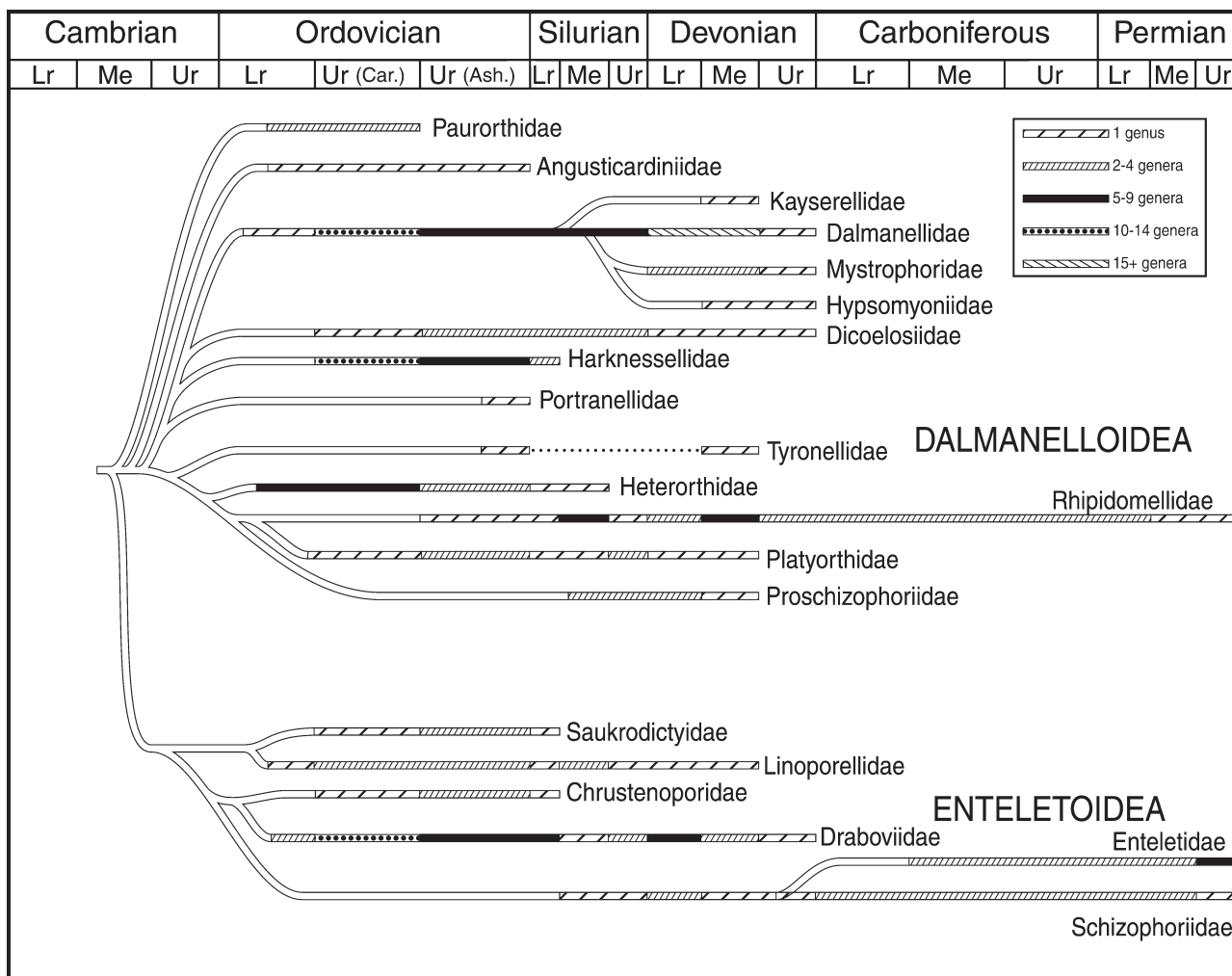


Fig. 2 Classification of the Dalmanellidina: Phylogenetic tree for the dalmanellidine brachiopods superimposed on a stratigraphical framework. The tree was developed from the published character set in the revised Treatise (Williams – Harper 2000b) and the tree together with its diversity data forms the basis for the analysis presented here.

The Gap Excess Ratio (GER) measures the congruence between the cladogram and the fossil record by calculating the difference between minimum implied gap and the minimum possible ghost range as a fraction of the range of possible values for the stratigraphical data on a tree (Wills 1999). The best-fit solution is indicated by 1 and zero congruence is indicated by 0.

All three metrics have been graphically explained with a series of hypothetical data by Benton et al. (2000, Fig. 2). SCI, RCI and GER values have been calculated for the orthidine and dalmanellidine trees (Table 1) using GHOSTS (Wills 1999).

Table 1 Tree metrics for the Orthidina and Dalmanellidina trees.

	SCI	RCI	GER
Orthidina	0.375	78.79	0.830
Dalmanellidina	0.350	48.47	0.395

Although the SCI values for both suborders are similar there are marked differences between the RCI and GER metrics. Whereas the consistency of the stratigraphical

order of appearance of taxa in both groups does not differ, the stratigraphical record of the dalmanellidines is markedly less complete. This is exaggerated by the cryptogenetic appearance of groups such as the linoporellids, portranellids, saukrodictyids and the tyronellids that are difficult to classify.

Disparity and diversity

Disparity has been defined in a number of different ways. Despite considerable debate there is currently no agreed definition or standard measurement of disparity. Wills et al. (1994) defined disparity as the range or significance of morphology in a given sample of organisms. The raw data matrices, which formed the basis for the new classifications of the orthidines (Fig. 1) and the dalmanellidines (Fig. 2), have been analysed herein to generate a range of disparity and variety indices.

The raw data matrices were first processed by MATRIX 1.0 (Wills 1999) to generate near-Euclidean triangular distance matrices; two disparity measures were cal-

Table 2 Disparity and distance indices calculated for Orthidina and Dalmanellidina.

Taxa	Number	Product of variances	Product of ranges	Σ of variances on all axes	Σ of ranges on all axes	Mean Euclidean distance	Mean Manhattan distance
Orthidina	26	0.39	2.53	8.72	55.43	4.15	17.48
Dalmanellidina	20	0.47	2.64	7.96	44.42	3.97	16.07
Orthidina Caradoc	17	0.26	1.94	8.53	40.73	4.11	17.25
Dalmanellidina Caradoc	11	0.42	2.05	7.88	27.13	3.99	16.24
Orthidina Wenlock	6	0.18	1.08	6.67	13.92	3.83	14.93
Dalmanellidina Wenlock	9	0.27	1.58	7.17	22.16	3.82	14.69
Orthidina Pragian	2	0.99	1.41	2.23	2.90	3.61	13.00
Dalmanellidina Pragian	12	0.26	1.77	7.36	28.19	3.84	15.09
Caradoc Orthida	28	0.14	1.63	9.12	60.81	4.24	18.26
Wenlock Orthida	15	0.38	2.11	8.33	35.12	4.07	16.78
Pragian Orthida	14	0.27	1.80	8.01	32.33	4.01	16.44

culated, the mean Euclidean distance between all taxa and the mean Manhattan distance between all taxa. Output files from MATRIX were then processed by Principle Coordinate Analysis (PCO) using MVSP 3.1 (Kovach 1993–1998); the scores of taxa on the eigenvectors were further analysed by RARE 1.1 (Wills 1999) to generate an additional four disparity indices: sum of ranges, product of ranges, sum of variances and product of variances. Rarefaction profiles were also generated based on the disparity values for all the sample sizes between two and the maximum number of taxa in the data set; these data were input to EXCEL and graphed.

Overall, with the exception of the measures of range and variance products, the Orthidina show greater disparity values than those of the Dalmanellidina although the differences are not large (Table 2). This reinforces the commonly held view that the taxonomic differences are more finely drawn within the punctate orthides; this is probably even more marked at the generic level. Over the three time slices investigated, the orthidines show a greater disparity than the dalmanellidines during the late Ordovician (Caradoc) radiation (excepting the value for the variance product) whereas the dalmanellidines show a greater disparity than the orthidines during the mid Silurian (Wenlock) and the early Devonian (Pragian). During the Wenlock all values for disparity suggest greater disparity within the dalmanellidines, excepting values for the mean Euclidean and mean Manhattan distances which are convergent for both suborders. Values for the Pragian taxa also indicate a greater disparity amongst the dalmanellidines except again for the variance product. This is not surprising since the middle Devonian orthidines comprise only two families in contrast to 12 dalmanellidine families. The number of taxa, particularly higher taxa, commonly correlates with the amount of morphological diversity, although there are exceptions (Valentine 1969); moreover the taxonomic status of a particular group need not act as a proxy for a particular level of morphological difference (Wills et al. 1994).

The variance and range of characters along any given axis are used as a proxy of variation (Foote 1991); these

parameters were calculated for the greater orthide clade (Table 2). The product of variance and range simulates the hypervolume occupied by the data set. This product is scaled to a single dimension by taking the n^{th} root, where n is the number of dimensions in the measurement space, to reduce the inflation of the product as more dimensions are added. Alternatively the sum of variances or ranges for the sample may be calculated (Foote 1992). This may be a more robust measure for this type of data (Wills 1998a).

Based on estimates of hypervolume, overall the dalmanellidines show a slightly greater disparity than that for the orthidines, and this is also evident in each of the three time slices selected. Using the alternative method of summing the variances and ranges the orthidines have a greater disparity than the dalmanellidines. Inconsistencies with the use of product-based measures of disparity were not resolved in the present study although these problems are not unique (see also Wills 1998a, b).

Rarefaction techniques are frequently used to compensate for the effects of sample size in a range of sample-based analyses. Rarefaction curves for the Orthidina and Dalmanellidina, based on the sum of variances on all axes describe similar paths with the track of the orthidines above the dalmanellidines. Orthides reached a peak disparity and diversity during the late Ordovician and despite differences in sample size the orthidines have a greater disparity than the dalmanellidines (Fig. 3a). Over the three time slices investigated, the Ordovician orthides demonstrated a significantly greater disparity than those in the Silurian and Devonian (Fig. 3b) that were competing within cyrtomatodont-dominated sessile benthos. Rarefaction curves for late Ordovician (Fig. 3c), mid Silurian (Fig. 3d) and early Devonian (Fig. 3e) for orthidine and dalmanellidine brachiopods indicate that during the first interval orthidines developed the greater disparity; during the subsequent two intervals the dalmanellidines developed the greater disparity.

The protorthides (Williams – Harper 2000b) contain only four taxa and not surprisingly disparity values are smaller than those corresponding values for the orthidines

and dalmanellidines. Nevertheless the differences between the mean Manhattan distances for all the protorthide taxa and those of the dalmanellidines are not especially large (Table 3); and the mean Euclidean distance between all protorthide taxa is very close to that for the dalmanellidines. But the other indices indicate that the protorthides are less disparate than the orthidines and the dalmanellidines.

Diversity profiles have been developed for each of the orthide superfamilies together with the protorthoids (Fig. 4). Major radiation and extinction events within these groups have been identified at the family and series level. These analyses are relatively broad but are derived directly from the new classifications of the greater orthide group and revised data available for its geographical and stratigraphical distributions. Peaks are developed sequentially for the protorthoids, orthoids, plectorthoids, dalmanelloids and enteletoids.

Rarefaction Curves for Orthidina and Dalmanellidina

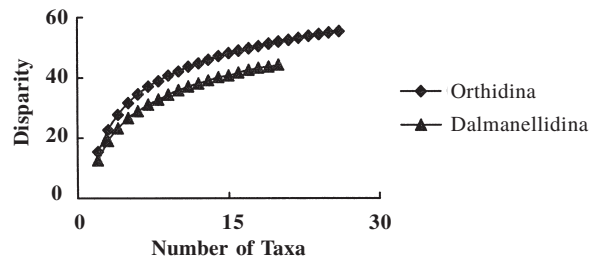


Fig. 3a Rarefaction curves for mid to late Ordovician orthidine and dalmanellidine brachiopods: During this interval the orthidines developed the greater disparity.

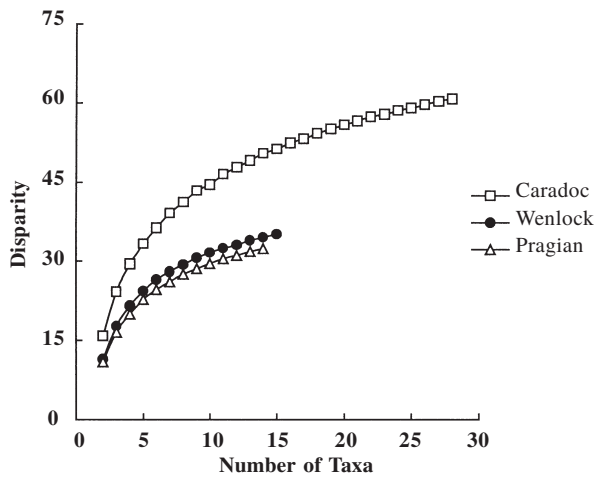


Fig. 3b Rarefaction curves for Caradoc, Wenlock and Pragian orthide brachiopods: Orthide brachiopods had a greater morphological disparity during the late Ordovician than in the mid Silurian and early Devonian.

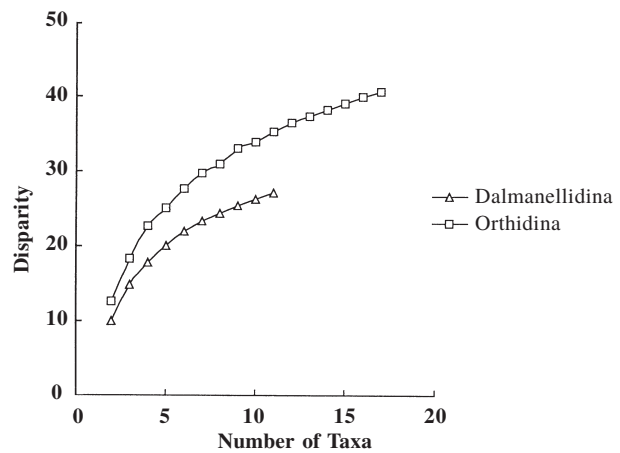


Fig. 3c Rarefaction curves for late Ordovician orthidine and dalmanellidine brachiopods: During this interval the dalmanellidines developed the greater disparity.

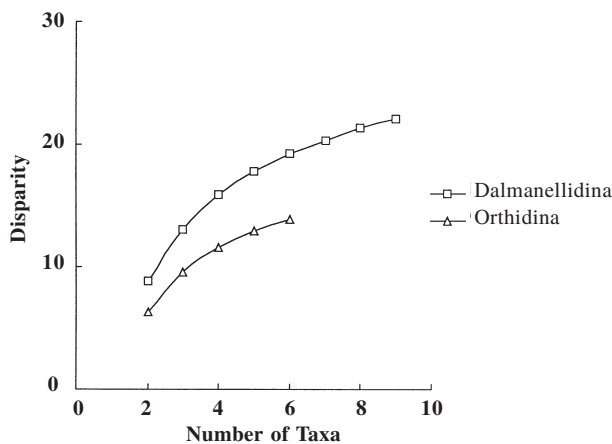


Fig. 3d Rarefaction curves for mid Silurian orthidine and dalmanellidine brachiopods: During this interval the dalmanellidines developed the greater disparity.

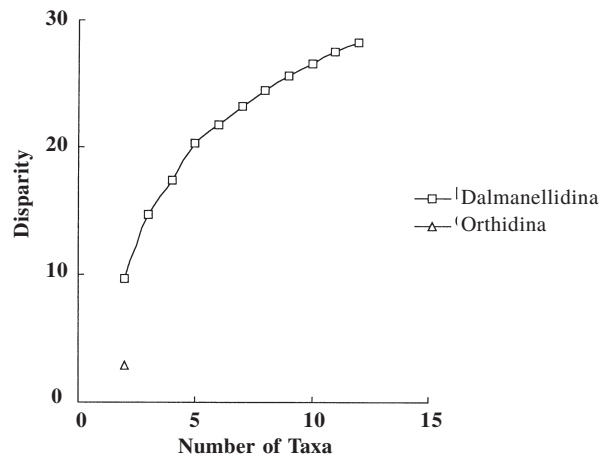


Fig. 3e Rarefaction curves for early Devonian (Pragian) Dalmanellidina and Orthidina.

