

# Global analyses of brachiopod faunas through the Ordovician and Silurian transition: reducing the role of the Lazarus effect

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**Abstract:** Global analyses of 88 families and 284 genera of brachiopods from middle Ashgill, Late Ordovician, to early–middle Rhuddanian, Early Silurian, indicate that 18.6% and 12.5% of families and 51.0% and 41.3% of genera were eliminated in the first and second phases of the end-Ordovician mass extinction, respectively, with the total loss of 28.4% of families and 69.0% of genera in the crisis. New investigation demonstrates that brachiopods, at both generic and familial levels, suffered greater during the first phase than during the second phase. Four groups (victims, relicts, survivors, and new arrivals) are distinguished by their stratigraphical ranges. Generic survivors, occurring in the Kosov Province during the Hirnantian, can be split into three types with respect to their changing abundance: increasing, declining, and Lazarus taxa. Among the 88 genera that survived, numerous declining genera occurred in the Hirnantian: 16 Lazarus families and 18 Lazarus genera are provisionally known and may be regarded as end members of the declining type. Comparison of the abundance, population size, and distribution patterns of declining and Lazarus taxa shows important similarities between these two types which contribute to a better understanding of the nature of Lazarus taxa. In addition to these biological attributes, taphonomic failure and generally poor preservation, together with collecting bias and inadequate systematic data, are clearly involved. More collections will undoubtedly globally reduce the number of Lazarus taxa. A single, common refugium for end-Ordovician brachiopods probably did not exist; rather, these taxa used paleogeographically scattered locations in a range of environments for survival.

**Résumé :** Des analyses globales de 88 familles et de 284 genres de brachiopodes de l'Ashgill moyen (Ordovicien tardif) au Rhuddanien précoce à moyen (Silurien précoce) indiquent que 18,6 % et 12,5 % des familles et 51 % et 41,3 % des genres ont disparu durant les première et deuxième phases, respectivement, de l'extinction massive de la fin de l'Ordovicien, pour une disparition totale de 28,4 % des familles et 69 % des genres durant cette crise. Une nouvelle étude démontre que les brachiopodes, tant au niveau du genre qu'à celui de la famille, ont été plus touchés durant la première phase que durant la seconde. Quatre groupes distincts (victimes, reliques, survivants et nouveaux venus) peuvent être établis selon leurs distributions stratigraphiques respectives. Les survivants génériques, qui se trouvent dans l'Hirnantien de la province du Kosovo, peuvent être divisés en trois types selon l'évolution de leur abondance : les taxons dont l'abondance augmente, les taxons dont l'abondance diminue et les taxons lazars. Des 88 genres survivants, bon nombre ont connu une diminution de leur abondance durant l'Hirnantien; 16 familles et 18 genres lazars sont provisoirement connus et peuvent être considérés comme représentant les membres extrêmes des taxons dont l'abondance diminue. Une comparaison de l'abondance, de la taille des populations et de la distribution des taxons dont l'abondance diminue et des taxons lazars révèle d'importantes similitudes qui permettent une meilleure compréhension de la nature des taxons lazars. Une taphonomie imparfaite et la piètre préservation généralisée, combinées à la subjectivité des collections et à des données systématiques inadéquates sont toutefois d'importants facteurs. L'intégration d'autres collections à ce type d'étude mènera indubitablement à une diminution du nombre de taxons lazars. Il est peu probable qu'un refuge unique commun aux brachiopodes de la fin de l'Ordovicien ait existé. Ces taxons se sont plutôt repliés sur divers sites paléogéographiques présentant un éventail d'environnements propices à leur survie.

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## Introduction

The Ordovician–Silurian transition is one of the best studied of the five major mass-extinction events (e.g., Brenchley 1984; Sheehan 1988, 2001; Sheehan and Coorough 1990; Harper and Rong 1995, 2001; Sheehan et al. 1996; Armstrong 1996). Intensive research on the location of the boundary in time and space has provided an initial impetus for a range of research projects involving faunal distributions through the boundary (e.g., Chen et al. 2000) and environmental and isotopic changes (Brenchley et al. 1994, 1995, 2003; Marshall et al. 1997). In particular, a brachiopod database within the framework of a stable and precise graptolitic zonation within this interval (Rong et al. 2002) can provide tests for hypotheses associated with the Lazarus effect.

Although various major groups of brachiopods suffered greatly during the extinction, there was phylogenetic and ecological continuity between the Late Ordovician and Early Silurian shelf faunas (Droser et al. 1997). Baarli and Harper (1986) demonstrated that the end-Ordovician mass extinction of brachiopods did not cease at the earliest Silurian with the presence of a relict Ordovician association. The initial Silurian fauna consists of the more eurytopic taxa of the regressive succession that survived the extinction in the deeper parts of the intracratonic basin of the Oslo region. They were subsequently able to create and participate within new community structures during the Early Silurian transgression (Rong and Harper 1999).

The Lazarus effect has been manifested in different ways among major fossil groups. The rare occurrence of numerous taxa following mass extinction is related to several factors. Biological factors are objective indicators of extinction events, including the reduction of population size and the number of silicified assemblages. In addition, the incompleteness of the fossil record (e.g., an extended interval of poor preservation) involves stratigraphical factors (e.g., development of facies), artificial factors (e.g., collection bias, sampling failure), and a combination of all these factors (Wignall and Benton 1999; Fara 2001; Twitchett 2001). Some collections are too small to yield rare and uncommon forms. It is important to analyse the nature and implications of the rarefaction (collector) curve (Boucot 1975). A biomass reduction model has been proposed to suggest a mechanism by which the Early Triassic marine fossilization low was created (Twitchett 2001). Inadequate taxonomic study may also lead to large numbers of Lazarus taxa.

Through a global analysis of the Late Ordovician and Early Silurian brachiopods, recognition of different groups of brachiopod genera, particularly the surviving genera, and a comparison of the Lazarus genera with declining genera (see later in the paper) are made herein for a better understanding of the brachiopod turnover from the middle to late Ashgill and Rhuddanian.

## Global data for the latest Ordovician

Up-to-date information on major groups within this phylum at familial and generic levels known through the Ordovician–Silurian transition is available chiefly in the revised version of the *Treatise on invertebrate paleontology: Part H: Brachiopoda* (Williams et al. 2000, 2002). The familial and

generic record is given by time interval in Appendices A and B. The number of extinct families and genera at the two phases of the extinction and the number of newly established taxa are provided in Table 1 and can be compared with those of Sheehan and Coorough (1990) in Table 1.

Paleogeographically, the latest Ordovician (Hirnantian) brachiopods have been grouped into three provinces (Rong and Harper 1988). The Kosov (K) Province, a cool-water biogeographical unit, contains a *Hirnantia* fauna occurring in many blocks, mainly in the temperate and subtropical zones during the crisis. There are two subunits recognized: (1) a typical subunit possessing a real *Hirnantia* fauna; and (2) an atypical, scattered subunit characterized by the presence of some elements of the fauna associated with unknown or uncommon genera in the typical *Hirnantia* fauna (more discussion later in the paper).

The Edgewood (E) Province, a warm-water unit mainly in lower latitudes, includes some genera (e.g., *Leptoskelidion*, *Parastrophinella*, *Thebesia*) unknown in the K Province, lacks a typical *Hirnantia* fauna, but yields some eurytopic and common elements of the *Hirnantia* fauna (e.g., *Dalmanella*, *Leptaena*, *Eostropheodonta*, *Hindella*) in Laurentia (e.g., central US and Anticosti Island) (Amsden 1974; J. Jin, personal communication, 2002; P. Copper, personal communication, 2002), Kolyma (Oradovskaya 1983), parts of Estonia (e.g., Harper and Hints 2001; M. Rubel, personal communication, 2002), and Tadzhikistan (Menakova 1991). The *Thebesia* Association of Hovedøya S 10, Oslo, and the *Brevilamnulella* Association of Hvalsbakken 20, Asker (Brenchley and Cocks 1982; Cocks 1982), in which no typical *Hirnantia* fauna is present, show close affinities with the Edgewood Province. Khingan-Altai (Kul'kov and Severgina 1987) may possibly be assigned to this unit.

The Bani (B) Province, a cold-water unit in higher latitudes with low-diversity associations, marked the margin of the polar ice sheets in Morocco, Algeria, Libya (Havlíček 1989, 1990), and possibly South Africa (Cocks et al. 1970). *Hirnantia* and *Plectothyrella*, two distinctive genera of the *Hirnantia* fauna, occur with endemic forms (*Destombesium*, *Arenorthis*, and *Undithyrella*) absent in the other two provinces. There are also differences at the species level between the Bani and Kosov *Plectothyrella* (Villas et al. 1999).

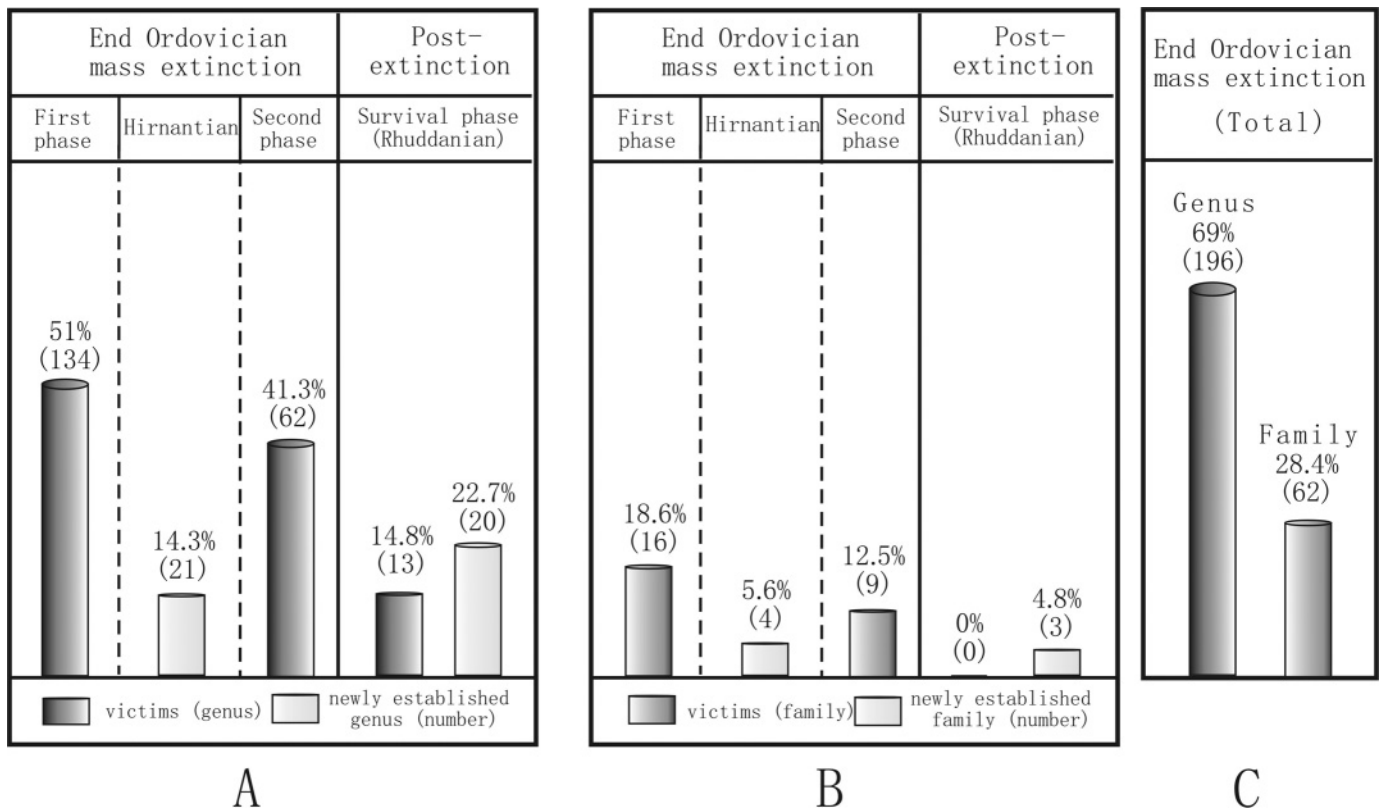
## Four groups of taxa recognized across the extinction

With respect to the stratigraphical ranges of taxa through the Ordovician–Silurian transition, there are four groups of brachiopod taxa that may be treated at different taxonomic levels: (1) victims, (2) relicts, (3) survivors after the different pulses of the terminal Ordovician extinction, and (4) newly established taxa after the first pulse of the extinction (Appendix A) Different views of the stratigraphic range of brachiopod families and genera across the crisis are shown in Figs. 2–5.

### (1) Victims

The victims went extinct at different time intervals (Appendix A). Among 88 families, 28.4% (25) were wiped out in the extinction, and 18.6% (16/(88 – 4)) and 12.5%

**Fig. 1.** Percentages of extinct and newly established genera (A) and families (B) in different time intervals through the Ordovician–Silurian transition. (C) Totals for all genera and families.



**Table 1.** Counts at generic level in this paper compared with those of Sheehan and Coorough (1990).

Count items	Sheehan and Coorough 1990	This paper
Eliminated at the 1st phase of the extinction	92 (44.0%)	134 (51.0%)
Eliminated at the 2nd phase of the extinction	63 (51.0%)	62 (41.3%)
Total number of lost genera in the extinction	141 (67.0%)	196 (69.0%)
Number of new genera arising in the Hirnantian	21 (17.0%)	21 (14.3%)
Number of genera in the Hirnantian	124	147

(9/(88 – 16)) vanished during the first and second pulses, respectively. At the generic level, the total rate of extinction is 69.0% ((134 + 62)/284); 51.0% (134/(284 – 21)) and 41.3% (62/(284 – 134)) disappeared at the first and second pulses, respectively (Figs. 6, 7). Our investigation demonstrates that brachiopods, at both generic and familial levels, suffered greater at the first pulse than at the second pulse, contrary to the results of Sheehan and Coorough (1990). It may be noted that nearly 14% of brachiopod genera became extinct in the earliest Llandovery.

## (2) Relicts

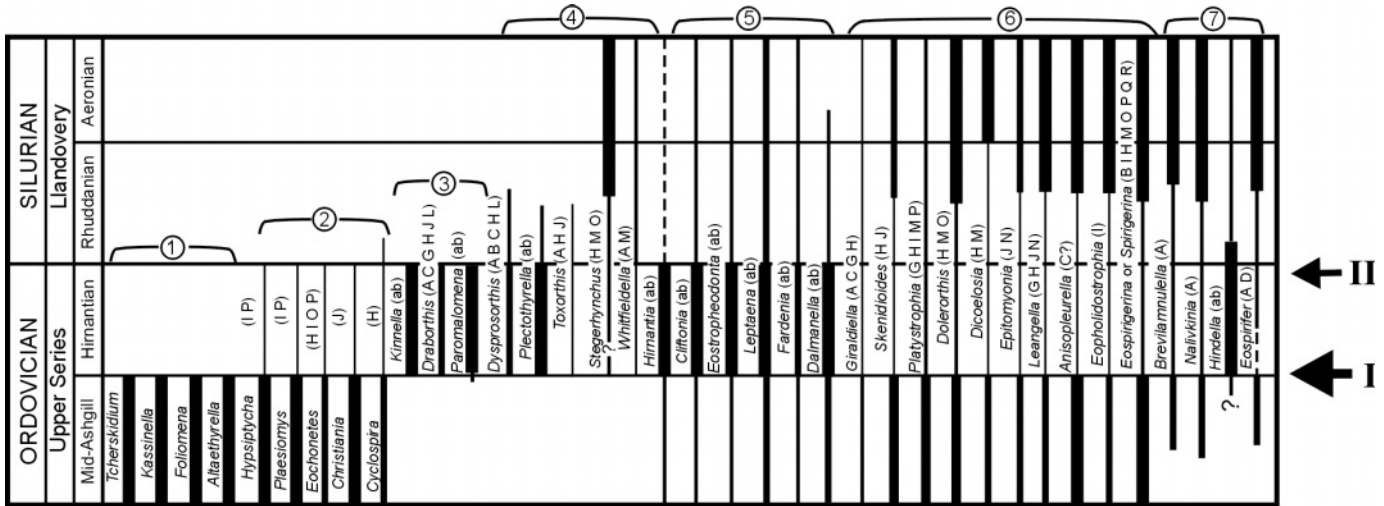
This group consists of taxa that survived one or two phases of the extinction without recovery (Appendix A). This phenomenon has been recently termed “dead clade walking” by Jablonski (2002). Fifty-one genera in the Hirnantian and 13 in the Rhuddanian may be assigned to this group. All, except a few taxa (e.g., *Aegiromena*), are known from relatively few localities. The great majority of this group is recorded

from the K Province, with nearly 1/3 and 1/10 from E and B provinces, respectively. Some (e.g., *Hebertella*, *Thaerodonta*) occurred only in the E Province (Lespérance 1985; Jin 2001; M. Rubel, personal communication, 2002), and others (e.g., *Plaesiomys*, *Hypsiptycha*) in both K Province (Temple 1968; Harper 1979; Williams and Wright 1981) and E Province (J. Jin, personal communication, 2002) and rarely in B Province. Many of them were common in the middle Ashgill and rare in the Hirnantian, indicating a drastic reduction in population size and individual abundance with a scattered distribution pattern.

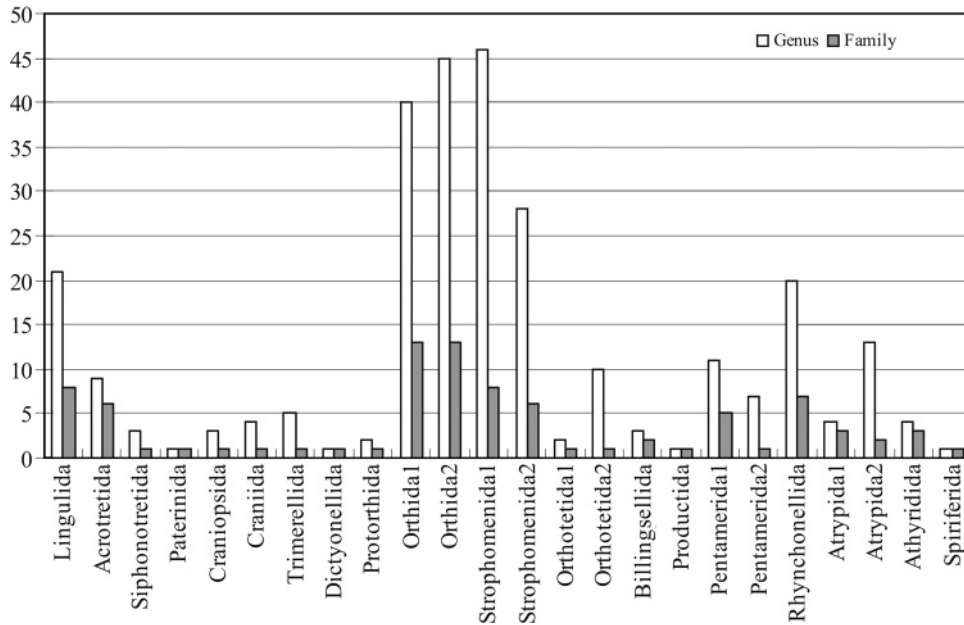
## (3) Survivors

Among 88 families, 71.6% (63) survived the extinction, with 16 Lazarus families. Among the total 88 genera that survived the crisis (relicts included), 57 (nearly 2/3 of the total) ranged from the middle Ashgill through the Hirnantian into the Silurian, with 18 Lazarus genera (20.5%), and 12 (13.6%) from the Hirnantian into the Llandovery (Figs. 5, 8, 9).

**Fig. 2.** Range of common brachiopod genera through the Ordovician–Silurian transition: 1, victims in the first phase of the extinction; 2, relicts in the Hirnantian or Rhuddanian; 3, new arrivals (some disaster taxa) within the Hirnantian; 4, new arrivals extended into early Llandovery or later; 5, increasing survivors; 6, declining survivors; 7, progenitors (they are not grouped with the sixth, since they appeared just before the extinction). Genera occur in the following areas: A, south China; B, Tibet; C, Sibumasu; D, Tasmania; E, Argentina; F, Kazakhstan; G, Baltica; H, Avalonia; I, southern Scotland; J, northern Maine; K, Quebec; L, southern Europe; M, central US; N, Gornyi Altai; O, Kolyma; P, Anticosti Island; Q, Estonia; R, Tadzhikistan. Arrows I and II represent the first and second phases, respectively, of the end-Ordovician extinction.



