Available online at www.sciencedirect.com

SCIENCE DIRECT®

Journal of Asian Earth Sciences 26 (2006) 405–423

Journal of Asian Earth Sciences

www.elsevier.com/locate/jaes

Isogramma Meek and Worthen, 1870 (Dictyonellida, Brachiopoda) from the upper Palaeozoic of East Asia: Implications for biogeography and evolutionary trends

Z.Q. Chen[a,*], G.R. Shi[b]

[a]*School of Earth and Geographical Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia*
[b]*School of Ecology and Environment, Deakin University, Melbourne Campus, 221 Burwood Highway, Burwood, Vic. 3125, Australia*

Received 13 January 2005; accepted 2 April 2005

Abstract

Isogramma manchoukuoensis from the Upper Carboniferous of northeast China is redefined based on re-examination of the type specimens. *Isogramma* specimens from the Middle Permian of northeastern Japan are reassigned to *I.* aff. *paotechowensis*. A new family, Schizopleuroniidae, is proposed to include *Schizopleuronia,* but excludes *Megapleuronia*, which belongs to the Megapleuroniidae Liao, 1983. The family Isogrammidae is considered to be a transitional group in the eichwaldid-isogrammid-schizopleuronid evolutionary lineage within the Dictyonellida. A review of the global distribution of *Isogramma* species reveals that the genus has a total of 56 species ranging from the Mississippian (Early Carboniferous) to the Lopingian (Late Permian). *Isogramma* diversified rapidly after its origination in the middle Viséan and its species diversity remained high throughout the Mississippian. The genus possibly suffered a severe mid-Carboniferous boundary mass extinction, with no Early Carboniferous species surviving this event. Bashkirian *Isogramma* species show low diversity, followed by a global recovery in the Moscovian. During the latest Carboniferous *Isogramma* became highly diversified again. At the Carboniferous–Permian (C/P) transition *Isogramma* underwent another dramatic diversity drop, followed by several stepwise declines in diversity during the Early–Middle Permian. The Wuchiapingian *I. sinosa* is the last *Isogramma* species.

Ukraine was the possible centre of origin for *Isogramma*. From Ukraine *Isogramma* spread over the Moscow Basin of Russia, Central Europe (Germany, Austria), South Europe (Spain) and West Europe (England, Ireland and Scotland), and migrated to the North American midcontinent and South China during the late Viséan (Early Carboniferous). In Europe, *Isogramma* migrated to Spain and eastern Europe (Serbia) in the Moscovian, from there it then dispersed into Central Asia (Uzbekistan and Kazakhstan) in the Kasimovian-Gzhelian. In the Palaeo-Tethys *Isogramma* migrated from South China to northeast and northwest China in the Moscovian, spread over the North China Block during the C/P transition, moved to Russian Siberia, Japan and the Qiangtang terrane of the Palaeo-Tethys during the Early–Late Permian. In North America *Isogramma* spread over the midcontinent during the Late Carboniferous and Early–Middle Permian and migrated to South America (Bolivia) in latest Carboniferous.

Biogeographically, *Isogramma* was confined principally to the palaeo-tropical and warm to temperate zones throughout the Late Palaeozoic, with the possible exception of the Artinskian, as a questionable species of the genus also occurs in the Transbaikal region of southeast Russia.

Keywords: Isogramma; Brachiopoda; Evolution; Migration; Carboniferous; Permian

---

1. Introduction

Isogramma Meek and Worthen (1870) is perhaps one of the most morphologically characteristic genera among Late Palaeozoic brachiopods; however, it remains poorly understood in terms of its morphology, phylogeny, classification and biogeography, despite several past studies (e.g. Cooper, 1952; Brand, 1970; Cooper and Grant, 1974; Wardlaw et al., 1987) and recent re-classification (Holmer, 2000). Much of the difficulty associated with the genus has been due to the lack of well-preserved material necessary for determining its morphological relationships with other

---

* Corresponding author.
E-mail address: zqchen@cyellene.uwa.edu.au (Z.Q. Chen).

1367-9120/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jseaes.2005.04.002

similar genera. Because of this lack of information, the systematic position of *Isogramma* in relation to other Late Palaeozoic dictyonellid genera has long been a subject of conjecture, and its evolutionary trends and palaeobiogeographical history also remain obscure. Herein, we attempt to provide an updated review on the global stratigraphical and geographical distributions of *Isogramma,* based on a refined understanding of its morphology. This new data set further permits us to elucidate the evolutionary course and biogeographical history of *Isogramma* since its origin in the Mississippian (Early Carboniferous). In addition, we have also re-examined the previously described *Isogramma* material from the Upper Carboniferous of northeastern China and the Middle Permian of northeastern Japan (Fig. 1). Material used for this review includes type collections housed in the Tohoku University, Sendai, Niigata University, Niigata, Japan and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

2. Stratigraphy of studied material

Specimens named *Isogramma manchoukuoensis* by Hatai and Omura (1941; see also Fig. 2) were said to be from the black shale of the Nisiyama (=Western Hill) area of Honkei-ken (=Benxi city), Hoten Province of Manchoukuo. These locality names have long been abandoned since the Second World War and they are therefore rarely known. However, in a report by Noda (1939) on the regional geology of Benxi, it is possible to trace some details of the this fossil locality and even the stratigraphical horizon of *I. manchoukuoensis*. According to Noda (1939). The Western Hill (Nisiyama) area is actually

Fig. 1. Locations of *Isogramma* in northeastern China and northeastern Japan.

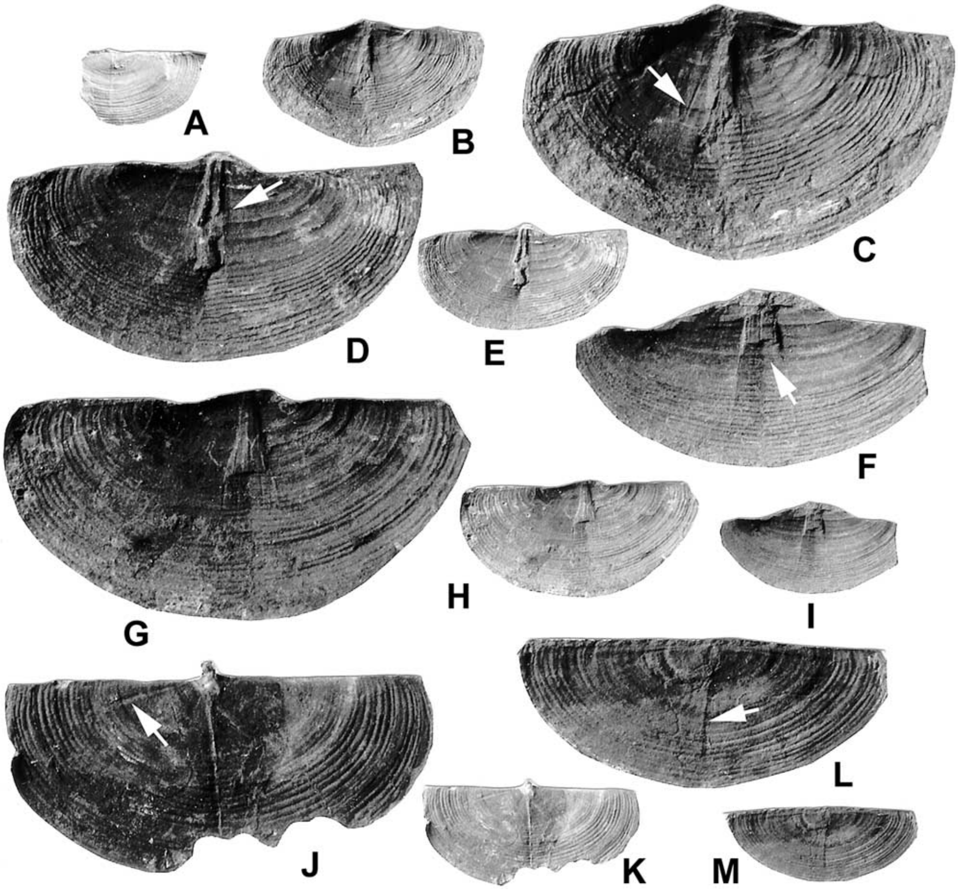

Fig. 2. *Isogramma manchoukuoensis* Hatai and Omura (1941) from the Moscovian Penchi Formation of northeastern China and housed in the Natural History Museum of the Tohoku University, Sendai, Japan. A, IGPS 64401-07, a broken dorsal valve, ×1.5; B–C, IGPS 64401-02, a ventral valve showing collepax bearing radiating muscle scars (arrowed), ×1.5, ×5; D–E, IGPS 66401-03, a ventral valve showing collepax (arrowed) and concentric growth lines, ×5, ×1.5; F, I, IGPS 66401-08, a ventral valve showing collepax covered anteriorly by outer shell layers (arrowed), ×3, ×1.5; G–H, a ventral valve showing collepax covered anteriorly by outer shell layers, ×5, ×1.5; J–K, IGPS 64401-04, a dorsal valve showing cardinal process with a broad shaft, a long median septum and anterolaterally extending lateral ridges (arrowed), ×5, ×1.5; L–M, IGPS 66401-05, a dorsal valve showing impression of cardinal process, median septum (arrowed) and lateral ridges, ×3, ×1.5.

near the Benxi Coal Mine district, Benxi City, Liaoning Province, northeast China (Fig. 1). In the same report, Noda (1939) also detailed the stratigraphy of the Benxi area, where the Penchi Series is typically exposed (Chao, 1928; Wang, 2000a). Sheng (1958) described abundant fusulinid faunas from the Penchi (=Benchi) Series of this region. It should be noted that the 'Penchi Series' is now officially treated by Chinese geologists as a formation and generally regarded as spanning the entire fusulinid *Fusulina-Fusulinella* Zone of the late Moscovian (Wang, 1990). The lithology of the Penchi Formation in the Benxi area, even in the entire Taitsuho Valley region (Sheng, 1958), is rather uniform and comprises alternations of yellow sandstone, black shale, thin-bedded argillaceous limestone and coal measures.

The examined material named '*I. paotechowensis*' by Nakamura (1970; see also Fig. 3) was collected from the lower Kanokura Series at Imo, Yahagi-machi, Rikuzen-takada City, Iwate Prefecture, northeastern Japan (Fig. 1). Although Nakamura (1970) attributed the *Isogramma*-bearing strata to the Early Permian, the lower Kanokura Series is now generally considered to be Guadalupian (Middle Permian) in age, either Roadian-Wordian (Tazawa and Ibaraki, 2001) or Wordian age (Shi, in Shi and Tazawa, 2001; see also Shi and Chen, 2003).

3. Morphology, phylogeny and classification of *Isogramma*

Isogramma is an unusual brachiopod genus for its broad, flat valves, the nature of its pedicle attachment and the 'punctate' shell structure (Cooper and Grant, 1974). The pedicle attachment is represented by a smooth, triangular area at the umbo, which is enlarged by shell resorption, is covered posteriorly by a plate, and has a slit-like opening to the interior (Holmer, 2000). Williams and Brunton (1997) suggested that this triangular area was covered by a tissue

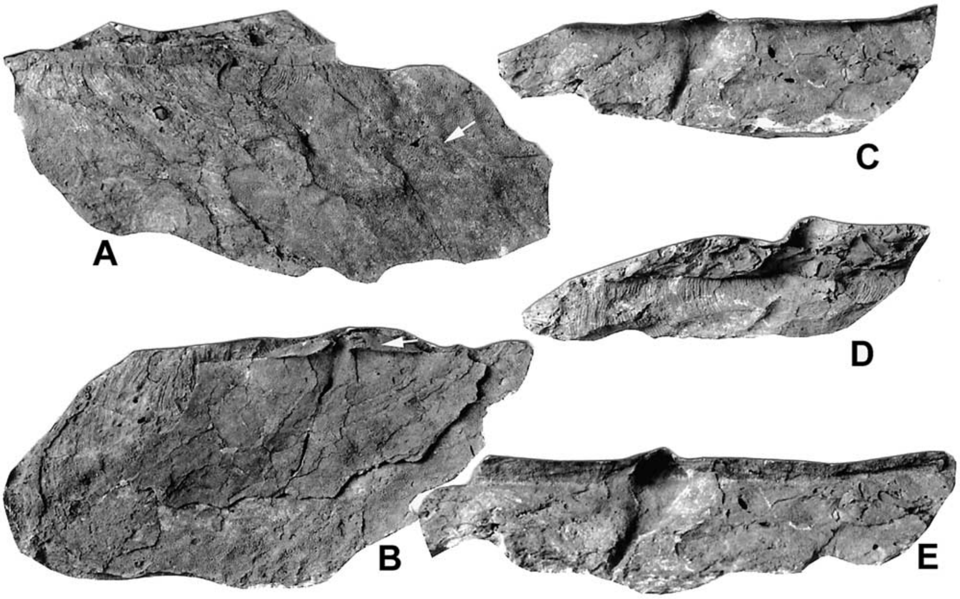

Fig. 3. *Isogramma* aff. *paotechowensis* (Grabau and Chao in Chao, 1928) from the lower Kanokura Series, Kitakami Mountains, northeastern Japan and housed in the Niigata University, Niigata, Japan. A, UHR 19040, external mould of a dorsal valve together with parts of the ventral beak, showing distinct interareas and impressed punctae (arrowed), ×0.7; B, UHR 19040, internal mould of a dorsal valve showing high interareas (arrowed), ×0.7; C–E, close-up of cardinal process and articulation, ×0.8, ×0.8, ×0.9.

coated with adhesive polymers. This peculiar structure has been variably termed: an ‘umbonal plate’ (Rowell, 1965), ‘notch’ (Brand, 1970), ‘pedicle plate’ (Cooper and Grant, 1974; Wardlaw et al., 1987), or a ‘collepax’ (Wright, 1981). Of these suggested names Wright’s (1981) collepax is followed here. Internally, the ventral valve is characterised by a distinct platform, formed by the depressed collepax, serving as muscle attachment; and the dorsal valve is defined by the presence of a strong median septum, which usually unites with the shaft of a large cardinal process. The inner shell layer is perforated by dense punctae of varying sizes, forming one of the most significant characters of the genus (Cooper and Grant, 1974, p. 252).

The collepax, beak regions, shell structure, and absence of teeth of *Isogramma* are similar to those of the Ordovician–Devonian *Eichwaldia* and *Eodictyonella* to which it is related. However, *Isogramma* differs from both of these Early Palaeozoic genera externally in its very strong concentric ornament and possessing a much larger size and a transversely oval shell outline. Internally, *Isogramma* is also distinguished from the latter two genera in having a lophophore platform and a large cardinal process serving the articulation system. Most of these distinctions are also criteria distinguishing the Isogrammidae from the Eichwaldiidae, which include *Eichwaldia* and *Eodictyonella*. In addition, Wardlaw et al. (1987) argued that the collepax of *Isogramma* is made of impunctate shell material, whereas the collepax of both *Eichwaldia* and *Eodictyonella* are punctate. As such, Wardlaw et al. (1987) considered that the Isogrammidae is phylogenetically closer to the Strophomenida, while the Eichwaldiidae is morphologically closer to the Rhynchonellida. However, the super-familial classification of *Isogramma* used here follows Holmer (2000) in that the Isogrammidae is placed in the Eichwaldioidea Schuchert, 1893 of the Dictyonellida Cooper, 1956.

The other two closely allied genera are the Middle Permian *Megapleuronia* Cooper, 1952 and the Late Permian *Schizopleuronia* Liao, 1983. Although Wardlaw et al. (1987) considered *Schizopleuronia* to be a junior synonym of *Megapleuronia*, the difference between the two is distinct: the former is much larger and more transverse, has a ventral median sulcus, and lacks a muscle platform in the dorsal valve; moreover, *Megapleuronia* has a highly distinctive diductor attachment scar lying on a high platform in the dorsal valve. For these reasons, we agree with Holmer (2000) that *Schizopleuronia* is a distinct genus.

When compared with *Isogramma*, both *Schizopleuronia* and *Megapleuronia* are distinct in having a biconvex or concavoconvex profile, a rather narrow (or absent) interarea in both valves, and conspicuous plicae on both valves. These common characteristics may link the latter two genera together to form a distinct family. However, as mentioned above, *Megapleuronia* possesses a distinct muscle platform in the dorsal valve that *Schizopleuronia* lacks. This adventitious articulated attachment distinguishes *Megapleuronia* from most articulated brachiopods (Holmer, 2000). This means that *Megapleuronia* may be different superfamilially from other dictyonellid genera and represents a high-level classificatory unit within the Dictyonellida. Therefore, its placement within the eichwaldid-isogrammid-schizopleuronid evolutionary lineage is unsuitable. For these reasons the Megapleuroniinae Liao (1983), with *Megapleuronia* as the type genus cannot include *Schizopleuronia*. We herein upgrade the Megapleuroniinae Liao (1983) to the family status and propose the new family Schizopleuroniidae to include *Schizopleuronia*. The Megapleuroniidae Liao, 1983 may belong to an independent superfamily from the eichwaldid-isogrammid-schizopleuronid evolutionary lineage. Within the latter lineage, the Isogrammidae is different from the Schizopleuroniidae principally in having a prominent delthyrium and interareas in both valves. These distinctive features of the Isogrammidae also link the family with the Eichwaldiidae. It thus appears possible that the Isogrammidae, ranging from Carboniferous to early Late Permian in age, may represent a transitional group between the Ordovician–Devonian Eichwaldiidae and the Late Permian Schizopleuroniidae. These three families are possibly linked, as they all have a colleplax on the ventral valve and punctate shells. If this is true, *Isogramma* may be considered to represent a transitional form in the eichwaldid-isogrammid-schizopleuronid evolutionary lineage within the Dictyonellida.

4. Global review of *Isogramma*

At present, a total of 56 species (including 17 uncertain species) are known from the Carboniferous–Late Permian strata of nine regions around the world (Figs. 4 and 5). Below we provide a detailed review of the global stratigraphical and geographical occurrences of these species and address their taxonomic revisions and updated stratigraphical information. These confirmed species and their occurrences are not discussed herein, but listed in the Appendix.

4.1. North America

In the North American midcontinent, *I. millepunctata* Meek and Worthen, 1870, originally named as *Chonetes*? *millepunctata* from the Upper Coal Measures, Marion County, Illinois, has been widely reported from the Pennsylvanian and Permian (Appendix), but some of the earlier identifications under this name have since been

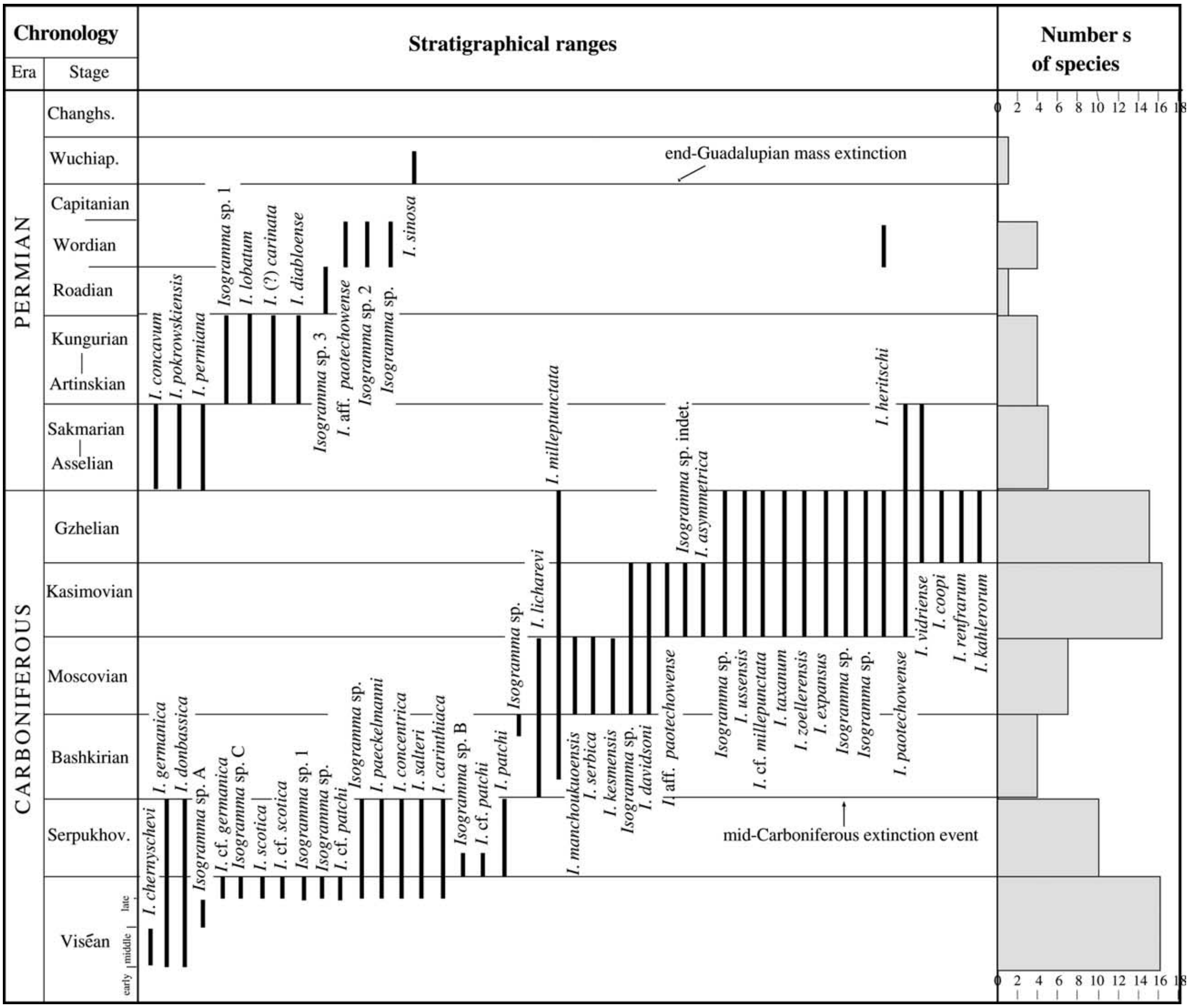

Fig. 4. Stratigraphical distributions and diversity curves for *Isogramma* throughout the Carboniferous and Permian.

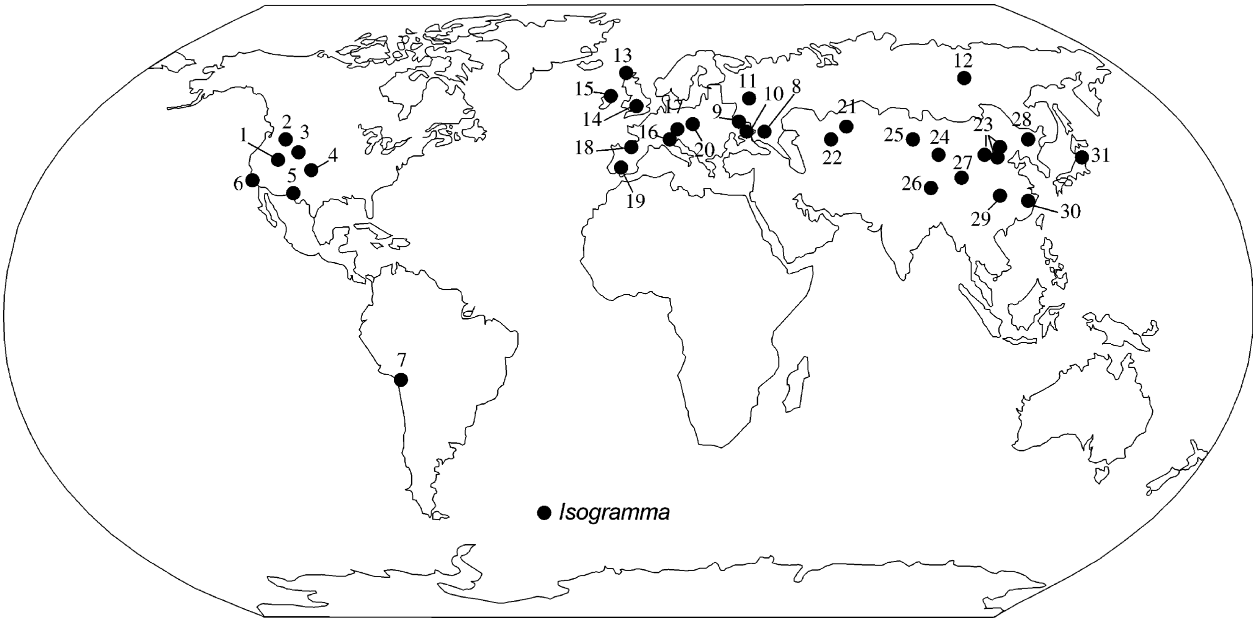

Fig. 5. Geographical distributions of *Isogramma*. 1—Illinois, USA; 2—Ohio, USA; 3—Nebraska, USA; 4—Texas, USA; 5—New Mexico, USA; 6—California, USA; 7—Parquipujio and Lake Titicaca, Bolivia; 8—Donets Basin, Ukraine, 9—Lovo Basin, Ukraine; 10—Bachmat region, Ukraine; 11—Moscow region, Russia; 12—Southern Siberia, Russia; 13—Fefe and Ayrshire areas, Scotland; 14—Somerset area, England; 15—Northern Ireland; 16—Nötsch area, Carnic Alps, Austria, Italy; 17—Hansdorf, Falkenberg and Schlesien areas of Germany; 18—Cantabrian Mountains, northern Spain; 18—Cantabrian Mountains, northern Spain; 19—Sierra de Córdoba, southern Spain; 20—Northwestern Serbia; 21—Fergana, Uzbekistan; 22—Eastern Kazakhstan; 23—Taiyuan, North China; 24—Gansu, Northwest China; 25—Xinjiang, Northwest China; 26—Batang, eastern Tibet, West China; 27—Southern Shaaxi, West China; 28—Liaoning, northeastern China; 29—Hunan, South China; 30—Fujian, South China; 31—Kitakami Mountains, northeastern Japan.

revised and re-assigned to other species. For example, Cooper (1952) moved part of the material named *I. millepunctata* by Dunbar and Condra (1932, pl. 42, fig. 21) to his new species *I. texanum*; and Cooper and Grant (1974, p. 254) re-assigned the Permian material identified as *I. millepunctata* by King (1931, p. 65, pl. 10, fig. 8) to their new species *I. vidriense*. As a result, the true *I. millepunctata* is now confined to the Pennsylvanian in the North American midcontinent. In addition, Dutro (1955) described *I.* cf. *pachti* from the late Mississippian Baird Formation of Shasta County, California. Permian forms of *Isogramma* are very diverse, but are confined to the Texas region (Appendix).

4.2. South America

In Bolivia, except for *Isogramma* sp. illustrated by Branisa (1965) from the lower Copacabana Group of the Parquipujio areas (Appendix), Ishibashi and Fujikawa (1999) also figured *Isogramma* sp. from the lower Copacabana Group of the Yampupata area of the Lake Titicaca region. Later, Fujikawa et al. (2003) re-assigned the Yampupata specimen to *I. paotechowensis* and constrained it to the latest Carboniferous (Kasimovian-Gzhelian) age, based on faunal correlations of brachiopods and associated foraminifera. Having re-examined the Yampupata material (by CZQ) housed in the Niigata University, Japan, we consider that the incompletely preserved Bolivian material does not permit a full comparison with *I. paotechowensis*, a species originally described from North China (see below).

4.3. Russia

In the Moscow Basin, both *I. pachti* (Dittmar, 1872) and *I. ussensis* (Dittmar, 1872) are the earliest known *Isogramma* species; the former came from the Steshevsky Horizon (C_1^{st}) of early Serpukhovian age (Sarycheva and Sokolskaya, 1952), while the latter is Kasimovian (Ilkhovsky, 1978). Sarycheva and Sokolskaya (1952) described *I. germanica* from the Alexinsky Horizon (C_1^{al}) and Mikhailovsky Horizon (C_1^{mkh}), which are equivalent to the C_1^{vf} horizon (late Viséan) of the Donets Basin, Ukraine (Table 1). However, Dutro (1955) rejected this specific assignment and considered that the true *I. germanica* bears much coarser concentric growth lines than the Moscow specimens. In addition, *Isogramma* also occurs in the Moscovian–Gzhelian strata of the Moscow Basin (Appendix).

From the Transbaikal region of southern Siberia, Maslennikov (1960) reported a questionable species of *Isogramma* as *I.* (?) *carinata* from a supposedly Artinskian–Kungurian locality. However, the real identity and the reported stratigraphical position of this species remain elusive as neither Kotlyar and Poepeko (1967) nor Kotlyar

Table 1
Viséan–Gzhelian chronostratigraphical correlations of Central-West Europe (Scotland, Ireland, Germany–Austria), the Donets region of Ukraine, the Moscow region of Russia, China and North America midcontinent. Datum sources: 1—George et al. (1976), Ramsbottom et al. (1978); 2—Aisenverg et al. (1979), Poletaev et al. (1990), Reitlinger et al. (1996); 3—Aisenverg et al. (1979), 4—Wang (1990), 5—Lane et al. (1999)

Strati.		West-Central Europe 1					Donets Basin 2			Moscow Basin 3		China 4		North America 5	
Subsys.	Sta.ge	England, Ireland, Scotland			Belgium, Germany, Austria		Stage	Suite	Zone	Stage	Horizon				
Pennsylvanian	Gzhelian	Stephanian	Stephanian D Stephanian C		A		Gzhelian	$C_3{}^3$(P)	------- $C_3{}^d$	Gzhelian	Noginsky Pavlovo-Possadsky Amerevsky Russavkinsky	Mapingian	Xiaodushanian	Pennsylvanian	Virgilian
	Kasimovian		Stephanian B Stephanian A				Kasimovian	$C_3{}^2$(O) $C_3{}^1$(N)	$C_3{}^c$ $C_3{}^b$ $C_3{}^a$	Kasimovian	Yauzky Dorogomilovsky Khamovnichesky Kreviakinsky				Missourian
	Moscovian	Westphalian	Westphalian D Westphalian C				Moscovian	$C_2{}^7$(M) $C_2{}^6$(L) $C_2{}^5$(K)	$C_2{}^{m}e$ $C_2{}^{m}d$ $C_2{}^{m}c$ $C_2{}^{m}b$ $C_2{}^{m}a$	Moscovian	Myachkovsky Podolsky Kashirsky Vereisky	Weiningian	Dalan		Desmoinesian Atokan
	Bashkirian	Namurian	Westphalian B Westphalian A Yeadonian Marsdenian Kinderscoutian	G_2 G_1 R	G_2 G_1 $R_1 + R_2$		Bashkirian	$C_2{}^4$(I) $C_2{}^3$(H) $C_2{}^2$(G) $C_2{}^1$(F) $C_1{}^5$(E)	$C_2{}^{b}e$ $C_2{}^{b}d$ $C_2{}^{b}c$ $C_2{}^{b}b$ $C_2{}^{b}a$ $C_1{}^{n}e$	Bashkirian	Melekessky Cheremshansky Prikamsky Severo-Keltmensky Krasnopolyansky		Huashibanian Luosuan		Morrowan
Mississippian	Serpukhovian		Alportian Chokierian Arnsbergian Pendleian	H E_2 E_1	H E_2 E_1	Cu_3	Serpukhovian	$C_1{}^4$(D) $C_1{}^3$(C) $C_1{}^2$(B)	$C_1{}^{n}d$ $C_1{}^{n}c$ $C_1{}^{n}b$ $C_1{}^{n}a$ $C_1{}^{v}g$	Serpukhovian	Voznessensky Zapaltubinsky Protvinsky Steshevsky Tarussky	Tatangian	Dewuan	Mississippian	Chesterian
	Viséan	Viséan	Brigantian Asbian Holkerian Arundian Chadian	D_2 P_2 P_1 D_1 S_2 S_1 | C_2	V_{3c} V_{3b} V_{3a} V_{2b} V_{2a} V_{1b} V_{1a}	Cu_2	Viséan	$C_1{}^1$(A)	$C_1{}^{v}f$ $C_1{}^{v}e$ $C_1{}^{v}d$ $C_1{}^{v}c$ $C_1{}^{v}b$ $C_1{}^{v}a$	Viséan	Venevsky Mikhailovsky Alexinsky Tulsky Bobrikovsky Radajevsky Elkhovsky		Shangsian Jiusian		Meramecian Osagean

et al. (2002) included this species in their lists of Permian brachiopods of Transbaikalia. Also, we have not been able to locate Maslennikov's species in any of the synonyms of Permian–Carboniferous brachiopods in the two later Russian publications just mentioned.

4.4. Ukraine and Serbia

In the Donets Basin of Ukraine, Aisenverg (1964) described several *Isogramma* species from the Viséan to Bashkirian (Appendix). Of these, *I. chernyschevi* was described from the lower Efremovsky (C_1^{ef}), *I. donbassica* from the horizons C_1^{ef} to C_1^{sb}, and *I. germanica* from the horizons C_1^{ef} to D_4. According to Aisenverg et al. (1979) and Poletaev et al. (1990), the C_1^{ef} is middle Viséan, while both C_1^{sb} and D_4 are early and latest Serpukhovian, respectively (Table 1). Accordingly, these three species are likely the oldest *Isogramma* forms of the world (Fig. 4). In addition, Aisenverg (1964) demonstrated that his new species *I. licharevi* ranges from the D_7 Suite (topmost C_1^4) to the C_2^{am} Suite in Donets. Of these, the D_7 Suite was regarded as the uppermost Lower Carboniferous (Poletaev et al., 1990) and the C_2^{am} Suite is Moscovian (Aisenverg et al., 1979). *I. licharevi* therefore ranges from the Early Carboniferous to Moscovian in age (Brand, 1970). However, the D_7 Suite is characterised by the presence of the conodont

Declinognathodus noduliferus (Poletaev et al., 1990, fig. 3), which now is a zonal species of the *D. noduliferus* Zone, a marker for the beginning of the Bashkirian (Pennsylvanian) in the world (Lane et al., 1999). As a result, *I. licharevi* is confined to the Bashkirian–Moscovian. Aisenverg (1964) also described *Isogramma* sp. 1 and *I. paeckelmanni* from the Ustiluzhskaya Suite of the Lovo Basin (Appendix). This suite is equivalent to the Mikhailovsky Horizon (C_1^{mkh}) of the Russian Platform, both being late Viséan (Reitlinger et al., 1996).

In Serbia, eastern Europe, *Isogramma serbica* Stojanoviæ-Kuzenko (1968, pl. 1, figs. 8, 9; pl. 2, fig. 1; see also Stojanoviæ-Kuzenko et al., 1995, pl. 65, figs. 6, 6a) from the Obradoviæi Assemblage in the Likodra Nappe of northwestern Serbia was found in association with a diverse early Moscovian brachiopod fauna.

4.5. Central Asia (Uzbekistan and Kazakhstan)

In Uzbekistan both *I. millepunctata* and *I. paotechowensis* have been described frequently from the Uchbulak and Dastarsky Horizons of the Fergana Basin (Appendix). The Uchbulak and Dastarsky Horizions are of late Kasimovian age and late Gzhelian age, respectively (Bensh et al., 1996). Thus, *Isogramma* in Fergana is confined to the Kasimovian-Gzhelian. In the eastern Kazakhstan, Sarycheva (1968) described *I. licharevi* from the Keregetasskaya Suite of Bashkirian–Moscovian age.

4.6. China

In North China, Chao (1928) first proposed *I. paotechowensis* (Grabau and Chao) from the Taiyuan Formation, which is Asselian–Sakmarian (Early Permian) in age (Wang, 2000b; see also Table 2). In northeast China *I. manchowensis* Hatai and Omura (1941) was described from the Moscovian Penchi Formation. The type specimens are also re-illustrated here (Fig. 2). In northwest China, *Isogramma* was described from the Moscovian Shiqiantan Formation of the Qitai area of Xinjiang Province as *I. paotechowensis* by Zhang et al. (1983) and as *I. millepunctata* by Wang and Yang (1998). Judging the illustrated material and taxonomic descriptions given by these authors, we consider that the Xinjiang specimens are better assigned to *I. manchowensis* than to either *millepunctata* or *paotechowensis* due to their significant smaller size and concentric lamellae closely comparable with those seen in *manchowensis*. *Isogramma* also occurs in the Upper Carboniferous and the Upper Permian of northwest and west China, as well as in the upper Datangian (= Viséan; see Table 1) and Lower–Middle Permian of South China (Appendix).

4.7. Japan

Minato (1955, p. 29, fig. 1) first reported *I. paotechowensis* from the Kanokura Series of the Kitakami Mountains, northeastern Japan. Later, Nakamura (1970) also described *Isogramma* from the lower Kanokura Series of the Kitakami region. He assigned the larger specimens to *I. paotechowensis* and the smaller specimens to his new species *I. heritschi*. As discussed above, *Isogramma* from the Kitakami region is Middle Permian in age (Table 2). In this paper we have re-examined *I. paotechowensis* of Nakamura (1970) (see below, also Fig. 3).

4.8. Central–South Europe (Austria, Germany and Spain)

In the Carnic Alps, Austria, *Isogramma* has long been described from the Lower Carboniferous (e.g. Dittmar,

Table 2
Correlations of the Permian *Isogramma*-bearing strata of USA, China and Japan

Epo.	International standard	Japan		South China		North America	
Lopingian	Changhsingian	Toyoman	Mitaian	Lopingian	Changhsingian		▨
	Wuchiapingian				Wuchiapingian		Ochoan
							La Colorado
Guadalupian	Capitanian	Kanokuran	Kuman	Maokoun	Lengwuan	Guadalupian	Capitanian
	Wordian		Akasakian		Kuhfengian		Wordian
	Roadian			Chihsian	Xiangboan		Roadian
Cisuralian	Kungurian	Sakamotozwa	Nabeyaman		Luodianian	Leonard.	Cathedralian
			Kabayaman				
	Artinskian			Chuanshanian	Longlinian		Hessian
	Sakmarian		Kawaguchian		Zisongian	Wolfcamp.	Lenaxian
	Asselian	Nagatoan					Nealian

1872; Aigner, 1931; Aigner and Heritsch, 1931). Aigner and Heritsch (1931) considered that *Chonetes koninckiana* d'Koninck (1873, p. 41, pl. 2, fig. 3) was conspecific with *I. paeckelmanni*. The Pennsylvanian species of *Isogramma* are very diverse in the Carnic Alps (Appendix). Nakamura (1970, p. 308) considered that specimens figured by Aigner and Heritsch (1931) as *I. paotechowensis* could represent two distinct species of different sizes: he therefore retained *I. paotechowensis* for the larger specimens while proposing *I. heritschi* to accommodate the smaller specimen of Aigner and Heritsch (1931, pl. 5, fig. 52).

In Germany, Semenow (1854) described *Chonetes concentrica* d'Koninck from a Lower Carboniferous shale unit. Later, Paeckelman (1930) moved some of Semenow's specimens to *I. germanica*, a species established on type material from the late Viséan Culm successions of Hansdorf, Falkenberg and Schlesien. Aigner and Heritsch (1931) redefined *I. germanica* and reassigned the small specimens of the species to *I. paeckelmanni* (Appendix). The type specimens of *I. germanica* were later re-illustrated by Brand (1970) who diagnosed the species as having coarse, distinct concentric growth lines.

In Spain, Barrois (1882) first described *Isogramma davidsoni*, which was originally assigned to *Aulacorhynchus*, from the Moscovian–Kasimovian successions of the Asturias areas, northern Spain. Later, Delépine (1943, p. 74) reported this species from the Westphalian D (Moscovian) of the same area. Since then, *I. davidsoni* and its variate forms have been frequently reported from the Moscovian and Kasimovian successions of the Cantabrian Mountains, northern Spain (Appendix). Sánchez de Posada et al. (1999, 2002) also listed *I.* aff. *paotechowensis* from the Austrian Kasimovian. *Isogramma* sp. was often reported in the literature from the Moscovian–Kasimovian of Austrias (e.g. Martínez-Chacón and Winkler Prins, 1985; Río García, 1998; Sánchez de Posada et al., 1999, 2002). Wagner et al. (2002, fig. 9) considered that Asturian *Isogramma* ranges from late Moscovian to Kasimovian in age. In southern Spain, Liñán Guijarro (1978) reported *Isogramma* sp. from the upper Viséan of the Sierra de Córdoba area. Accordingly, *Isogramma* occurs in the Lower Carboniferous and the Moscovian–Kasimovian successions in Spain. However, although they may belong to true *Isogramma* (Martinez-Chacon, personal communication, 2005), most of these *Isogramma* specimens have not been illustrated and described and thus require a modern re-study.

4.9. Western Europe (England, Ireland and Scotland)

Records of *Isogramma* from both England and Ireland are rare. Brand (1970) stated that *I. salteri* and *I.* cf. *germanica* are the only species recorded in England, both occurring in the Hotwells Limestone (D_2) of Brigantian (= late Viséan) age (Table 1) of the Somerset area. In Ireland, only *I.* cf. *pachti* has been recorded (Brand, 1970, p. 73). This species is known from subsurface strata equivalent to the Upper Limestone Group (E_2) of early Arnsbergian (= early Serpukhovian) age (Table 1).

In Scotland, Davidson (1863) first reported *I. concentricus* (d'Koninck) from the Lower Carboniferous. These *Isogramma* specimens however belong to various species (Davidson, 1884; Aigner and Heritsch, 1931; Brand, 1970). Brand (1970, p. 75) erected *I. scotica* using *Chonetes concentricus* of Davidson (1863, p. 278, pl. 55, fig. 13) (= *Aulacorhynchus davidsoni* Barrois of Davidson, 1884, p. 283), as its holotype. In addition, Brand (1970) described several *Isogramma* species from the Upper Limestone Group (E_2) of the Serpukhovian age and Passage Groups of Bashkirian age (Table 1). It is noteworthy that *Isogramma* sp. A of Brand (1970) from the Dinwoodie Beds (D_1) of the Asbian (early late Viséan) of the Archerbeck Borehole is the oldest known *Isogramma* species in western Europe.

5. Diversity and evolutionary trends of *Isogramma*

As reviewed above, the known oldest *Isogramma* forms appear to be those from the Viséan of the Mississippian and comprise 16 species (including five uncertain species), 7 of which (*I. donbassica*, *I. germanica*, *I. salteri*, *I.* sp., *I. paeckelmanni*, *I. concentrica*, and *I. carinthiaca*) persisted into the Serpukhovian when three new forms (*Isogramma* sp. B, *I. patchi* and *I.* cf. *patchi*) emerged (Fig. 4). The species diversity of *Isogramma* in the Serpukhovian remained high and its species composition is very similar to that of the Viséan (Fig. 4), implying that the *Isogramma* lineage remained stable through both stages. However, the Serpukhovian–Bashkirian boundary, also the Mississippian–Pennsylvanian boundary, marked a major change for the *Isogramma* lineage as all of the Serpukhovian *Isogramma* species disappeared just below the boundary. This mid-Carboniferous boundary extinction event, clearly indicated from the stratigraphical distribution of *Isogramma* species (Fig. 4), has also been recognised in several other studies (e.g. