

Statistical comparisons of late Caradoc (Ordovician) brachiopod faunas around the Iapetus Ocean, and terranes located around Australia, Kazakhstan and China

Yves CANDELA

Department of Natural Sciences, National Museums of Scotland,
Building 8, West Granton Centre, 242, West Granton Road,
Edinburgh EH5 1JA (United Kingdom)
y.candela@nms.ac.uk

Candela Y. 2006. — Statistical comparisons of late Caradoc (Ordovician) brachiopod faunas around the Iapetus Ocean, and terranes located around Australia, Kazakhstan and China. *Geodiversitas* 28 (3): 433-446.

ABSTRACT

Statistical comparisons, based on 173 genera distributed in 27 Caradoc localities from around the world, show strong faunal similarities between North and South China and the Chu-Ili terrane, the Chingiz terrane and Australia/Tasmania. The Scoto-Appalachian fauna of the Laurentian terrane shows closer similarities to faunas from the Gornoi-Altai terrane (belonging to the Kazakhstan terrane) than to faunas from Baltica and Avalonia that are generally regarded as being closer to Laurentia. This suggests a peri-equatorial location for the Gornoi-Altai terrane that would allow the migration of taxa to the west. The faunas from North and South China are typical deep water *Foliomena* faunas that are restricted to peri-equatorial palaeo-latitudes. The North China terrane is best positioned closer to the Equator than other palaeogeographical reconstructions suggest. The three different Kazakhstan terranes group each with a different cluster (i.e. the Gornoi-Altai terrane with Laurentia, the Chu-Ili terrane with North and South China and the Chingiz terrane with the Australian, including Tasmania, part of Gondwana). This suggests that Kazakhstan is best regarded as having been divided into several terranes, each possessing an individual developing history, rather than a single entity.

KEY WORDS

Brachiopoda,
Caradoc,
Ordovician,
palaeogeography,
provinciality.

RÉSUMÉ

Comparaisons statistiques de faunes de brachiopodes fini-caradociennes (Ordovicien) autour de l'océan Iapetus, et de terrains situés autour de l'Australie, du Kazakhstan et de la Chine.

Des comparaisons statistiques, basées sur 173 genres distribués dans 27 localités dans le monde, montrent de fortes similarités fauniques entre les terrains de Chine du Nord et du Sud, de Chu-Ili, de Chingiz et d'Australie/Tasmanie. La faune Scoto-Appalachienne de la Laurentia démontre des similarités plus proches des faunes du terrain de Gornoi-Altai (faisant partie du terrain du Kazakhstan) que de Baltica et Avalonia qui sont généralement considérés comme étant plus proches de la Laurentia. Ceci suggère une position péri-équatoriale du terrain de Gornoi-Altai qui permettrait la migration des taxons vers l'ouest. Les faunes de la Chine du Nord et du Sud sont des faunes typiques à *Foliomena* qui sont considérées avoir une distribution autour de paléolatitudes péri-équatoriales. Le terrain de Chine du Nord est plus adéquatement positionné plus proche de l'Équateur que d'autres reconstructions paléogéographiques le proposent. Les trois différents terrains du Kazakhstan se connectent avec des groupes différents (à savoir le terrain de Gornoi-Altai avec la Laurentia, le terrain de Chu-Ili avec la Chine du Nord et du Sud et le terrain de Chingiz avec la partie australienne, incluant la Tasmanie, du Gondwana). Ceci suggère qu'il est plus judicieux de considérer le Kazakhstan comme étant constitué de plusieurs terrains possédant chacun une histoire de développement individuel plutôt qu'une seule et unique entité.

MOTS CLÉS
Brachiopoda,
Caradocien,
Ordovicien,
paléogéographie,
provincialisme.

INTRODUCTION

In a previous publication (Candela 2003), Late Ordovician brachiopod faunas from Laurentia, Baltica, Avalonia and Armorica were compared using cluster analysis. The results discriminated three clusters: a first cluster grouping assemblages with Armorican affinities, a second with Laurentian affinities and a third with Avalonian affinities. Remarks focused, firstly, on the strong affinities between assemblages from Baltica and Avalonia, which grouped at high similarity coefficient. This illustrated the breakdown of brachiopod provinciality that had started during the Middle Ordovician. Secondly, the stronger similarity of brachiopod assemblages from Pomeroy (Northern Ireland) and Kilbucho (South of Scotland), that are found on

opposite sides of the Southern Upland Fault, rather than with assemblages from Girvan (Scotland) (which is on the same side of the SUF as Pomeroy), suggested a short post-Caradoc displacement. In the present paper, data from Kazakhstan (Klenina *et al.* 1984; Kulkov & Severgina 1989; Popov *et al.* 2002), China (Rong & Zhan 1996; Cocks & Zhan 1998; Rong *et al.* 1999), Sibumasu (Cocks & Zhan 1998), Australia/Tasmania (Laurie 1991; Percival 1991) and Armorica (Villas 1985, 1992) is integrated to enable a wider understanding of the distribution of faunas from Ordovician shelf, slope and basinal settings around palaeocontinents.

Brachiopods were important elements of the benthic fauna during the Early-Middle Palaeozoic. They are an ideal group for palaeobiogeographic studies, because they were sessile, most of them lived

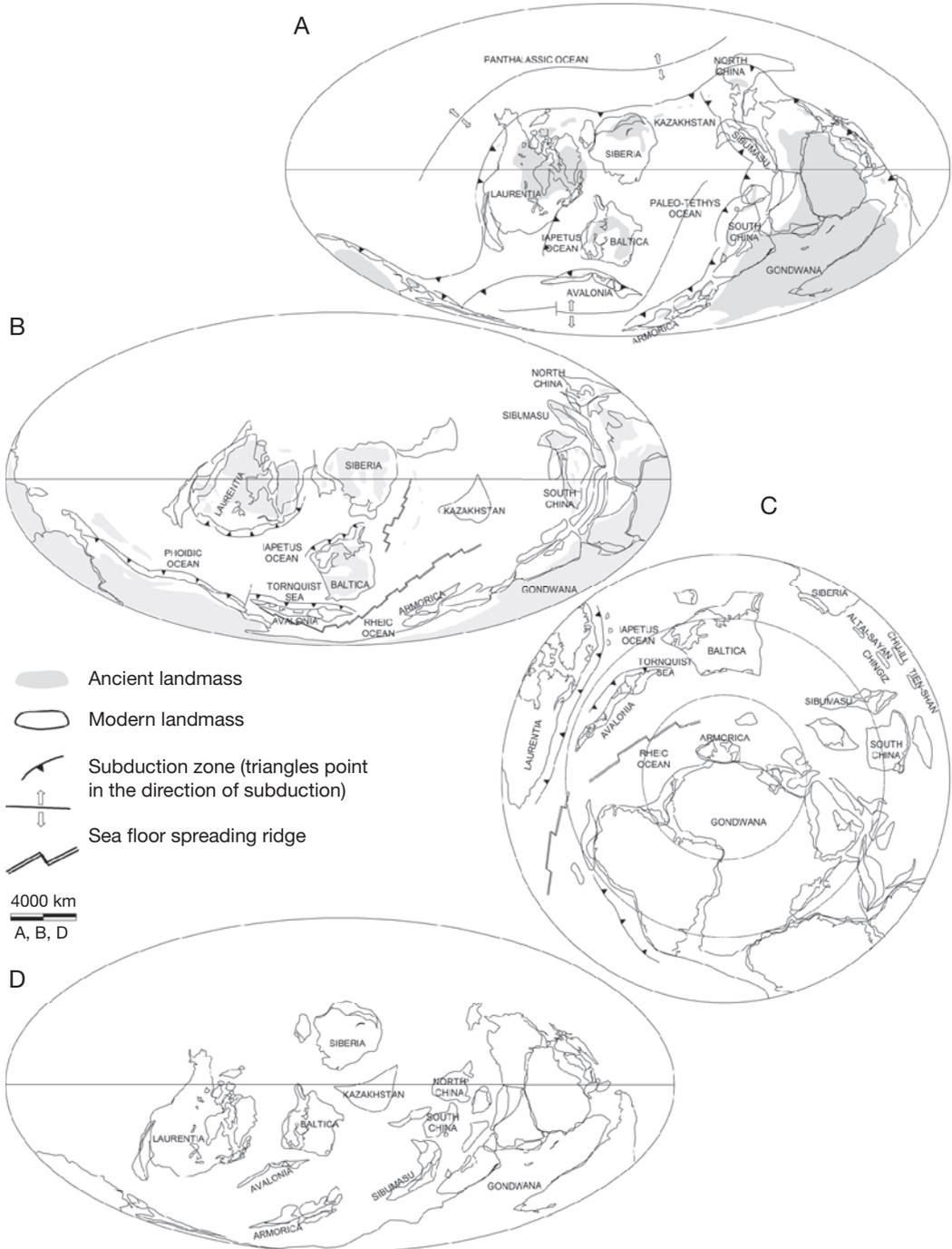


FIG. 1. — Reconstructions for Mid-Ordovician (460 Ma) times. Redrawn from: **A**, Scotese (2002); **B**, Golonka (2002); **C**, Cocks & Fortey (2002) amended by Fortey & Cocks (2003); **D**, Rong *et al.* (1999).

in relatively shallow water, their shells accumulated in large numbers, and they could survive transport, burial and diagenesis (Tychsen & Harper 2004). The last feature enables an accurate identification of the animals at the generic and specific levels.

PLATE TECTONIC MODELS

Various palaeogeographic maps have been produced since the important work of Scotese & McKerrow (1990). Reconstructions have relied principally on palaeomagnetic and sedimentologic data (Golonka 2002; Scotese 2002). Because continental palaeomagnetic evidence is less precise for the Early Palaeozoic (Lees *et al.* 2002), the relative longitudinal position of plates and its representation have been arbitrary (Mound & Mitrovica 1998). At best, relative longitude is known to $\pm 30^\circ$ and latitude $\pm 15^\circ$ (Scotese & McKerrow 1990). However, the use of key fossil groups such as brachiopods and trilobites, combined with palaeomagnetic data, has allowed Cocks & Torsvik (2002) to produce palaeogeographic reconstructions for the period ranging from 500 to 400 Ma. Fortey & Cocks (2003) have presented the advantages of using palaeontologic evidence in global continental reconstructions for the Ordovician and the Silurian. For example, fossil evidence helps resolve longitudinal problems that cannot be solved by palaeomagnetism alone (Fortey & Cocks 2003). Selected models proposed by Scotese (2002) (Fig. 1A), Golonka (2002) (Fig. 1B) and Cocks & Torsvik (2002), amended by Fortey & Cocks (2003) (Fig. 1C) are discussed below.

The reconstructions proposed by Cocks & Torsvik (2002) differed greatly from those published by Golonka (2002) and Scotese (2002), the latter two being dissimilar in only few details. Consensus is achieved in the relative position of Laurentia, Baltica, Siberia and Avalonia, although the latter is placed south of Baltica by Scotese (2002), whereas in Golonka's (2002) map it is placed west of Baltica (see also McKerrow *et al.* [2000]). Cocks & Torsvik (2002) also positioned Avalonia west of Baltica, and separated Siberia and Laurentia by over 6000 km of ocean. In the maps proposed by Golonka (2002) and Scotese (2002), Siberia and

Laurentia are closer together as Siberia was colliding (arc collision) with Laurentia throughout the Caradocian (McKerrow *et al.* 1991), causing the Taconian Orogeny.

The position of Gondwana, centered at the palaeosouth pole, has not been modified since Scotese & McKerrow (1990), although Golonka (2002) placed South America closer to the southern margins of Laurentia than Scotese (2002) and Cocks & Torsvik (2002). The main differences regard the relative position of Sibumasu, North China and South China. In a first scenario (Cocks & Torsvik 2002), these have drifted away from the Paleo-Tethys margins of Gondwana, with Sibumasu and South China located at 30°S , while North China is located in the Northern Hemisphere, although there cannot have been very great distances between it and the neighbouring terranes (Fortey & Cocks 2003). A second scenario involves Sibumasu, North China and South China remaining peri-Gondwanan terranes (Metcalf 1998; Golonka 2002; Scotese 2002): North China is located 30°N , South China is at the Equator and Sibumasu is intermediate.

Scotese (2002) proposed a North Hemisphere position for Kazakhstan, forming an island arc between Siberia to the west and North China to the east. Şengör *et al.* (1993) and Şengör & Natal'in (1996) proposed an Ordovician configuration for the Kazakh terranes (*sensu* Şengör 1987 and Şengör *et al.* 1993) as strung out in a huge arc (Kipchak Arc) stretching from the east coasts of Siberia to Baltica (see also Golonka 2002). Fortey & Cocks (2003) have discussed and rejected this configuration. The clear Sino-Australian signature, for the Late Ordovician, of trilobites and brachiopods indicated a peri-Gondwanan position for the terranes forming the Kipchak Arc. A new reconstruction was proposed by Fortey & Cocks (2003: fig. 15) (see also Figure 1C herein).

DATA AND TECHNIQUES

The present study integrates a compilation of fossil brachiopod data from published sources only (list in Appendix) with personal data. Older references have been updated to modern taxonomic standards

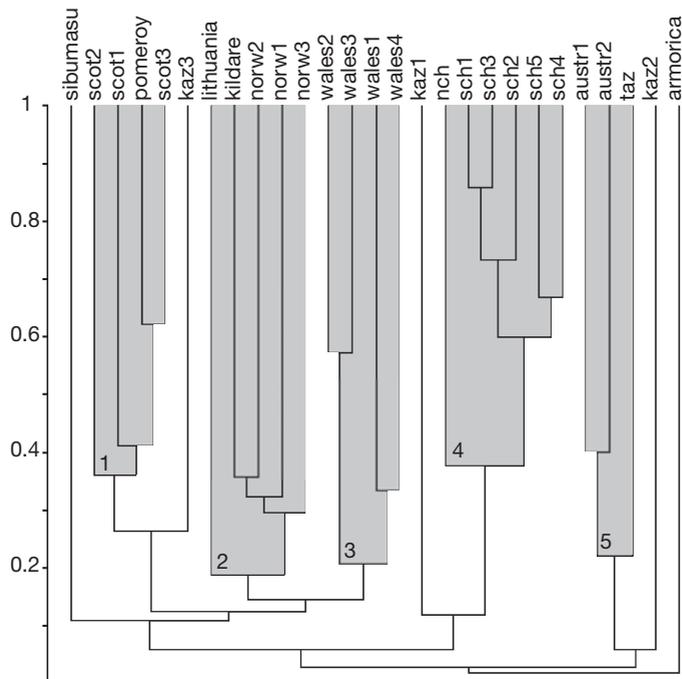


FIG. 2. — Cluster analysis on presence/absence data of 27 localities using 173 genera; UPGMA, Dice Index of similarity (values are displayed on the vertical axis). Data: see Appendix. Shaded areas represent the five clusters numbered 1 to 5. Key for assemblage: see Appendix.

to form a stable database. A total of 173 genera (detailed list in Appendix) were used, recorded in 27 localities, which correspond to such terranes as defined by Cocks & Torsvik (2002) and Fortey & Cocks (2003). The analyses discarded the pandemic genera found in more than 10 localities (*Leptaena*, *Skenidioides* and *Sowerbyella*): they bias the result by over-estimating the correlation between assemblages. The generic database is founded primarily on possible biases in relation to conditions of preservation (moulds and casts, deformed shells, decalcified material, etc.) and to appropriate generic assignment by various authors. Some of the genus names used may therefore not be possible to validate, and may be incorrect. Multivariate analysis techniques included in the PAST software (Hammer *et al.* 2005) were used. Firstly, cluster analysis (Fig. 2) used the Dice index of similarity, which is suitable for the use of presence/absence data (Hammer *et al.* 2005) and recommended for palaeobiogeographic

analysis (Rong *et al.* 1995). Cluster analysis is a straightforward method of visualizing association data, although the confidence of the nodes is highly dependent on data quality and levels of similarity for cluster nodes is dependent on the similarity index used (Tychsen & Harper 2004). The mean linkage (UPGMA) method is chosen here because clusters are joined on the basis of the average distance between all members in the two groups. A second analysis (Fig. 3) used detrended correspondence analysis (DCA), to bring an objective and critical approach and to investigate palaeobiogeographic trends in the data.

ANALYSIS OF DATA AND DISCUSSION

CLUSTER ANALYSIS

The data groups into five distinct clusters (Fig. 2): cluster 1 assembles faunas of Scoto-Appalachian

affinities lying on the eastern margin of Laurentia (Williams 1962; Candela 2003); cluster 2 groups faunas of Baltoscandian affinities (Harper & Owen 1984; Harper *et al.* 1984; Paškevičius 1994), also including the assemblage from the south east of Ireland (Parkes 1994); cluster 3 groups faunas of Avalonian affinities (Hurst 1979; Pickerill & Brenchley 1979; Lockley 1980); cluster 4 links faunas from North China (Rong & Zhan 1996) and South China (Rong *et al.* 1999); cluster 5 groups faunas from the core of “east” Gondwana (as defined by Fortey & Cocks 2003), i.e. Tasmania (Laurie 1991) and Australia (Percival 1991).

Cluster 5 and high latitude peri-Gondwanan faunas of Armorica are linked to the rest of the data at a very low similarity index, which reflects the taxonomic structure of these faunas composed of many exclusive genera (e.g., *Australispira*, *Trigrammaria*, *Wiradjurella* for Australia, *Hebertella* and *Tasmanella* for Tasmania, and *Aegiromena*, *Gelidorthis* and *Svobodaina* for Armorica). The term exclusive is used *sensu* Sánchez & Babin (2003) here instead of endemic for the same reasons. For obvious opposite palaeoecologic conditions (Armorica positioned at high, circum-polar latitude whereas elements from cluster 5 are located around the palaeo-equator), these two groups are not connected faunally to each other.

During the Middle to Late Ordovician, Gondwana provinciality had not broken down yet, although its early dispersal history had started with the rifting from Avalonia that drifted rapidly northward between 480 and 460 Ma (Cocks & Torsvik 2002) to reach palaeo-latitudes similar to the southern margins of Baltica. Avalonia had lost its Gondwanan affinities due to the substantial breadth that the Rheic Ocean had reached by the Caradoc. The absence of common fauna is also emphasized by the strong gradient in water temperature between the warmer water conditions around Avalonia and the colder circumpolar waters of Armorica. Avalonia had changed its brachiopod signature with the presence of genera with ancestors mainly from Baltica (for example *Leptaena*, *Sericoides* both from the lower Caradoc) (Fig. 2, connection between clusters 2 and 3). Reciprocally, genera that originated in Avalonia (for example *Dalmanella* in the Arenig) had taken

the opportunity of colonising the margins of Baltica during the Caradoc as the Tornquist Ocean, which divided the two palaeocontinents was shrinking. Williams *et al.* (2003) noted an identical migration route during the mid Caradoc for ostracods from the “North Atlantic” region. The assemblage from Lithuania groups with assemblages from Scandinavia (Fig. 2, cluster 2), at a lower level of similarity, perhaps due to differences in facies.

The brachiopod assemblage from south east Ireland [kildare], although palaeo-geographically belonging to Avalonia (Fortey & Cocks 2003), is related to the Norwegian assemblage from Oslo-Asker [norw2] (Fig. 2). It contains a higher number of taxa common to Baltica, as well as Laurentia, than to the Anglo-Welsh province. Owen & Parkes (2000) compared the trilobite faunas from Kildare, SE Ireland, with coeval Scoto-Appalachian and Avalonian trilobite faunas, and concluded that the strong Scoto-Appalachian faunal link during the lower Upper Ordovician may indicate that the Leinster terrane occupied a more oceanward setting than the Anglo-Welsh area.

Central Kazakhstan is composed of a series of accreted terranes (Şengör 1987; Şengör *et al.* 1993) whose current juxtaposition does not reflect their original geographic position (Fortey & Cocks 2003). Their geologic structure suggests that in the Palaeozoic, these terranes formed either a series of island arcs, known collectively as the “Kipchak Arc” (Şengör 1987; Şengör *et al.* 1993), that extended between Baltica and Siberia, or were regarded as microcontinents separated by small oceanic basins, each having its own history of development (Fortey & Cocks 2003). Three of these terranes are integrated in the analysis: the Chu-Ili [kaz1], Chingiz [kaz2] and Altai-Sayan [kaz3] terranes (see Appendix for faunal detail). In the Lower to Middle Ordovician, the Laurentian (at least Scoto-Appalachian) and Siberian signature of the Gornoi Altai [kaz3] brachiopod faunas is relatively strong (Fortey & Cocks 2003). The Scoto-Appalachian signature is still strong in the Caradoc, as shown by the link with faunas from cluster 1 (Fig. 2). This is due to the presence of genera such as *Bimuria*, *Dactylogonia*, *Dolerorthis*, *Glyptorthis*, *Hesperorthis*, *Isophragma*, *Paurorthis*, *Sowerbyella* and *Sower-*

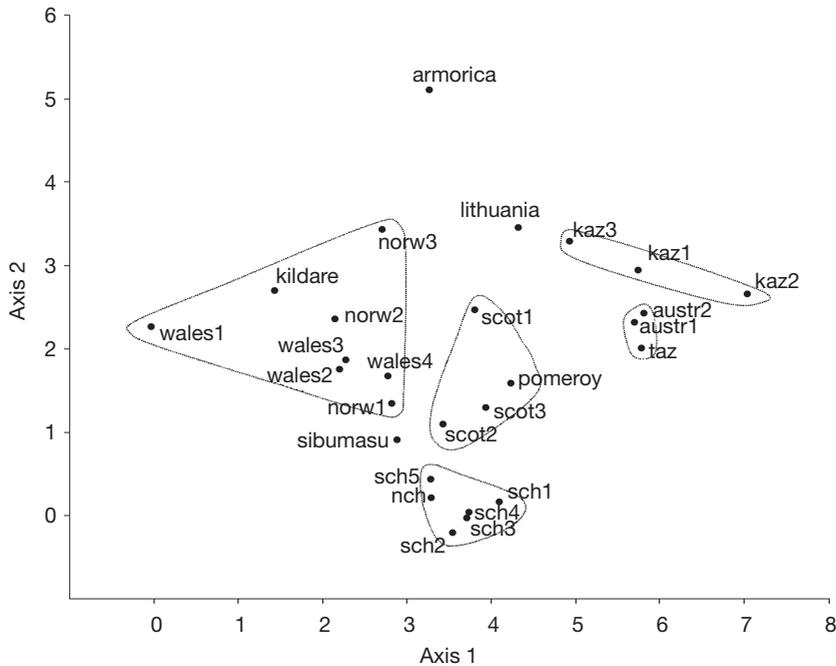


FIG. 3. — Assemblage scores on axes 1 and 2 of detrended correspondence analysis (DCA) based on presence/absence of genera. Key: same as Figure 2.

byites that are common in Laurentia (including the Scoto-Appalachian province). The analysis of Caradoc brachiopod faunas by Cocks & Zhan (1998: table 1) also emphasized the link between the faunas from Gornoi Altai and the Laurentian continent.

Although having many genera in common with Laurentia during the Middle Ordovician (Llanvirn) (Fortey & Cocks 2003), the brachiopod signature of the Anderken Formation of the Chu-Ili terrane clearly shows Chinese affinities by the Upper Ordovician (Caradoc) (Fig. 2). Popov *et al.* (2002) emphasized the relation of the Anderken Formation brachiopod assemblage with those of north-west China.

Finally the Caradoc brachiopod fauna [kaz2] of the Sargaldak Formation of the Chingiz terrane shows affinities with faunas grouped in cluster 5 (from Tasmania and New South Wales, Australia), although genera such as *Aulie* and *Dulankarella* are restricted to Kazakhstan during the Caradoc.

These remarks on the Kazakh terranes corroborate the idea that, during the Caradoc, these terranes were located at a low latitude, along the Equator and extended to the margins of “East” Gondwana as suggested by Zhylykaidarov (1998), Fortey & Cocks (2003) and Alexyutin *et al.* (2005), rather than forming an arc stretching from Baltica to Siberia as proposed by Şengör (1987), Şengör *et al.* (1993) and Şengör & Natal’in (1996). Popov *et al.* (1997) argued that the model proposed by Şengör *et al.* (1993) may explain post-Silurian tectonic development of the Kazakhstanian orogen, however “some terranes in Central Kazakhstan may not be incorporated easily into this model” (e.g., Chingiz terrane). Popov *et al.* (1997) assumed the microplates and island arcs associated with Kazakhstan to be situated between Baltica and the Australian part of Gondwana.

According to Zhan & Jin (2005), the brachiopods from the Upper Yangtze Platform (South China), Sibumasu and Kazakhstan (Chu-Ili) palaeo-

geographic regions constitute a distinct faunal province, characterised by endemic taxa and several regional taxa (i.e. *Saucrorthis* and *Martiella*). Popov *et al.* (1999) also noted the strong affinities between North and South China and Kazakhstan (see also Figure 2 herein) for being the place where early atrypidides and athyridides originated and first diversified.

The brachiopod assemblages from North China [nch] and South China ([sch1] to [sch5]) are typical deep water *Foliomena* faunas as first defined by Sheehan (1973) and amended by Rong *et al.* (1994, 1999). The strophomenoid brachiopod *Foliomena* originated in South China in early Caradoc black graptolitic shales of the Miaopo Formation (BA 4). The typical *Foliomena* fauna appeared in the middle Caradoc in South China in the carbonate facies of the Pagoda Formation (BA 5) (Rong *et al.* 1999). The *Foliomena* fauna is typical of deep water benthic regimes, marginal to continents, which helps with reconstructing the position of palaeo-plates. This evidence suggests that North China, South China and Sibumasu (which possesses an early Ashgill *Foliomena* fauna) with their *Foliomena* faunas “faced” oceanward (Palaeo-Tethys Ocean), as proposed by Rong *et al.* (1999: fig. 9) and Fortey & Cocks (2003: fig. 15). This differs from reconstructions of Scotese (2002) and Golonka (2002). According to Rong *et al.* (1999), the *Foliomena* fauna occurs within a restricted latitudinal range of between 18–25° in the southern hemisphere, supported later by Fortey & Cocks (2003), who postulated a peri-equatorial to subtropical location for South China, Sibumasu and North China. Golonka (2002) positioned North China at 45°N and South China at 30°S, and the Sibumasu terrane in an intermediate position. Webby (2002), in his study of the Ordovician reefs, stressed that the palaeoposition of North China in palaeolatitudes of 30–45°N, as proposed by Golonka (2002) and Scotese (2002), is problematic. The reefs (coral, algal and stromatoporoid) found in North China are typical of the tropics, which has a latitudinal range not greater than between 25°N and 25°S (see Webby 2002: fig. 7).

In the present study, the Sibumasu terrane (comprising the western part of the Malay Peninsula,

Thailand and Burma (Cocks & Torsvik 2002; Fortey & Cocks 2003) has a low level of similarity with the circum-Iapetus assemblages (i.e. clusters 1 to 3). Several genera are found outside Sibumasu (e.g., “*Cyclospira*”: [Avalonia, Laurentia]; *Nicolella*: [Avalonia, Baltica, Laurentia]; *Onniella*: [Avalonia, Baltica]; *Skenidiodides*: [Avalonia, Baltica, Laurentia]; “*Protozyga*”: [Avalonia, Laurentia]) indicating some communication between these terranes or possibly relatively warm and uniform global temperatures (Cocks & Torsvik 2002). These genera are generally typical of subtropical latitudes. No common taxa are recorded in high-latitude circum-polar terranes. The breakdown of terrane provinciality during rising sea-level echoed the middle Caradoc brachiopod diversification that drastically increased the number of genera over about 20 Ma (from 470–450 Ma). Cluster 4 (including North and South China) and the assemblage from the Chu-Ili terrane have similarities with the Sibumasu assemblage. The small orthid *Saucrorthis*, formerly thought to be restricted to the early Caradoc of South China is also present in the younger assemblage from Sibumasu, and, *Bekkerella* and *Dirafinesquina* are restricted to the Naungkangyi Group in Sibumasu. Although the Sibumasu terrane has been demonstrated to have geographical affinity with South China (Fortey & Cocks 1998), this new evidence indicates some separation from South China (Fortey & Cocks 2003). The small number of common genera between the Chinese and the Sibumasu terranes (“*Cyclospira*” and *Skenidiodides*) may denote different palaeoecological conditions. The Chinese assemblages have a typical low diversity *Foliomena* faunas (deep water, BA 5), whereas the assemblage from Sibumasu is a shallower water assemblage (BA 2 to 3) (Cocks & Zhan 1998).

ORDINATION ANALYSIS

A bivariate plot (Fig. 3) shows the result of the detrended correspondence analysis (DCA). Both assemblages from Australia and the assemblage from Tasmania form a tight cluster in DCA displaying little variation along axis 1. The small variation along axis 2 (Fig. 3) can be explained by the presence of exclusive genera such as *Australispira*, *Doleroides*,

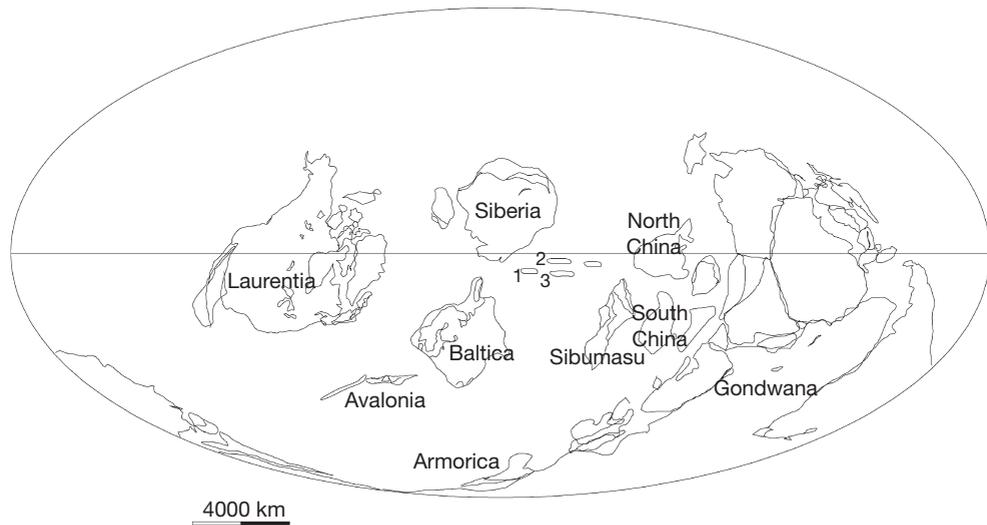


FIG. 4. — Proposed palaeogeographic reconstruction; Kazakh terranes: 1, Altai-Sayan; 2, Chu-Ili; 3, Chingiz; limits of terranes unknown. Scale bar: 4000 km.

Molongcola, *Paraonychoplecia*, *Quondongia*, *Trigrammaria*, *Tylambonites* and *Wiradjurella* in the two Australian assemblages and *Hebertella* and *Tasmanella* in Tasmania. Taxonomic differences between these contemporaneous and adjacent assemblages existed because of different tectono-sedimentary regimes and thus environments for benthic life. The assemblage from Tasmania was a former Gondwana shelf margin assemblage, whereas the assemblages from Australia were offshore, island-arc shelf area assemblages (Webby 1987, 1991). Webby (1991) also noted stromatoporoid genus and species provincial differences between Tasmania and Australia. The stromatoporoid fauna showed affinities with faunas from North America, but closer biogeographic links are shown with Asian terranes such as North China, Kazakhstan and Malaysia (Webby 1991). Brachiopod assemblages also demonstrate ties between Australia, Laurentia, North and South China and Kazakhstan.

The Welsh assemblage [wales1] plots apart from the rest of the Avalonia cluster including the other Welsh assemblages ([wales2], [wales3] and [wales4]). It is characterized by shallow water brachiopod faunas including *Heterorthis alternata* and *Sowerbyella sericea*. Coeval rocks to the north-west, on the op-

posite side of the Welsh Borderland Fault System (WBFS) ([wales2] and [wales3]), are characterized by deeper water brachiopod faunas including *Eoplectodonta*, *Onniella* and *Sericoidea*. The contrast between [wales1] and the other Avalonia assemblages expressed by variations along DCA axis 2 (Fig. 3) is probably related to palaeoenvironmental settings: as the direction along a north west transect of these localities across the WBFS represents a transition from shallow water platform to an offshore deeper water environment.

Armorica keeps its palaeogeographic and taxonomic (*Aegiromena*, *Gelidorthis* and *Svobodaina*) individuality (Fig. 3).

Sibumasu retains its position close to the Baltica-Avalonia and Scoto-Appalachian clusters (Fig. 3 and Fig. 2), but also holds a close position near the Chinese cluster. This latter relationship is well established (Fortey & Cocks 1998, 2003) and documented, and is, therefore not surprising. Laurie & Burrett (1992) proposed an Early Ordovician juxtaposition of Sibumasu and western Australia. On the basis of faunal distribution and palaeomagnetic data, the North China terrane suggests proximity to Australia and Sibumasu (Burrett & Stait 1987).

CONCLUSIONS

The palaeogeographic reconstruction proposed herein (Fig. 4) is based on this revised faunal analysis and also on previous works (Rong *et al.* 1999; Cocks & Torsvik 2002; Fortey & Cocks 2003). North and South China, Sibumasu and the Kazakh terranes and their faunas suggest:

- North China was close to Equator;
- Sibumasu and South China lay in tropical latitudes, and were close to North China;
- Kazakhstan was not a single entity, but divided into several terranes located at the equator, rather than being part of an arc between Siberia and Baltica;
- these geographic positions allowed an exchange and spread of taxa via currents as shown by Herrmann *et al.* (2004).

Acknowledgements

I am very grateful to Paul Copper (Laurentian University, Ontario, Canada) whose comments and advices have significantly improved the manuscript. I am also grateful to the second anonymous reviewer. I thank Tatiana Modzalevskaya (St. Petersburg, Russia) for her kind help with some Russian translation.

REFERENCES

- ALEXUYUTIN M. V., BACHTADSE V., ALEXEIEV D. V. & NIKITINA O. I. 2005. — Palaeomagnetism of Ordovician and Silurian rocks from the Chu-Yili and Kendyktas mountains, south Kazakhstan. *Geophysical Journal International* 162: 321-331.
- BURRETT C. & STAIT B. A. 1987. — China and Southeast Asia as part of the Tethyan margin of Cambro-Ordovician Gondwanaland, in MCKENZIE K. G. (ed.), *Shallow Tethys* 2. Balkema, Rotterdam: 65-77.
- CANDELA Y. 2003. — Late Ordovician brachiopods from the Bardahessiagh Formation of Pomeroy, Ireland. *Monograph of the Palaeontological Society*, London, 95 p., 12 pls. (Publ. No. 618, part of Vol. 156 for 2002).
- COCKS L. R. M. & TORSVIK T. H. 2002. — Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society*, London 159: 631-644.
- COCKS L. R. M. & ZHAN R.-B. 1998. — Caradoc brachiopods from the Shan States, Burma (Myanmar). *Bulletin of the Natural History Museum, (Geology)*, London 54 (2): 109-130.
- FORTEY R. A. & COCKS L. R. M. 1998. — Biogeography and palaeogeography of the Sibumasu terrane in the Ordovician: a review, in HALL R. & HOLLOWAY J. D. (eds), *Biogeography and Geological Evolution of SE Asia*. Backhuys, Leiden: 43-56.
- FORTEY R. A. & COCKS L. R. M. 2003. — Palaeontological evidence bearing on global Ordovician-Silurian continental reconstructions. *Earth-Science Reviews* 61: 245-307.
- GOLONKA J. 2002. — Plate-tectonic maps of the Phanerozoic, in KIESSLING W., FLÜGEL E. & GOLONKA J. (eds), *Phanerozoic reef patterns*. *SEPM Special Publication*, Tulsa 72: 21-75.
- HAMMER Ø., HARPER D. A. T. & RYAN P. D. 2005. — PAST: Palaeontological STatistics. <http://folk.uio.no/ohammer/past/>
- HARPER D. A. T. & OWEN A. W. 1984. — The Caradoc brachiopod and trilobite fauna of the upper Kirkerud Group, Hadeland, Norway. *Geologica et Palaeontologica* 18: 21-51.
- HARPER D. A. T., OWEN A. W. & WILLIAMS S. H. 1984. — The Middle Ordovician of the Oslo region, Norway, 34. The type Nakholmen Formation (upper Caradoc), Oslo, and its faunal significance. *Norsk Geologisk Tidsskrift* 64: 293-312.
- HERRMANN A. D., HAUPT B. J., PATZKOWSKY M. E., SEIDOV D. & SLINGERLAND R. L. 2004. — Response of Late Ordovician paleoceanography to changes in sea level, continental drift, and atmospheric pCO₂: potential causes for long-term cooling and glaciation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 210: 385-401.
- HURST J. M. 1979. — The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop. *Bulletin of the British Museum of Natural History (Geology)*, London 32 (4): 183-304.
- KLENINA L. N., NIKITIN I. F. & POPOV L. E. 1984. — [Brachiopods and Biostratigraphy of the Middle and Upper Ordovician of the Chinghiz Ranges]. Nauka, Alma-Ata, 196 p. (in Russian).
- KULKOV N. P. & SEVERGINA L. G. 1989. — [Ordovician and Early Silurian Stratigraphy and Brachiopods from Gorny Altai]. Nauka, Moscow, 221 p. (in Russian).
- LAURIE J. R. 1991. — Articulate brachiopods from the Ordovician and Lower Silurian of Tasmania. *Memorior of the Association of Australasian Palaeontologists* 11: 1-106.
- LAURIE J. R. & BURRETT C. 1992. — Biogeographic significance of Ordovician brachiopods from Thailand and Malaysia. *Journal of Paleontology* 66 (1): 16-23.
- LEES D. C., FORTEY R. A. & COCKS L. R. M. 2002. — Quantifying paleogeography using biogeography: a test case for the Ordovician and Silurian of Avalonia

- based on brachiopods and trilobites. *Paleobiology* 28: 343-363.
- LOCKLEY M. G. 1980. — The Caradoc faunal associations of the area between Bala and Dinas Mawddwy, north Wales. *Bulletin of the British Museum of Natural History, (Geology)*, London 33 (3): 165-235.
- MCKERROW W. S., DEWEY J. F. & SCOTese C. R. 1991. — The Ordovician and Silurian development of the Iapetus Ocean, in BASSETT M. G., LANE P. D. & EDWARDS D. (eds), The Murchison symposium; proceedings of an international conference on the Silurian System. *Special Papers in Palaeontology* 44: 165-178.
- MCKERROW W. S., MAC NIOCAILL C. & DEWEY J. F. 2000. — The Caledonian Orogeny redefined. *Journal of the Geological Society*, London 157: 1149-1154.
- METCALFE I. 1998. — Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography, in HALL R. & HOLLOWAY J. D. (eds), *Biogeography and Geological Evolution of SE Asia*. Backhuys, Leiden: 25-41.
- MOUND J. E. & MITROVICA J. X. 1998. — True polar wander as a mechanism for second-order sea-level variations. *Science* 279: 534-537.
- OWEN A. W. & PARKES M. A. 2000. — Trilobite faunas of the Duncannon Group: Caradoc stratigraphy, environments and palaeobiogeography of the Leinster terrane, Ireland. *Palaeontology* 43 (2): 219-269.
- PARKES M. A. 1994. — The brachiopods of the Duncannon Group (Middle-Upper Ordovician) of southeast Ireland. *Bulletin of the Natural History Museum, Geology Series* 50 (2): 105-174.
- PAŠKEVICIUS J. 1994. — *Baltijos Respublikų Geologija* [= *The Geology of the Baltic Republics*]. Vastybinis leidybos centras, Vilnius, 447 p. (in Lithuanian).
- PERCIVAL I. G. 1991. — Late Ordovician articulate brachiopods from central New South Wales. *Memoir of the Association of Australian Palaeontologists* 11: 107-177.
- PICKERILL R. K. & BRENCHELY P. J. 1979. — Caradoc marine benthic communities of the south Berwyn Hills, North Wales. *Palaeontology* 22 (1): 229-264.
- POPOV L. E., COCKS L. R. M. & NIKITIN I. F. 2002. — Upper Ordovician brachiopods from the Anderken Formation, Kazakhstan: their ecology and systematics. *Bulletin of the Natural History Museum, (Geology)*, London 58 (1): 13-79.
- POPOV L. E., HOLMER L. E. & GORJANSKY V. J. 1997. — Late Ordovician and early Silurian trimerellide brachiopods from Kazakhstan. *Journal of Paleontology* 71 (4): 584-598.
- POPOV L. E., NIKITIN I. F. & SOKIRAN E. V. 1999. — The earliest atrypides and athyridides (Brachiopoda) from the Ordovician of Kazakhstan. *Palaeontology* 42 (4): 625-661.
- RONG J.-Y., HARPER D. A. T., ZHAN R.-B. & LI R.-Y. 1994. — Kassinea-Christiania associations in the early Ashgill Foliomena brachiopod fauna of South China. *Lethaia* 27: 19-28.
- RONG J.-Y., LI R.-Y. & KULKOV N. P. 1995. — Biogeographic analysis of Llandovery brachiopods from Asia with a recommendation of use of affinity indices. *Acta Palaeontologica Sinica* 34: 428-453.
- RONG J.-Y. & ZHAN R.-B. 1996. — Distribution and ecological evolution of the Foliomena fauna (Late Ordovician brachiopods), in WANG H.-Z. & WANG X.-L. (eds), *Centennial Memorial Volume of Prof. Sun Yunzhu: Palaeontology and Stratigraphy*. China University of Geosciences Press, Beijing: 90-97, pls 1, 2.
- RONG J.-Y., ZHAN R.-B. & HARPER D. A. T. 1999. — Late Ordovician (Caradoc-Ashgill) Brachiopod faunas with *Foliomena* based on data from China. *Palaios* 14: 412-432.
- SÁNCHEZ T. M. & BABIN C. 2003. — Distribution paléogéographique des mollusques bivalves durant l'Ordovicien. *Geodiversitas* 25 (2): 243-259.
- SCOTese C. R. & MCKERROW W. S. 1990. — Revised World maps and introduction, in MCKERROW W. S. & SCOTese C. R. (eds), *Palaeozoic palaeogeography and biogeography. Geological Society Memoir* 12: 1-21.
- SCOTese C. R. 2002. — <http://www.scotese.com> (PALEO-MAP website).
- ŞENGÖR A. M. C. 1987. — Tectonics of the Tethyides: orogenic collage in a collisional setting. *Annual Reviews of Earth and Planetary Science* 15: 213-244.
- ŞENGÖR A. M. C. & NATAL'IN B. A. 1996. — Palaeotectonics of Asia: fragments of a synthesis, in YIN A. & HARRISON T. M. (eds), *The Tectonic Evolution of Asia*. Cambridge University Press, Cambridge: 486-640.
- ŞENGÖR A. M. C., NATAL'IN B. A. & BURTMAN V. S. 1993. — Evolution of the Altai tectonic collage and Palaeozoic crustal growth in Eurasia. *Nature* 364: 299-307.
- SHEEHAN P. M. 1973. — Brachiopods from the Jerrestad Mudstone (Early Ashgillian, Ordovician) from a boring in southern Sweden. *Geologica et Palaeontologica* 7: 59-76.
- TYCHSEN A. & HARPER D. A. T. 2004. — Ordovician-Silurian distribution of Orthida (Palaeozoic Brachiopoda) in the greater Iapetus Ocean Region. *Palaeontologica Electronica* 7 (3): 1-15.
- VILLAS E. 1985. — Braquiópodos del Ordovícico Medio y Superior de las Cadenas Ibéricas Orientales. *Memorias del Museo Paleontológico de la Universidad de Zaragoza* 1: 1-223.
- VILLAS E. 1992. — New Caradoc brachiopods from the Iberian Chains (Northeastern Spain) and their stratigraphic significance. *Journal of Paleontology* 66 (5): 772-793.
- WEBBY B. D. 1987. — Biogeographic significance of some Ordovician faunas in relation to East Australian

- Tasmanide suspect terranes, in LEITCH E. C. & SCHEIBNER E. (eds), *Terrane Accretion and Orogenic Belts*. Geodynamics Series 19. American Geophysical Union, Washington D. C.: 103-117.
- WEBBY B. D. 1991. — Ordovician stromatoporoids from Tasmania. *Alcheringa* 15: 191-227.
- WEBBY B. D. 2002. — Patterns of Ordovician reef development, in KIESSLING W., FLÜGEL E. & GOLONKA J. (eds), Phanerozoic reef patterns. *SEPM Special Publication*, Tulsa 72: 129-179.
- WILLIAMS A. 1962. — The Barr and Lower Ardmillan Series (Caradoc) of the Girvan District, south west Ayrshire, with description of the Brachiopoda. *Memoir of the Geological Society of London* 3: 1-267.
- WILLIAMS M., FLOYD J. D., SALAS M. J., SIVETER D. J., STONE P. & VANNIER J. M. C. 2003. — Patterns of ostracod migration for the “North Atlantic” region during the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195: 193-228.
- ZHAN R.-B. & JIN J. 2005. — Brachiopods from the Middle Ordovician Shihtzupu Formation of Yunnan Province, China. *Acta Palaeontologica Polonica* 50 (2): 365-393.
- ZHYLKAIDAROV A. 1998. — Conodonts from Ordovician ophiolites of central Kazakhstan. *Acta Palaeontologica Polonica* 43 (1): 53-68.

*Submitted on 11 May 2005;
accepted on 22 June 2006.*

APPENDIX

List of faunas used in the analyses.

- [**armorica**]: Peña del Tormo member of the Fombuena Formation, central Spain (Villas 1985, 1992); *Aegiromena*, *Gelidorthis*, *Rafinesquina*, *Rostricellula*, *Svobodaina*.
- [**austr1**]: Billabong Creek Limestone Member, Billabong Creek, New South Wales, Australia (Percival 1991); *Anoptambonites*, *Australispira*, *Bowanorthis*, *Didymelasma*, *Dinorthis*, *Doleroides*, *Eridorthis*, *Paraonychoplectia*, *Protozyga*, *Quondongia*, *Rhynchotrema*, *Sowerbyella*, *Sowerbyites*, *Trigrammaria*, *Wiradjuriella*, *Zygospira*.
- [**austr2**]: Quondong Limestone, Palin Yard Creek, New South Wales, Australia (Percival 1991); *Australispira*, *Bowanorthis*, *Hesperorthis*, *Molongcola*, *Phaceloorthis*, *Ptychopleurella*, *Trigrammaria*, *Tylambonites*, *Wiradjuriella*, *Zygospira*.
- [**kaz1**]: Unit 5 of the Anderken Formation, Chu-Ili Range, south-eastern Kazakhstan (Popov *et al.* 2002); *Acculina*, *Anoptambonites*, *Bellimurina*, *Bowanorthis*, *Christiania*, *Craspedelia*, *Didymelasma*, *Dolerorthis*, *Foliomena*, *Glyptorthis*, *Grammoplectia*, *Ilistrophina*, *Kajnarina*, *Kellerella*, *Limbimurina*, *Liostraphina*, *Nikolaispira*, *Nushbiella*, *Parastrophia*, *Pectenospira*, *Phaceloorthis*, *Phragmorthis*, *Placotriplesia*, *Plectorthis*, *Plectosyntrophia*, *Rhynchotrema*, *Schizostrophia*, *Skenidioides*, *Sortanella*, *Sowerbyella*, *Triplesia*.
- [**kaz2**]: Sargaldak Formation, Chingiz Range, Kazakhstan (Klenina *et al.* 1984); *Archaeorthis*, *Aulie*, *Austinella*, *Camerella*, *Craspedelia*, *Dulankarella*, *Ectenoglossa*, *Eoanastrophia*, *Leptaena*, *Perimecocoelia*, *Productorthis*, *Ptychoglyptus*, *Rhynchotrema*, *Sowerbyella*, *Tuvinia*.
- [**kaz3**]: Khankhar Horizon, Gornoi Altai, Russia (Kulkov & Severgina 1989); *Bimuria*, *Boreadorthis*, *Dactylogonia*, *Dolerorthis*, *Eoanastrophia*, *Eridorthis*, *Glyptorthis*, *Hesperorthis*, *Isophragma*, *Leangella*, *Mimella*, *Multicostella*, *Onniella*, *Ortbambonites*, *Palaeostrophomena*, *Paurorthis*, *Plectorthis*, *Rhynchotretoides*, *Rostricellula*, *Severginella*, *Sowerbyella*, *Sowerbyites*, *Titanambonites*, *Togaella*, *Triplesia*.
- [**kildare**]: Grange Allen Formation, Co. Kildare, Ireland (Parkes 1994); *Cremnorthis*, *Dalmanellida* gen. indet., *Hedstromina*, *Kullervo*, *Leptaena*, *Leptestiina*, *Lingulella*, *Nicolella*, *Orthisocrania*, *Petrocrania*, *Philhedra*, *Platystrophia*, *Rhactorthis*, *Salopia*, *Sericoides*, *Skenidioides*, *Sowerbyella*.
- [**lithuania**]: Oandu Stage, Lithuania (Paškevičius 1994); *Boreadorthis*, *Camerella*, *Glossorthis*, *Hesperorthis*, *Holtedahllina*, *Holderleyella*, *Howellites*, *Leptaena*, *Nicolella*, *Oanduporella*, *Onniella*, *Platystrophia*, *Rafinesquina*, *Sampo*, *Skenidioides*, *Sowerbyella*, *Strophomena*, *Vellano*, *Zygospira*.
- [**nch**]: Pingliang Formation, Longxian, Shaanxi Province, Northwest China (Rong & Zhan 1996); *Anisopleurella*, *Bellimurina*, *Bicuspina*, *Christiania*, *Cyclospira*, *Dolerorthis*, *Foliomena*, *Glyptorthis*, *Gunnarella*, *Kiaeromena*, *Leangella*, *Leptaena*, *Leptestiina*, *Longxianirhynchia*, *Nubialba*, *Paracraniops*, *Skenidioides*, *Sowerbyella*.
- [**norw1**]: Furuberg Formation, Hadeland, Norway (Harper *et al.* 1984); *Dalmanella*, *Dolerorthis*, *Eoplectodonta*, *Gunnarella*, *Leptaena*, *Leptestiina*, *Mcewanella*, *Mjoesina*, *Nicolella*, *Parastrophinella*, *Petrocrania*, *Platystrophia*, *Plectorthis*, *Porambonites*, *Skenidioides*, *Sowerbyella*, *Strophomena*.
- [**norw2**]: Nakkholmen Formation, Oslo-Asker, Norway (Harper *et al.* 1984); *Chonetoides*, *Dalmanellida* gen. indet., *Glyptorthis*, *Hisingerella*, *Holderleyella*, *Kjaerina*, *Kjaerulfina*, *Leptaena*, *Leptestiina*, *Nicolella*, *Onniella*, *Petrocrania*, *Platystrophia*, *Porambonites*, *Skenidioides*, *Sowerbyella*, *Spiriferida* gen. indet.
- [**norw3**]: Norderhov Formation, Ringerike, Norway (Harper *et al.* 1984); *Dalmanellida* gen. indet., *Hedstromina*, *Kjaerulfina*, *Leptaena*, *Mjoesina*, *Nicolella*, *Orbiculoidea*, *Oxoplectia*, *Plectorthis*, *Rhactorthis*, *Sowerbyella*, *Strophomena*, *Triplesia*.
- [**pomeroy**]: member III of the Bardahessiagh Formation, Pomeroy, Co. Tyrone, Northern Ireland (Candela 2003); *Anisopleurella*, *Anoptambonites*, *Apatomorpha*, *Bicuspina*, *Bilobia*, *Bimuria*, *Caeroplecia*, *Campylorthis*, *Christiania*, *Colaptomena*, *Dactylogonia*, *Dalmanella*, *Diambonia*, *Dicoelosia*, *Dinorthis*, *Dolerorthis*, *Drummuckina*, *Eochonetes*, *Eoplectodonta*, *Fascifera*, *Foliomena*, *Glossorthis*, *Glyptambonites*, *Glyptomena*, *Glyptorthis*, *Gunnarella*, *Hesperorthis*, *Idiospira*, *Isophragma*, *Laticrura*, *Leptaena*, *Leptellina*, *Leptellininae* gen. indet., *Leptestiina*, *Mimella*, *Mjoesina*, *Oanduporella*, *Oepikina*, *Palaeostrophomena*, *Paucicrura*, *Paurorthis*, *Platymena*, *Plectorthis*, *Protozyga*, *Pseudolingula*, *Ptychoglyptus*, *Ptychopleurella*, *Rostricellula*, *Rugosowerbyella*, *Salopina*, *Scaphorthis*, *Sericoides*, *Skenidioides*, *Sowerbyella*, *Sowerbyites*, *Strophomena*, *Sulevorthis*.
- [**sch1**]: Pagoda Formation, Mianxian County, Shaanxi Province, South China (Rong *et al.* 1999); *Christiania*, *Foliomena*, *Leangella*, *Skenidioides*.
- [**sch2**]: Pagoda Formation, Nanzhen County, Shaanxi Province, South China (Rong *et al.* 1999); *Anisopleurella*, *Christiania*, *Cyclospira*, *Foliomena*, *Leangella*, *Nubialba*, *Skenidioides*.
- [**sch3**]: Pagoda Formation, Guangyuan County, Sichuan Province, South China (Rong *et al.* 1999); *Christiania*, *Cyclospira*, *Foliomena*, *Leangella*, *Skenidioides*.
- [**sch4**]: Pagoda Formation, Wangcang County, Sichuan Province, South China (Rong *et al.* 1999); *Anisopleurella*, *Foliomena*, *Leangella*, *Skenidioides*.
- [**sch5**]: Pagoda Formation, Ningqiang County, Shaanxi Province, South China (Rong *et al.* 1999); *Foliomena*, *Leangella*, *Petrocrania*.
- [**scot1**]: Craighead Limestone Formation, Girvan, Scotland (Williams 1962); *Anisopleurella*, *Anoptambonites*, *Bilobia*, *Bimuria*, *Camerella*, *Christiania*, *Conotreta*, *Cyclospira*, *Dactylogonia*, *Dalmanella*, *Dinorthis*, *Dolerorthis*, *Drepanorhynchia*, *Eoplectodonta*, *Eparoplecia*, *Fardenia*, *Fascifera*, *Glossella*, *Glyptorthis*, *Hesperorthis*, *Idiospira*, *Laticrura*, *Leptaena*, *Lingulella*, *Nicolella*, *Obolus*, *Oligorhynchia*, *Orbiculoidea*, *Orthorhynchuloides*, *Oxoplectia*, *Palaeostrophomena*, *Parastrophia*, *Parastrophinella*, *Paucicrura*, *Philhedra*, *Pionodema*, *Platystrophia*, *Plectorthis*, *Porambonites*, *Protozyga*, *Rafinesquina*, *Reuschella*, *Rostricellula*, *Sericoides*, *Schizambon*, *Schizotreta*, *Skenidioides*, *Sowerbyella*, *Strophomena*, *Sulevorthis*, *Zygospira*.
- [**scot2**]: Ardwell Farm Formation, Girvan, Scotland (Williams 1962); *Bilobia*, *Bimuria*, *Cyclospira*, *Diambonia*, *Dinorthis*, *Dolerorthis*, *Eoplectodonta*, *Glyptorthis*, *Idiospira*, *Laticrura*, *Leangella*, *Leptaena*, *Leptellina*, *Oxoplectia*, *Paucicrura*, *Reuschella*, *Skenidioides*.
- [**scot3**]: Kirkcolm Formation, Kilbucho, SE Scotland (unpublished data); *Bilobia*, *Bimuria*, *Camerella*, *Campylorthis*, *Christiania*, *Colaptomena*, *Dactylogonia*, *Eoplectodonta*, *Glyptambonites*, *Glyptorthis*, *Hesperorthis*, *Idiospira*, *Isophragma*, *Laticrura*, *Leangella*, *Leptaena*, *Leptellina*, *Leptellininae* gen. indet., *Leptestiina*, *Mcewanella*,

Oanduporella, *Palaeostrophomena*, *Paucicrura*, *Paurorthis*, *Petrocrania*, *Pholidostrophia* (*Eopholidostrophia*), *Plaesiomys*, *Rugosowerbyella*, *Salopina*, *Scaphorthis*, *Sericoidea*, *Skenidioides*, *Sowerbyella*, *Sowerbyites*, *Strophomena*, *Sulevorthis*.

[sibumasu]: Naungkangyi Group, Shan States, Burma (Cocks & Zhan 1998); *Bekkerella*, *Bellimurina*, *Cyclospira*, *Dirafinesquina*, *Glyptomena*, *Ishimia*, *Leptellina*, *Nicolella*, *Onniella*, *Palaeoglossa*, *Plaesiomys*, *Porambonites*, *Protozyga*, *Saucrorthis*, *Skenidioides*.

[taz]: Benjamin Limestone, Florentine Valley, Tasmania (Laurie 1991); *Dinorthis*, *Hebertella*, *Hesperorthis*, *Ptychopleurella*, *Rhynchotrema*, *Tasmanella*.

[wales1]: Alternata Limestone Formation, Welsh Borderland (Hurst 1979); *Bancroftina*, *Dalmanella*, *Dolerorthis*, *Heterorthis*, *Kjaerina*, *Marionites*, *Paracraniops*, *Reuschella*, *Sowerbyella*, *Trematis*.

[wales2]: Cymerig Limestone Formation of the Bala District, North Wales (Lockley 1980); *Cyclospira*, *Dalmanella*, *Dalmanellida* gen. indet., *Eoplectodonta*, *Onniella*, *Palaeoglossa*, *Paracraniops*, *Paterula*, *Protozyga*, *Reuschella*, *Rhactorthis*, *Sericoidea*, *Skenidioides*, *Strophomenida* gen. indet.

[wales3]: Gelli-grŷn Calcareous Ashes of the Bala District, North Wales (Lockley 1980); *Cremnorthis*, *Dalmanella*, *Dalmanellida* gen. indet., *Dolerorthis*, *Eoplectodonta*, *Leptaena*, *Onniella*, *Sericoidea*, *Skenidioides*, *Strophomenida* gen. indet.

[wales4]: Cwm Rhiwarth Siltstones, south Berwyn Hills, North Wales (Pickerill & Brenchley 1979); *Bicuspina*, *Colaptomena*, *Dalmanella*, *Dinorthis*, *Dolerorthis*, *Howellites*, *Kiaeromena*, *Kjaerina*, *Leptaena*, *Leptestiina*, *Lingulella*, *Linguloid* gen. indet., *Orbiculoidea*, *Oxoplectia*, *Platystrophia*, *Reuschella*, *Skenidioides*, *Sowerbyella*.