**Fig. 3.** Total numbers of families and genera through the Ordovician–Silurian transition. The faunas are composed largely of genera in Orthida 1 and 2 and Strophomenida 1, with less diverse Strophomenida 2. At family level, the most diverse is the Orthida. Nineteen orders through this interval have been recorded in the literature. For common usage and convenience, we split the following five orders into two parts: Orthida 1 and 2 (impunctate and punctate group), Strophomenida 1 and 2 (Plectambonitoidea and Strophomenoidea), Orthotetida 1 and 2 (Orthotetidina and Triplesiidina), Pentamerida 1 and 2 (Syntrophidina and Pentameridina), and Atrypida 1 and 2 (smooth and ribbed atrypids). Altogether, there are 24 major groups investigated. Numbers of extinct families and genera are shown at two phases of the extinction. The numbers for the Lazarus taxa are included in survivors. Origination indicates those taxa newly established in the Hirnantian, with some extended into the Silurian.

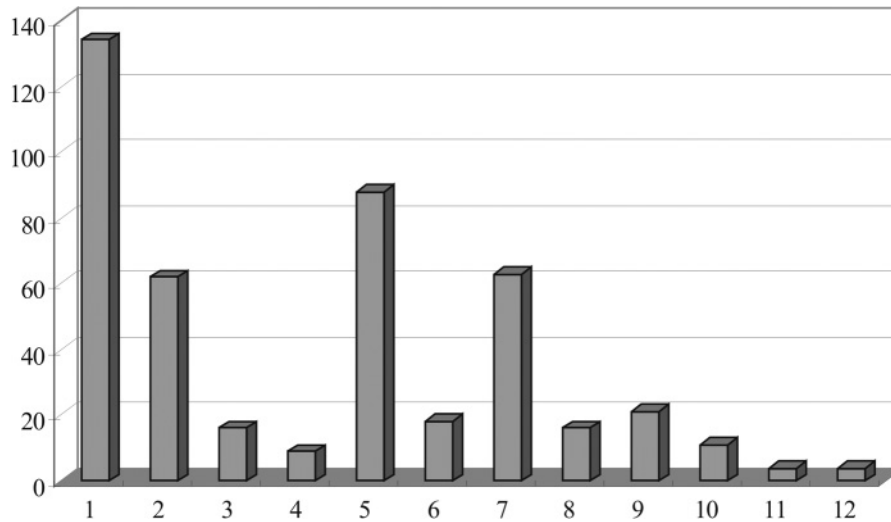


About 3/5 of the survivors were from expanded warm-water regions in the middle Ashgill (Boucot et al. 2003). More than 2/3 of this unit are known from the K Province, and nearly 1/3 in the latter are associated with elements of the *Hirnantia* fauna (Appendix A).

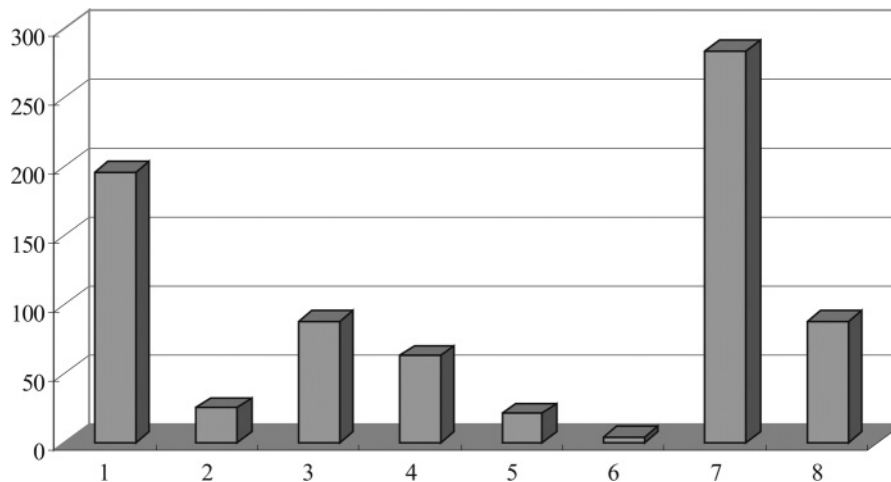
**(4) New arrivals**

Twenty-one new genera first appear in the Hirnantian, favourably compared to that of the Rhuddanian when 20 new genera appeared. Ten of these are restricted to the Hirnantian and 11 extended into the Silurian (Appendix A

**Fig. 4.** Total numbers of different types across the end-Ordovician crisis: 1–4, extinct genera and families at the first (1 and 3) and second (2 and 4) phases; 5, survival genera (Lazarus taxa included); 6, Lazarus genera; 7, survival families (Lazarus taxa included); 8, Lazarus families; 9–12, newly established genera and families after the first phase (9 and 11) and extended into the Llandovery (10 and 12).



**Fig. 5.** Total numbers of different types across the end-Ordovician extinction: 1, extinct genera; 2, extinct families; 3, survival genera; 4, survival families (Lazarus taxa included); 5 and 6, newly established genera (5) and families (6) after the first phase of the extinction; 7 and 8, genera (7) and families (8) through the transition.



and B, New arrivals). Taxonomically, orthids (38.1%) and strophomenids (19.05%) are common, whereas the phosphatic brachiopods and athyridids (both 9.5%) are rare (Figs. 10, 11). Rhynchonellids (23.8%) are rare in these faunas, however, but frequent among the new arrivals. Interestingly, there are no pentamerids, atrypids, spiriferids, or trimerellids in the new arrivals, indicating unfavourable conditions for them during the crisis. Geographically, nine genera (42.9%) occur in the E Province and 12 (57.1%) in the K Province. These two provinces shared only one genus (*Whitfieldella*). A single genus (*Undithyrella*) occurs in the B Province.

**Division of the Hirnantian survivors in the Kosov (K) Province**

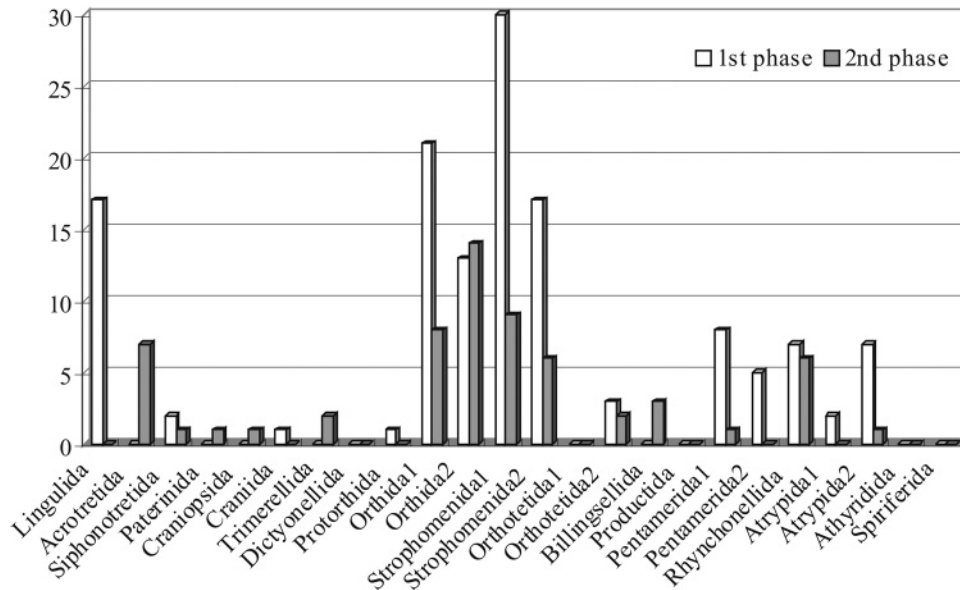
With the exception of the relicts that survived the different phases of the end-Ordovician extinction, the brachiopod survivors occurring in the K Province in the Hirnantian can

be divided into three groups: (1) increasing genera, (2) declining genera, and (3) Lazarus genera (Fig. 12). The increasing genera possess high abundance, large population size, and wide distributions between two phases of the extinction and became rare or extinct when the crisis terminated. The other two groups have the opposite properties. Investigation of the declining genera may help to provide a better understanding of the nature of the Lazarus genera.

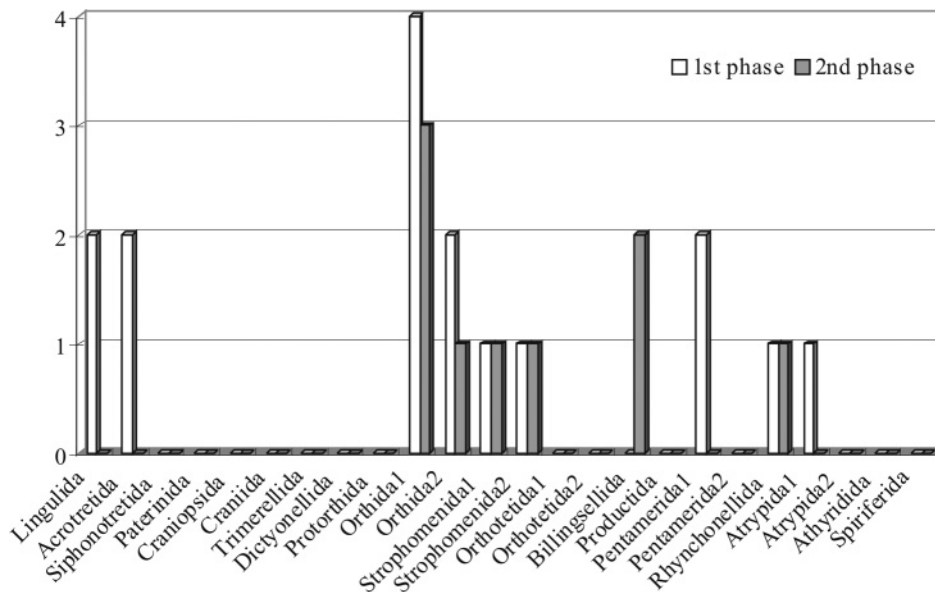
**(1) Increasing genera**

Increasing genera are marked by an intensive increase in population size with a large expansion in geographic range during crisis (some being disaster taxa, such as *Hirnantia* and *Eostropheodonta*). The minority of survivors occurred in the middle Ashgill and greatly expanded their ranges geographically in the early to middle Hirnantian when global environments were impoverished and disappeared again fleetingly or occurred rarely after the extinction (e.g., some

**Fig. 6.** Number of extinct genera at the two phases of the end-Ordovician extinction. Note that the scale of the second phase is generally smaller than that of the first phase. Orthida and Strophomenida possessed diverse subgroups in the Ordovician, suffered greatly during both phases of the extinction, and became dominant again for a short time in earlier Llandovery.



**Fig. 7.** Number of extinct families at the two phases of the extinction. None of the families in 14 major groups became extinct, indicating that in many cases they probably adopted a sort of strategy that reduced their population size and distribution escaping the crisis.



key constituents of the *Hirnantia* fauna). Some from the K Province (e.g., *Hindella*) may extend to the E Province, to some degree, in the Hirnantian.

**(2) Declining genera**

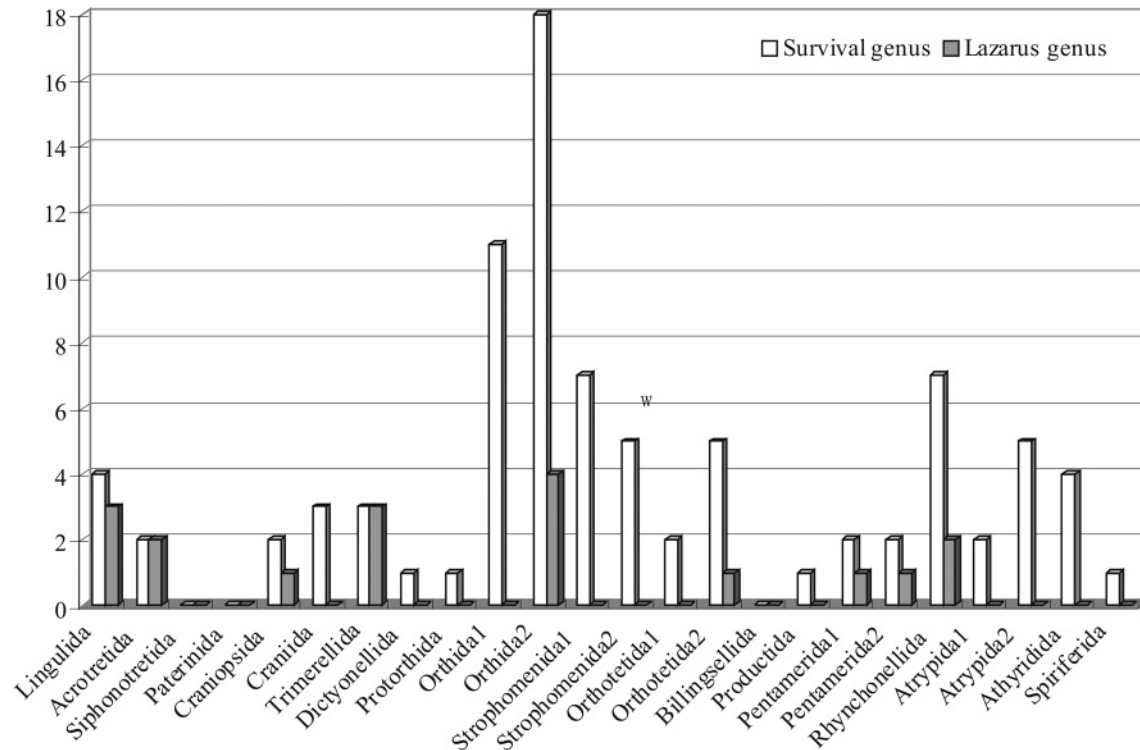
This group accounts for the majority of the survivors and includes mainly eurytopic and long-ranging taxa known before and after the extinction. They declined with lower abundance and scattered distributions between the two phases of the extinction and expanded geographically again in the Early Silurian. For example, *Dolerorthis* and *Eospirigerina* survived the first phase and cohabited rarely and sporadically with the typical *Hirnantia* fauna (Temple 1970; Harper

1981; Cocks 1982). Some genera, like *Skenidioides* (Temple 1970; Williams and Wright 1981), *Epitomomyia* (this paper), *Leangella* (Bergström 1968), and *Rugosowerbyella* (Nikitin 1980), are known scarcely and sporadically in the K Province. Their absence in the B Province indicates that cold-water environments were unsuitable for them. Others of this group were restricted to the warm-water E Province and are almost unknown in the K Province.

**(3) Lazarus genera**

This group was originally defined as taxa that disappeared from the fossil record (Flessa and Jablonski 1983) or below the detection limit of the record (Wignall and Benton 1999),

**Fig. 8.** Number of surviving genera with Lazarus genera across the end-Ordovician crisis. Only three orders (Siphonotretida, Paterinida, and Billingsellida) became extinct before the end of the Ordovician. Orthida (29 genera) and Strophomenida (12) account for 46.6% of the surviving genera, whereas Pentameridina (2), ribbed Atrypida (5), and Spiriferida (1) account for less than 10% of the total. Orthida and Strophomenida were significant constituents in the brachiopod surviving after the extinction, whereas Pentameridina, ribbed Atrypida, and Spiriferida, although extremely rare during the crisis, played an important role in the subsequent recovery and radiation (see explanation in Fig. 3).



above the minimum viable population size (Twitchett 2001), and existed at unknown site(s) during a mass extinction – survival interval (Jablonski 1986; Kauffman and Erwin 1995). Fara (2001) pointed out that there is confusion surrounding the recognition of Lazarus taxa, with a variety of definitions that obscured this concept; this statement was questioned by Rickards and Wright (2002). Based on this study, it seems that the Lazarus taxa declined substantially during the crisis time interval, a feature similar to the declining genera, noted earlier, but were not discovered in the fossil record during the crisis. Thus they may be considered an extreme member of the declining genera.

## Discussion of Lazarus genera

The concept of the Lazarus effect was applied to the Ordovician–Silurian boundary faunas on a single plate where the migration of the *Hirnantia* fauna taxa into south China during the crisis period (Rong and Harper 1999) added an important dynamic to the development of the post-extinction fauna. New investigations on a global scale indicate, however, that the more work focused on the Lazarus taxa, the smaller the number of these taxa that are recognizable. Clearly, continued collection and study of taxa through the crisis have reduced the number of Lazarus taxa. Nevertheless, a number of brachiopod groups had restricted their distributions during the crisis.

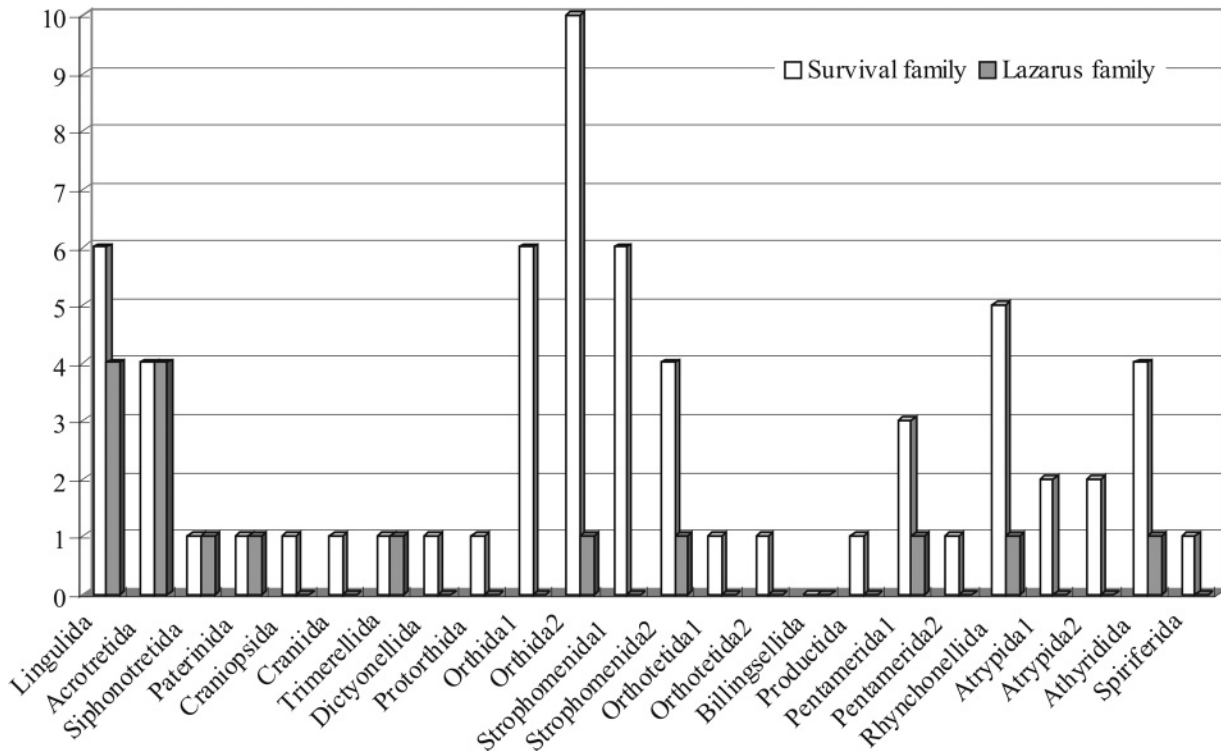
A Lazarus taxon cannot be recognized until substantial

and satisfactory collections have been obtained all over the world. This seems an endless quest. The fragmentary nature of the fossil record renders it virtually impossible to define a Lazarus taxon. A single record of the taxon, discovered in rocks deposited during a crisis interval, immediately cancels its status as a Lazarus taxon (Rickards and Wright 2002). Contrary, new data will also produce new Lazarus effects (Westerman 1999; Mergl 2001; Watkins 2002). The previous statements emphasize the instability and fragility of the Lazarus concept that, at least, has not proved to be helpful in understanding the end-Ordovician brachiopod extinction.

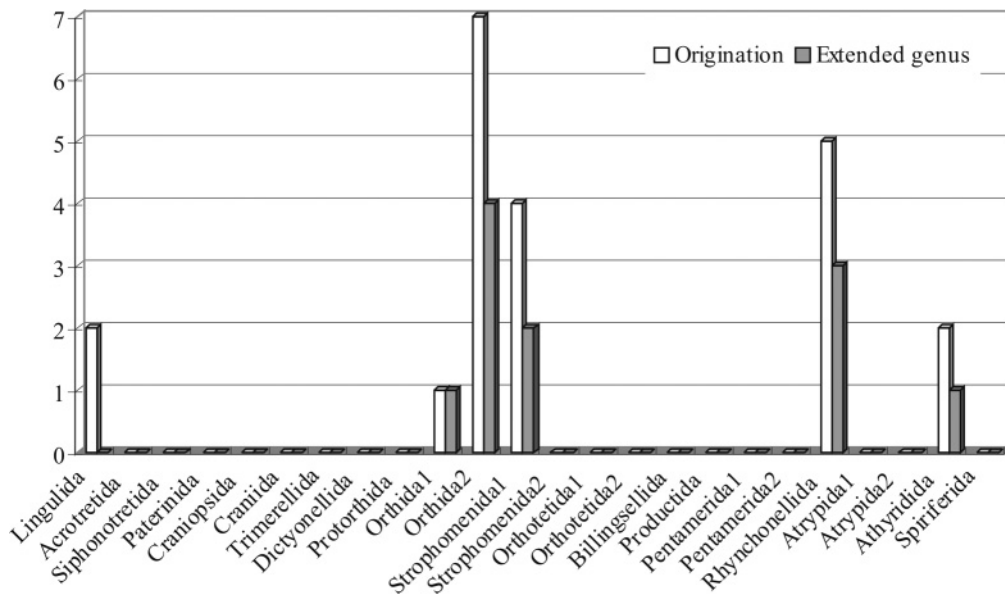
It seems that the Lazarus concept was partly based on the end-Permian extinction of some biotic groups (e.g., gastropods), followed by the monumentally low-diversity Early Triassic, followed in turn by the Middle Triassic major adaptive radiation. For example, many gastropod genera have been considered to be Lazarus taxa through the Late Permian to Early Triassic because of the lack of silicified specimens from the Lower Triassic (Pan and Erwin 1994; Erwin and Pan 1996; Erwin 1996, 1998; Tong and Erwin 2001), but only very few Lazarus genera of brachiopods have been recognized during this interval (Rong and Shen 2002). This may be partly linked to the upsurge of gastropods in the Modern Evolutionary Fauna and the dramatic decline of brachiopods of the Palaeozoic Evolutionary Fauna in the early Mesozoic.

Some geographical isolated remnants today form the basis of impressive stories, such as the rhipidistian crossopterygian *Latimeria* and the rhynchocephalian *Sphenodon*. Recent

**Fig. 9.** Number of survival families with Lazarus families through the Ordovician–Silurian transition. None of the extinct families is in Orthida 1 and Strophomenida 2, and Orthida 2 has a single extinct family at the second phase. There is no regularity in the distribution pattern of the Lazarus taxa among the various groups. Both artificial sampling bias and the reduction in population size resulted in greatly limited distribution areas that are apparent in the recognition of Lazarus taxa.



**Fig. 10.** The newly established genera after the first phase of the extinction are recorded from six of the 24 major groups. About half of the new genera can extend into the Silurian, but some are relicts that were soon wiped out afterwards.

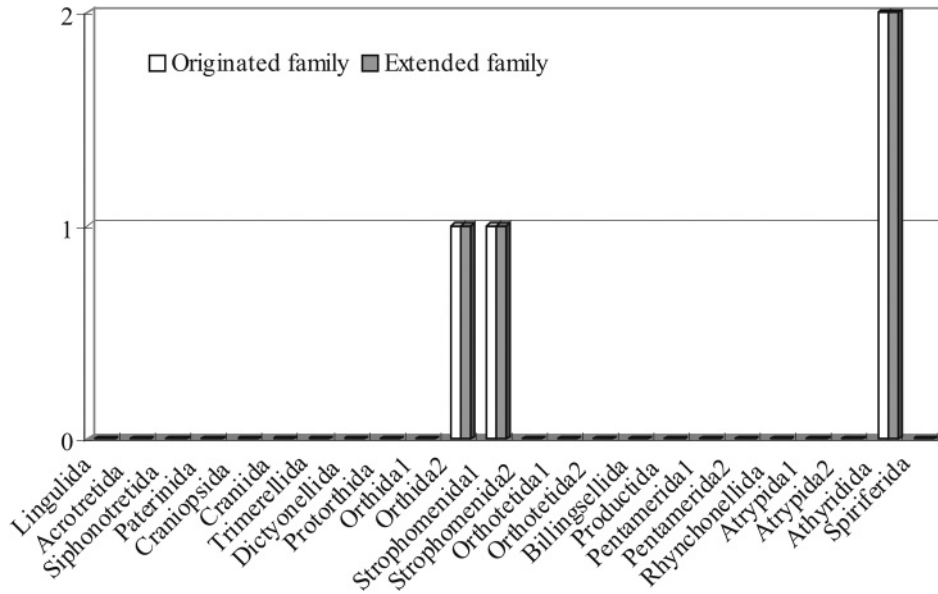


discovery of four specimens representing the first Paleocene European examples of the rare bizarre bivalve *Puvinites* is also worth noting (Pacaud 2001). These bivalves are fairly widespread from the mid-Jurassic through the Cretaceous, very rare in the Paleocene at a limited number of localities, still unknown in the post-Paleocene Cenozoic, but known in

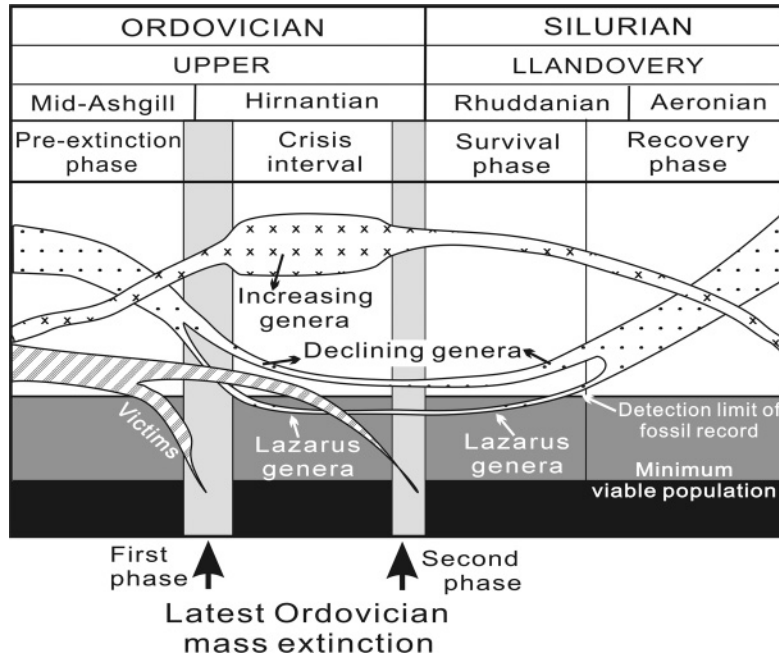
New Zealand and southeastern Australia today (Marshall 1998). A combination of rarity and lack of collecting is responsible for this condition. In fairness, one should wait for a while to determine whether they will vanish in their relict condition or eventually expand their number and area of occurrence significantly enough to forfeit their relict status.



**Fig. 11.** There are only four families among the 24 major groups, namely Templeellinae (Harper 2000), Strophonellidae, Rhynchospirinidae, and Meristellidae, that were newly established during the end-Ordovician crisis, indicating a low rate of origination at the family level in the Hirnantian.



**Fig. 12.** Diagram showing the three groups of survivors, namely increasing genera, declining genera, and Lazarus genera, through the Ordovician–Silurian transition. The Lazarus group is considered to be an extremity of the declining group and partly a distortion of the fossil record. The x axis represents sketch quantity.



**Comparison of Lazarus genera with declining genera**

The Lazarus genera that essentially belong in survivors can be regarded as extreme examples of the declining genera. Similar to the latter in nature, Lazarus genera were scattered across a range of environments on numerous continental blocks in terms of examples from this paper. The brachiopod data show that the declining genera and Lazarus genera share some common characters, such as low abundance, small

population size, and a scattered pattern of geographic distribution during the crisis interval.

**(1) Abundance**

The abundance of Lazarus genera during crisis was clearly so low that it would be very difficult to actually locate them in either new or existing collections. For example, the declining genera of the K Province were rare between the two pulses of the crisis. Further evaluation of declining genera requires more collections and taxonomic study; these taxa are rare

and poorly studied, for example, *Skenidioides* from Wales (Williams 1951), *Leangella* from Sweden (Bergström 1968), *Anisopleurella* from Kazakhstan (Nikitin 1980), and *Epitomomyia* from Maine (this paper) in the Hirnantian (Appendix C). They occurred in various areas together with the *Hirnantia* fauna, some in deeper water regimes (Temple 1970) and others in shallower water regimes (this paper).

## (2) Population size

In many cases, the Lazarus genera had small population sizes during the crisis, similar to those of the declining genera. The latter could invade the ecospace of the *Hirnantia* fauna (including marginal environments) but possessed rare individuals possibly because of ineffective competition in a relatively stable ecosystem, where the fauna had been successfully established. Population sizes fluctuated in response to pressure from predation, disease, habitat loss, and environmental changes in food supply (Twitchett 2001). The Hirnantian glaciation led to a global regression, with local uplift that induced habitat loss on some platforms like North America (Amsden 1974; Sheehan 1988, 2001), and is linked to a loss of endemic forms. Evidence for global cooling in the Hirnantian is robust. A temperature decline in the tropics of about 10 °C may have greatly affected population size as well (Brenchley et al. 1994).

## (3) Distribution

The scattered distribution pattern of the declining genera can also help us to achieve a better understanding of Lazarus taxa. Many in these two groups have a random geographic distribution in the Hirnantian and are known to occur rarely in the K Province (e.g., *Skenidioides*, *Epitomomyia*, *Dicoelosia*, and *Leangella*). Some from the E Province (e.g., *Dolerorthis*, *Rostricellula*, *Brevilamnulella*, and *Eospirigerina*) could enter a few areas of the K Province as rare elements in the *Hirnantia* fauna. As an extraordinary case, 12 relicts and 14 declining genera at least were recorded with some constituents of the *Hirnantia* fauna from the Hirnantian rocks at Garth, Wales (Williams and Wright 1981). Some of them occur in the same places as other low-abundance genera that expanded in the Silurian.