Table 3 Disparity and distance indices calculated for Protorthida.

Taxa	Number	Product of variances	Product of ranges	Σ of variances on all axes	Σ of ranges on all axes	Mean Euclidean distance	Mean Manhattan distance
Protorthida	4	1.09	2.20	5.32	9.54	3.85	15.17

Evolution of the Orthida in time and space

Many orthide groups apparently originated and developed in shallow-water environments but radiated later into quieter, deeper-water niches or more specialised cryptic habitats during their phylogeny (Sepkoski – Sheehan 1983; Harper et al. 1999). The pattern of radiations suggest step-wise waves of diversification simulating ecological displacements by successive individual superfamilies within the Orthida and through the early Palaeozoic (Fig. 4); peaks in diversity are matched by expansions in morphological disparity in the orthidines but this correlation is less clear in the dalmanellidines, where generic distinctions are less marked.

The initial early to mid-Cambrian radiation of the group, involving the protorthoids and early orthoids, apparently occurred at high latitudes; many of the earliest families have distributions associated with Gondwana and its adjacent terranes (Williams – Harper 2000a, b). But during the early Ordovician radiation most orthide fam-

ilies had widespread distributions although the geographical ranges of genera were more restricted. Macroevolutionary divergences presumably during the mid to late Cambrian, reflected at the family level, were apparently decoupled from later generic diversifications during the Ordovician together with abundance patterns of species and ecological events within superfamilial taxa (Harper et al. 1999).

During the Ordovician radiation approximately 75 % of all orthidine families occurred in over two distinct geographical regions with the more aberrant and arguably specialized taxa, such as the cyclocoelids, lycophoriids, porambonorthids and whittardiids having the more restricted distributions. When the dalmanellidines are added about 80 % of orthide families attained a relatively widespread geographic range during this interval probably associated with spread of taxa into deeper-water environments (Sepkoski – Sheehan 1983). In contrast during the Devonian approximately 50 % of families occurred in over two geographic regions. Many Devonian dalmanel-

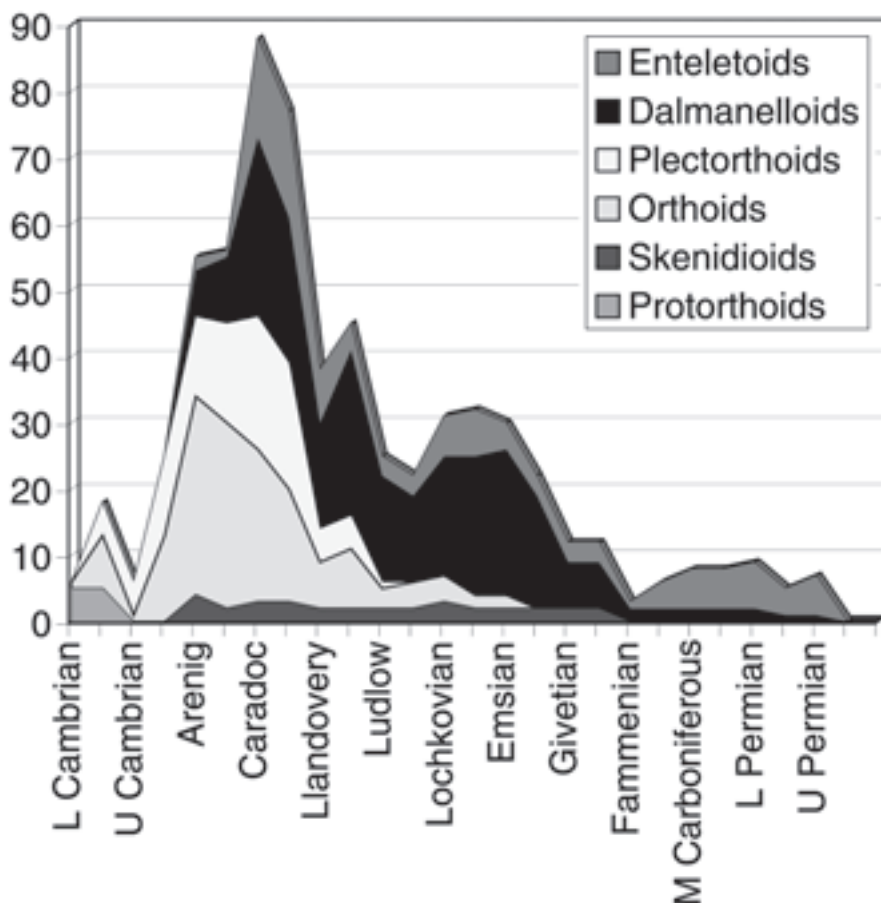


Fig. 4 Diversity tracks for the main groups of orthide and related brachiopods during the Palaeozoic. Peaks are developed sequentially for the protorthoids, orthoids, plectorthoids, dalmanelloids and enteletoids.

lidines, such as the kayserellids and mystrophorids, developed highly specialized morphologies during more local radiations or evolutionary bursts (Cooper – Williams 1952) commonly associated with narrower niches in carbonate environments.

Few of these deltidodont taxa are represented in later Palaeozoic faunas; these survivors, for example *Schizophoria* (Enteletoidea) and *Rhipidomella* (Dalmanelloidea), continued as a minor part of cyrtomatodont and productide-dominated epifaunal benthos. The patterns of local radiations continued during, for example, the late Permian when local radiations generated a range of highly-specialized taxa, commonly with relatively short ranges (Shen – Shi 1996).

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Diverzita, disparita a principy rozšíření mezi skupinami orthidních brachiopodů

Základní stavba misek deltidodontních artikulárních ramenonožců (strophomenárních a časných rhynchonellatních) se ustálila již ve spodním kambriu a diverzifikovala se do mnoha rozdílných morfologií v průběhu spodnoordovické radiace, před diverzifikací vývojově dokonalejších cyrtomatodontních typů. Deltidiotní skupina zahrnuje pedunkulární protorthidy (spodní kambrium až svrchní devon), orthidiny (střední kambrium až střední devon) a dalmanellidiny (spodní ordovik až pozdní perm). Nové klasifikace orthidních brachiopodů, které jsou použity v revidovaném vydání *Treatise*, jsou analyzovány s použitím tří indexů: linie orthidních brachiopodů má Stratigraphical Consistency Index (SCI), Relative Completeness Index (RCI) a Gap Excess Ratio: 0,375, 78,79 % a 0,83, zatímco u linie dalmanellididních brachiopodů jsou indexy SCI, RCI a GER v hodnotách 0,35, 48,47 % a 0,395. Poměrně nízké hodnoty u linie punktátních orthidů částečně odrážejí méně dokonalou znalost fylogenetické historie dalmanellididních brachiopodů. Mnoho orthidních brachiopodů vznikalo a rozvíjelo se v mělkovodních podmínkách, s radiací do klidnějších hlubokovodních ekologických nik nebo do speciálních kryptických prostředí. Radiace probíhala formou postupných kroků diverzifikace a sledovala ekologickou záměnu jednotlivými následnými nadčeledmi v rámci řádu Orthida v průběhu staršího paleozoika. Vrcholy diverzity jsou vyznačeny expanzí morfologické disparity. Spodno a střednokambriická radiace orthidních brachiopodů probíhala ve vysokých zeměpisných šířkách, avšak ve spodním ordoviku většina orthidních čeledí měla celosvětové rozšíření. Málo orthidních brachiopodů se vyskytuje ve faunách mladšího paleozoika. Makroevoluční rozdíly předpokládané během středního a svrchního kambria se projevily na úrovni čeledí, byly jak se zdá svázány s pozdější rodovou diverzifikací během ordoviku a rovněž s hojností druhů a ekologických strategií u taxonů úrovně nadčeledi.