## Comparison

Our investigation suggests that the majority of the middle Ashgill surviving genera occur as declining genera in the Hirnantian. To date, about 1/5 of the surviving genera are placed temporarily in the Lazarus category, including four genera of Orthida (*Chrustenopora*, *Fascifera*, *Jezercia*, and *Saukrodictya*); three of Lingulida (*Lingulops*, *Schizocrania*, and *Schizotreta*) or Trimerellida (*Gasconsia*, *Monomerella*, and *Trimerella*); two of Acrotretida (*Acrotretella* and *Opsiconidion*), Pentamerida (*Camerella* and *Holorhynchus*), or Rhynchonellida (*Lenatoechia* and *Orthorhynchula*); and one of Craniopsida (*Craniops*) or Triplesiidina (*Paraonychoplesia*). It is plausible that the phosphatic brachiopods, rhynchonellids, and some others contain Lazarus genera possibly due to inadequate systematic data or an insufficient fossil record. Furthermore, nearly 1/5 of the surviving families can be described as Lazarus taxa in which the phosphatic brachiopods account for more than 2/3, probably due to the same reasons. The Lazarus orthids are all known as relicts

that suffered great reductions in population size at the first phase of the extinction, disappeared during the crisis, reappeared in the earliest Silurian, but were wiped out soon after. The other Lazarus taxa (e.g., *Trimerella* of trimerellids and *Holorhynchus* of pentamerids) are considered to have been relatively warm-water forms with no occurrences known in the Hirnantian. No orthidines, strophomenids, atrypids, athyridids, or spiriferids can be described as Lazarus genera at the moment. It seems to the authors that there is no regularity in distribution pattern of the Lazarus taxa among various groups (Figs. 7, 8). Both artificial sampling bias and the reduction in population size resulted in limited distribution areas that have contributed to the recognition of Lazarus taxa.

Whether or not the occurrence of declining genera is related to biogeographical position and phylogenetic history should be considered. We take three examples for explanation. (1) The occurrence of *Eospirifer* in south China in the Hirnantian may be connected with its earliest known record in the same region in the middle Ashgill. *Eospirifer* did not reach Laurentia, Baltica, and Avalonia until late Aeronian (Rong and Zhan 1996) but occurred in Tasmania in late Hirnantian (Sheehan and Baillie 1981), showing a biogeographical affinity between Australia and south China. (2) *Platystrophia* has been known from Laurentia, Avalonia, and Baltica in the Hirnantian (Williams and Wright 1981; Harper and Hints 2001), whereas it was not found in south China in the Ordovician and Silurian. (3) The presence, although rare, of *Nalivkinia* in south China in the Hirnantian may be linked to its earliest known occurrence in south China in middle Ashgill (Xu 1996).

The relicts were recorded from many regions in the pre-Hirnantian Ashgill but reduced their population size and scope of distribution in the Hirnantian, showing some similarity to the Lazarus taxa. For example, rare specimens of *Plaesiomys*, *Hypsitycha*, and *Eochonetes* of Laurentian affinities have been found associated with the *Hirnantia* fauna in the shallow-water High Mains Sandstone in Girvan, Scotland (Harper 1981). *Dorytreta* of Laurentian affinities has been recorded along with some constituents of the shallow-water *Hirnantia* fauna in Guizhou, south China (Rong and Li 1999). *Christiania*, a cosmopolitan genus, variably occurs in the pre-Hirnantian Ordovician but declined dramatically in the Hirnantian, where it is known extremely rarely along with the *Hirnantia* fauna only in Maine (Appendix C). Synecologically, there is also a major community change in which *Christiania* occurs differentially from middle Ashgill (Zhan et al. 2002) and Hirnantian. All of these relicts survived the first or second phase of the extinction but soon vanished, without recovery, in the Silurian.

## Conclusions

Global analyses derived from this paper display the dynamics of brachiopod faunas through the Ordovician and Silurian transition: 28.4% of families and 69.0% of genera became extinct during the end-Ordovician events, with 18.6% and 12.5% of families and 51.0% and 41.3% of genera that were eliminated in the first and second phases of the extinction, respectively. This demonstrates that brachiopods, at both generic and familial levels, suffered greater in the first phase

than in the second phase. Regarding changing abundance, survivors occurring in the Kosov Province in the Hirnantian can be split into three groups: increasing, declining, and Lazarus taxa. The latter may be regarded as end members of the declining type. Comparison of the abundance, population size, and distribution patterns of the declining and Lazarus taxa shows essential similarities between these two groups which contribute to a better understanding of the nature of Lazarus taxa. As shown earlier, numerous declining genera (e.g., *Dicoelosia* and *Skenidioides*) occur at single localities with low abundance to cohabit with core elements of the *Hirnantia* fauna in many places, e.g., Avalonia (Temple 1970; Williams and Wright 1981), Baltica (Bergström 1968; Cocks 1982), Kazakhstan (Nikitin 1980), south China (Rong 1986; this paper), and marginal Laurentia (this paper). This may indicate that a dramatic decline of their population size may have taken place in various parts of the world in the crisis. Evidence of migration into a refugium has not been documented in the brachiopod data of the end-Ordovician extinction, and the migration may not have been a key mechanism for escaping from the extinction. The declining taxa may have persisted with significantly lower abundance and possessed paleogeographically scattered locations in a range of environments for survival after the extinction. This reduced the role of the Lazarus effect and may further agree with the supposition by Fortey (1989, p. 341) that well-defined marine refugia for the end-Ordovician brachiopods probably did not exist.

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## Appendix A

Data sources of brachiopod families and genera through the Ordovician–Silurian transition are as follows: Lingulida, Acrotretida, and Siphonotretida (Holmer and Popov 2000); Paterinida (Laurie 2000); Craniopsida and Trimerellida (Popov and Holmer 2000); Craniida (Bassett 2000); Dictyonellida (Holmer 2000); Clitambonitidina (Rubel and Wright 2000); Strophomenida (Cocks and Rong 2000); Orthotetidina (Williams and Brunton 2000); Triplesiidina (Wright 2000); Chonetidina (Racheboeuf and Copper 1986); Protorthida (Williams and Harper 2000a); Orthida (Williams and Harper 2000b; Harper 2000); Syntrophiidina (Carlson 2002); Pentameridina (Boucot et al. 2002; this paper); Rhynchonellida (Savage 1996; Savage et al. 2002); Atrypida (Copper 2001, 2002); Athyridida (Alvarez and Rong 2002; this paper); Spiriferida (Rong and Zhan 1996; this paper). Some regional data are provided by Cocks and Modzalevskaya (1997) for Taimyr, M. Rubel (personal communication, 2002) for Estonia, and J. Jin (personal communication, 2002) and P. Copper (personal communication, 2002) for Anticosti Island.

### Familial level

#### (1) *Victims*

Eighty-eight families are known in the middle to late Ashgill, with 25 families that became extinct during the end-Ordovician extinction (28.4%, 25/88). Sixteen families and nine families (those indicated with an asterisk) became extinct at the first pulse (18.6%, 16/(88 – 2)) and second pulse (12.5%, 9/(88 – 16)) of the extinction. Lingulida—Linguloidea: Zhanaellidae, Lingulasmatae. Acrotretida—Acrotretoidea: Ephipelasmatae, Eoconulidae. Strophomenida—Strophomenoidea: Foliomenidae, Christianiidae\*. Plectambonitoidea: Bimuriidae, Hesperomenidae\*. Billingsellida Clitambonitoidea: Clitambonitidae\*, Gonambonitidae\*. Orthida—Orthoidea: Nanorthidae, Plaesiomyidae\*, Productorthidae\*. Plectorthoidea: Plectorthidae\*, Cyclocoeliidae, Phragmorthidae, Rhactorthidae. Dalmanelloidea: Angusticardinae, Portranellidae\*, Tyronellidae. Pentamerida—Syntrophiidina: Syntrophiidae, Parallelelasmatae. Rhynchonellida Ancistrohynchoidea: Oligorhynchiidae, Sphenotretidae\*. Atrypida—Lissatrypoidea: Protozygidae.

#### (2) *Survivors*

Sixty-three families are known to extend into the Silurian with a continuation rate of family: 71.6% (63/88). Among them, all came from the pre-Hirnantian Ashgill, except two (Virginiatidae and Rhynchospiridae from late Ashgill). Sixteen families are provisionally regarded as Lazarus families (those indicated with an asterisk) (18.2%, 16/88). Lingulida—Linguloidea: Pseudolingulidae\*, Obolidae\*, Dysoristidae\* (Mergl 2001), Paterulidae\* (Mergl 2001). Discinoidea: Trematidae, Discinidae. Acrotretida—Acrotretoidea: Acrotretidae\*, Scaphelasmatae\*, Torynelasmatae\*, Biernatidae\*. Siphonotretida—Siphonotretoidea: Siphonotretidae\* (Mergl 2001). Paterinida—Paterinoidea: Paterinidae\* (Mergl 2001). Craniopsida—Craniopsoidea: Craniopsidae. Craniida—Cranioida: Craniidae. Trimerellida—Trimerelloidea: Trimerellidae\*. Dictyonellida—Eichwaldioidea: Eichwaldiidae.

Strophomenida—Strophomenoidea: Strophomenidae, Rafinesquinidae, Glyptomenidae, Eopholidostrophiidae, Leptostrophiidae, Strophonellidae. Plectambonitoidea: Leptellinidae\*, Leptestiidae, Xenambonitidae, Sowerbyellidae. Orthotetida—Orthotetidina: Chilidiopsidae. Triplesiidina: Triplesiidae. Productida—Chonetoidea: Strophochonetidae. Protorthida—Skenidioidea: Skenidiidae. Orthida—Orthoidea: Orthidae, Glyptorthidae, Hesperorthidae. Plectorthoidea: Giraldiellidae, Platystrophiidae, Toxorthidae (Rong 1984). Dalmanelloidea: Dalmanellidae, Dicoelosiidae, Harknessellidae\*, Heterorthidae, Platyorthidae, Rhipidomellidae. Enteleteoidea: Draboviidae, Chrustenoporidae, Linoporellidae, Saukrodictyidae. Pentamerida—Syntrophiidina: Porambonitidae\*, Camerellidae, Parastrophinidae. Pentameridina: Virganiidae. Rhynchonellida—Ancistrohynchoidea: Ancistrohynchidae. Rhynchotrematoidea: Orthorhynchulidae\*, Rhynchotrematidae, Trigonirhynchidae, Virginiatidae. Atrypida—Lissatrypoidea: Cyclospiridae, Septatrypidae. Atrypoida: Anazygidae, Atrypinidae. Athyridida—Meristelloidea: Hyattididae, Meristellidae, Meristidae\*. Retzioidea: Rhynchospiridae. Spiriferida—Cyrtioidea: Cyrtiidae.

### Generic level

#### (1) *Victims*

The total number of the genera through the end-Ordovician crisis is 284, in which 196 genera (69.0%, (134 + 62)/284) became extinct during the latest Ordovician extinction, with 134 and 62 genera (those indicated with an asterisk) wiped out at the first phase (51.0%, 134/(284 – 21)) and second phase (41.3%, 62/(284 – 134)), respectively. Lingulida—Linguloidea: *Anx*, *Apatobolus* (Mergl 1998), *Ectenoglossa* (Zhan and Cocks 1998), *Glossella* (Havlíček et al. 1994), *Leptobolus*, *?Lingulella* (Rong 1979), *Lingulasma*, *Palaeoglossa*, *Pseudolingula*, *Rafanoglossa* (Havlíček 1994), *Rowellella*. Discinoidea: *Acrosaccus*, *Chrustanotreta*, *Drabodiscina*, *Schizotretinia*, *Tethyrete* (Havlíček 1994 for the latter four), *Trematis*. Acrotretida—Acrotretoidea: *Biernatia*\*, *Eoconulus*\*, *Hisingerella*\*, *Rhinotreta*\*, *Scaphelasma*\*, *Spondylotreta*\*, *Veliseptum*\*. Siphonotretida—Siphonotretoidea: *Acanthambonia*\*, *Celdobolus* (Mergl 1994), *Multispinula*. Paterinida—Paterinoidea: *Dictyonites*\*. Craniopsida—Craniopsoidea: *Pseudopholidops*\*. Craniida—Cranioida: *Orthisocrania*. Trimerellida—Trimerelloidea: *Eodinobolus*\*, *Peritrimera*\*. Strophomenida—Strophomenoidea: *Actinomena* (Havlíček et al. 1994), *Bekkeromena*, *Costistrophomena*, *Christiania*\*, *Drum-muckina*, *Dzhebaglina*, *Fenomena*, *Foliomena*, *Furcitella*, *Geniculina*, *Gunnarella* (Dewing 1999), *Harjumena*, *Hedstroemia*\*, *Hesperinia* (Villas et al. 1989), *Hingganoleptaena*, *Holtedahlina*\*, *Iberomena*, *Kiaoromena* (Mitchell 1977), *Kjaerina*\*, *Kjerulfina*\*, *Limbimurina*, *Longvillia*, *Luhaia*, *Megamyonia*, *Mjoesina* (Hiller 1980), *Nasutimena* (Jin and Zhan 2001), *Nubialba*, *Odoratus*, *Oepikina* (Jin and Zhan 2001), *Origostrophia*, *Paromalomena*\*, *Pomeromena*, *Platymena*, *Proboscisambon*, *Rafinesquina*\*, *Rhactomena*\*, *Tashanomena* (= *Yushanomena*) (Zhan and Rong 1995), *Tetraphalerella*, *Titanomena*\*. Plectambonitoidea: *Aegiromena*\*, *Aegireretes* (Havlíček et al. 1994), *Leptellina*, *Anoptambonites*, *Bimuria*, *Chonetoidea*, *Dulankarella*, *Eochonetes*\*, *Kajnarina*, *Kassinella*, *Kozlowskites*, *Leptestiina*, *Mabella*, *Metambonites*, *Ptychoglyptus*, *Reversella*, *Rongambonites*, *Rugosowerbyella*\*, *Sampo*\*, *Sowerbyella*\*, *Synambonites*, *Thaerodonta*\* (Jin

2001), *Trimurellina*. Orthotetida riplesiidina: *Amphiplecia*, *Craigella*, *Grammoplecia*, ?*Ogmoplecia*\* (M. Rubel, personal communication, 2002), *Onychoplecia*\*. Billingsellida—Clitambonitidina: Clitambonitoidea: *Ilmarinia*\*, *Kullervo*\*, *Vellamo*\*. Protorthida—Skenidioidea: *Replicosenidioides*. Orthida—Orthoidea: *Austinella*, *Barbarorthis*\*, *Boreadorthis*, *Dinorthis*\* (Jin 2001), *Diocthofera*, *Diplonorthis*\*, *Lordorthis*, *Nicolella*\*, *Pionorthis*, *Plaesiomys*\* (Harper 1981), *Retrorsirostra*\*, *Spinorthis*, *Sulevorthis*\*. Plectorthoidea: *Aberia*, *Comatopoma*\*, *Cremnorthis* (Hiller 1980), *Cyclocoelia*, *Doleroides*, *Eriprifera*, *Hebertella*\*, *Laticrura* (Havlíček et al. 1994), *Mcewanella*, *Mimella*, *Plectorthis*, *Rhactorthis*, *Salacorthis*, *Scaphorthis*, *Schizophorella*, *Severginella*. Dalmanelloidea: *Apatorthis*, *Arenorthis*\*, *Dedzetina*, *Diceromyonia*\*, *Draborthis*\* (Bergström 1968), *Elsaella*\*, ?*Eremotrema* (Hiller 1980), *Horderleyella*\* (Bergström 1968), ?*Howellites*\*, *Karlicium*, *Onnizetina* (Havlíček et al. 1994), ?*Paucicrura*, *Phragmorthis*, *Portranella*\*, *Reuschella*\*, *Trucizetina*\*, *Tyronella*, *Wulogella*, *Wysogorskiella*. Enteletoidea: *Boticum*, *Destombesium*\*, *Drabovia*\*, *Drabovinella*\*, *Hulterstadia*, *Laticrura*, *Leptoskelidion*\*, *Pionodema*\*, *Wangyuella*. Pentamerida—Syntrophidina: *Didymelasma*, *Eoanastrophia*, *Eosotrophina* (Zhan and Rong 1995), *Equirostra* (M. Rubel, personal communication, 2002), *Liotrophia*, *Parastrophina*\* (Menakova 1991), *Porambonites*, *Stenocamara* (M. Rubel, personal communication, 2002), *Xenelasmopsis*. Pentameridina: *Eoconchidium*, *Galeatellina*, *Proconchidium*, *Prostricklandia*, *Tcherskidium*. Rhynchonellida—Ancistrorhynchoidea: *Dorytreta*\* (Rong and Li 1999), *Paraligorhynchia*, *Sphenotreta*\*, *Tonsella*\* (Jin 2001). Rhynchotrematoidea: *Altaethyrella* (Popov et al. 2000), *Evenkorhynchia*, *Hiscobeccus* (Jin and Zhan 2001), *Hypsiptycha*\* (Harper 1981; Jin and Zhan 2001), *Lepidocycloides*, *Lepidocyclus*, *Orthorhynchyllion*\*, *Otarorhynchia*, *Undithyrella*\*. Atrypida—Lissatrypoidea: *Protozyga*, *Xysila*. Atrypoida: *Antizygospira* (Zhan and Cocks 1998), *Catazyga*, *Eonalivkinia*, *Ovalospira* (Zhan and Cocks 1998), *Pronalivkinia* (Kul'kov et al. 1985; Popov et al. 2000), *Qilianotryma* (Copper 2001), *Sulcatospira* (Popov et al. 2000; Copper 2001), *Zygospira*\*.

## (2) Survivors

The following 88 survival genera have been recorded from the middle Ashgill through Silurian (31.0%: 88/284). Eighteen genera (20.5%, 18/88) (those indicated with an asterisk) unknown in the Hirnantian are provisionally regarded as Lazarus genera. Lingulida—Linguloidea: *Lingulops*\*. Discinoidea: *Orbiculoidea*, *Schizocrania*\*, *Schizotreta*\*. Acrotretida—Acrotretoidea: *Acrotretella*\*, *Opsiconidion*\*. Craniopsida—Craniopsoidea: *Craniops*\*, *Paracraniops*. Craniida—Craniioidea: *Acanthocrania*, *Philhedra*, *Petrocrania* (= *Philhedrella*). Trimerellida—Trimerelloidea: *Gasconsia*\* (Watkins 2002), *Monomerella*\*, *Trimerella*\* (= *Macaerocolella*, *Prosoponella*). Dictyonellida—Eichwaldioidea: *Eodictyonella*. Strophomenida—Strophomenoidea: *Biparetis*, *Eopholidostrophia*, *Eostropheodonta* (= *Aphanomena*), *Eostrophonella*, *Katastrophomena*, *Leptaena* (= *Leptaenopoma*), *Paromalomena*, *Strophomena*. Plectambonitoidea: *Anisopleurella*, *Eoplectodonta*, *Jonesea*, *Leangella*. Orthotetida—Orthotetidina: *Fardenia*, *Coolinia*. Triplesiidina: *Cliftonia*, *Oxoplecia*, *Paraonychoplecia*\*, *Streptis*, *Triplesia*. Productida—Chonetidina: Chonetoidea: *Archeochonetes* (Racheboeuf and Copper 1986). Protorthida Skenidioidea: *Skenidioides*. Orthida—Orthoidea: *Dolerorthis* (= *Schizonema*),

*Eridorthis*, *Glyptorthis*, *Gnamptorhynchus*, *Hesperorthis*, *Orthostrophella* (Amsden 1974), *Ptychopleurella*. Plectorthoidea: *Giraldibella*, *Giraldiella*, *Platystrophia*, *Toxorthis*. Dalmanelloidea: *Dalmanella*, *Dicoelosia*, *Dysprosorthis*, *Epitomyonia*, *Isorthis* (Havlíček et al. 1994), *Levenea*, *Mendacella*, *Mirorthis*, *Onniella*, *Ravozetina*, *Templeella*. Enteletoidea: *Chrustenopora*\* (Baarli 1987), *Fascifera*\* (Baarli 1987), *Hirnantia*, *Jezercia*\* (Baarli 1987), *Kinnella* (Cocks 1988), *Salopina*, *Saukrodictya*\*. Pentamerida—Syntrophidina: *Camerella*\*, *Parastrophinella*. Pentameridina: *Brevilamnulella*, *Holorhynchus*\* (Rong et al. 2004). Rhynchonellida—Rhynchotrematoidea: *Lenatoechia*\*, *Orthorhynchula*\*, *Rhynchotrema* (Jin 2001), *Rostricellula* (Jin 2001), *Stegerhynchus* (Amsden 1974; Oradovskaya 1983), *Plectothyrella* (Cocks 1988), *Thebesia* (known from the Wenlockian Cape Phillips Formation, Baillie Hamilton Island, Canadian Archipelago; Zhang 1989). Atrypida—Lissatrypoidea: *Cyclospira* (Copper 2001), *Idiospira*. Atrypoida: *Eospirigerina*, *Nalivkinia* (Xu 1996), *Plectatrypa*, *Schachriomonina*, *Sypharotrypa*. Athyridida: Meristelloidea: *Hindella* (including *Cryptothyrella*), *Homeospira*, *Hyattidina*, *Whitfieldella*. Spiriferida—Cyrtioidea: *Eospirifer*.

## (3) New arrivals 1

Ten genera arose in and are restricted to the Hirnantian: *Tethyrete* (Havlíček 1994); *Schizotretinia* (Mergl in Holmer and Popov 2000); *Leptoskelidion* (Amsden 1974; Cocks 1982); *Draborthis* (Bergström 1968; Temple 1968; Rong and Sun 1983; Rong 1984); *Trucizetina* (Havlíček 1982; Rong 1984); *Titanomena* (Bergström 1968); *Paromalomena* (including *Shanomena* in Cocks and Fortey 2002; e.g., Reed 1915; Temple 1965; Bergström 1968; Rong 1979, 1984; Nikitin 1980; Benedetto 1990; Cocks and Fortey 1997); *Orthorhynchillion* (Jin 1989); “*Homeospira*” (Amsden 1974); *Undithyrella* (Havlíček 1971).

## (4) New arrivals 2

Eleven genera arose in the Hirnantian and extended into the Silurian: *Toxorthis* (Temple 1968, 1970; Rong 1984); *Dysprosorthis* (Rong 1984; *Reuschella inexpectata*, Williams and Wright 1981); *Kinnella* (Bergström 1968; Cocks 1988); *Templeella* (Temple 1968; Rozman and Rong 1993); *Orthostrophella* (Amsden 1974; Williams and Harper 2000b); *Biparetis* (Amsden 1974; Dewing 1999); *Eostrophonella* (Dewing 1999; Cocks and Rong 2000); *Plectothyrella* (Bergström 1968; this paper); *Stegerhynchus* (Amsden 1974; Brenchley and Cocks 1982; Oradovskaya 1983; Jin 1989; Savage 1996); *Thebesia* (Amsden 1974; Brenchley and Cocks 1982; Kul'kov and Severgina 1989; Menakova 1991; Zhang 1989); *Whitfieldella* (Amsden 1974; Rong 1979; Menakova 1991; Alvarez and Rong 2002).

## Appendix B

In the earliest Silurian, there occur 76 brachiopod genera, with 20 new (those indicated with two asterisks) and 14 extinct (those indicated with one asterisk). The data are from Anticosti Island (Jin 1989; Jin and Copper 1997, 2000; Dewing 1999); Salta, Argentina (Isaacson et al. 1976); England (Harper and Williams 2002); Estonia (Rubel 1970; Cocks 1988; M. Rubel, personal communication, 2002); Kazakhstan (Modzalevskaya and Popov 1995); Kolyma (Oradovskaya



1983); midcontinental United States (Amsden 1974); Norway (Baarli and Harper 1986; Baarli 1988); south China (Rong et al. 2003; this paper); Venezuela (Boucot et al. 1972); and Wales (Williams 1951; Cocks 1988). The subdivision of middle and upper Rhuddanian is difficult in shelly facies, and revision of the results is needed.

Craniopsida: *Paracraniops*. Dictyonellida: *Eodictyonella*. Strophomenida: *Anisopleurella*, *Biparetis*\*, *Brachyprion*\*\*\*, *Eopholidostrophia*, *Eoplectodonta*, *Paromalomena*\*, *Eostropheodonta*, *Eostrophonella*, *Katastrophomena*, *Leangella*, *Leptaena*, *Palaeoleptostrophia*\*\*, *Ygerodiscus*\*\*. Orthotetida: *Coolinia*, *Fardenia*, *Saughina*\*\*, *Triplesia*. Orthida: *Chrustenopora*\*, *Dalejina*\*\*, *Dalmanella*, *Diceromyonia*\*, *Dicoelosia*, *Dolerorthis* (including *Schizonema*), *Dysprosorthis*\*, *Epitomyonia*, *Giraldiella*, *Glyptorthis*, *Hesperorthis*, *Isorthis*, *Jezercia*\*, *Kinnella*\*, *Levenea*, *Mendacella*, *Mirorthis*\*, *Onniella*, *Platystrophia*, *Ptychopleurella*, *Ravozetina*\*, *Resserella*\*\*, *Skenidioides*, *Templeella*, *Toxorthis*\*, *Visbyella*\*\*, gen. nov.\*\* (this paper). Pentamerida: *Borealis*\*\*, *Brevilamnulella*, *Parastrophinella*, *Stricklandia*\*\*, *Viridita*\*\*. Rhynchonellida: *Platyrochalis*, *Rhynchotrema*\*, *Rostricellula*, *Plectothyrella*\*, *Stegerhynchus*, *Thebesia*\*. Atrypida: *Alispira*\*\*, *Atrypina*\*\* (Copper 2002), *Atrypinopsis*\*\*, *Atrypopsis*\*\*, *Becscia*\*\*, *Clintonella*\*\*, *Cyclospira*\* (Copper 2001; Harper and Williams 2002), *Eospirigerina*, *Idiospira*, *Meifodia*\*\*, *Plectatrypa*, *Protatrypa*\*\*, *Protozyga*, *Sypharotrypa*, *Zygospiraella*\*\*. Athyridida: *Hindella*, *Whitfieldella* (including *Koigia*), *Homeospira*. Spiriferida: *Eospirifer*.

## Appendix C

### (1) Northern Maine (USA)

The locality is between Pond Pitch and Hasakell Rock on the east bank of the east branch of the Penobscot River, Penobscot County, northern Maine (also see Neuman 1967). Some declining genera are unknown in the typical *Hirnantia* fauna elsewhere but occur in the Hirnantian collections from northern Maine. The brachiopods with a moderate diversity, housed in the Smithsonian Institution (No. 13030), collected by David Roy and identified by RBN and J-yR in 1987 and 1997, contain four declining genera (*Skenidioides*, *Epitomyonia*, *Leangella*, and *Sowerbyella*?) associated with key taxa of the *Hirnantia* fauna (e.g., *Hirnantia*, *Kinnella*, *Eostropheodonta*, and *Plectothyrella*). This assemblage may be regarded as inhabiting deeper and quieter water, muddy bottom conditions with an assignment of probably upper BA4 (BA, Benthic Assemblage).

### (2) Keisley (England)

A high-diversity, deeper water Hirnantian association occurs at Keisley (Temple 1968) that consists of two groups of genera. Group 1 includes many genera (e.g., *Dysprosorthis*, *Draborthis*, *Hindella*, *Hirnantia*, *Kinnella*, and *Paromalomena*) with a low abundance, showing strong affinities with the high-diversity *Hirnantia* fauna (Rong and Harper 1988). Group 2 contains some declining genera (e.g., *Dicoelosia*, *Dolerorthis*, *Piono-*

*dema*, and *Skenidioides*), scarcely known or unknown in the typical *Hirnantia* fauna.

### (3) Garth (Wales)

Williams and Wright (1981) recorded diverse associations of brachiopods from the Hirnantian Wenalt Formation at Garth. Two principal occurrences (Nos. 19 and 21) are chosen for discussion. Some declining genera (e.g., *Dolerorthis*, *Eoplectodonta*, *Glyptorthis*, *Leangella*, *Platystrophia*, and *Skenidioides*) that are generally unknown from the *Hirnantia* fauna are associated with key taxa of the fauna (e.g., *Hirnantia*, *Kinnella*). High diversity, low abundance, and smaller shell size with some deeper water adapted genera may indicate a BA4 assignment.

### (4) Girvan (Scotland)

The Hirnantian brachiopods from the High Mains Formation in Girvan include a number of declining genera (e.g., *Eocho-netes*, *Eopholidostrophia*, *Eospirigerina*, *Glyptorthis*, *Hypsipytycha*, *Plaesiomys*, and *Rostricellula*) (Harper 1981), all unknown from the typical *Hirnantia* fauna (Rong and Harper 1988), associated with some key elements of the fauna (e.g., *Hirnantia*, *Eostropheodonta*, and *Hindella*), indicating a shallow-water assemblage.

### (5) Tongzi (northern Guizhou, south China)

A typical *Hirnantia* fauna including *Dalmanella*, *Hirnantia*, *Eostropheodonta*, *Paromalomena*, *Fardenia*, *Cliftonia*, *Plectothyrella*, and *Hindella* from the lower Kuanyinchiao Beds (AFA295-303: middle *Normalograptus extraordinarius* to lower *N. persculptus* zones) at Shanwangmiao, Tongzi, is associated with the trilobites *Dalmanitina* and *Eoleonaspis* (Chen et al. 2000). The upper Kuanyinchiao Beds (AFA304-311c: middle *N. persculptus* to *Akidograptus ascensus* zones) contain some common elements of the *Hirnantia* fauna (such as *Paracraniops*, *Dalmanella*, *Eostropheodonta*, *Paromalomena*, *Fardenia*, *Plectothyrella*, and *Hindella*), associated with a few declining genera (*Eospirifer* and *Nalivkinia*) that are usually unknown from the shelly fauna.

### (6) Zunyi (northern Guizhou, south China)

A brachiopod association of the Kuanyinchiao Bed (Hirnantian) at Zhujiapo, Zunyi contains the early athyridid *Whitfieldella* that is unknown in the *Hirnantia* fauna elsewhere, associated with rare *Paromalomena*, *Leptaena*, *Hindella*, and *Dalmanitina*. The low-diversity, paleogeographical position of near shore and more than 96% individuals of *Whitfieldella* show an assignment to BA2 (Rong 1979, 1986).

### (7) Yanhe (northeastern Guizhou, south China)

The Kuanyinchiao Bed (Hirnantian) at Shichang'ao, Yanhe, yields declining genera of orthid (*Giraldiella*) and virgianid (*Brevilamnulella*) with *Dalmanella testudinaria*, *Paromalomena polonica*, and *Hindella crassa incipiens*. Within the shelly beds are several layers, 3–5 cm thick, extremely rich in crinoidal debris, indicating nearshore, oxygen-rich, rough-water conditions (BA2). The occurrence of a single, abundant gastropod genus (*Holopea*) provides additional support for this conclusion.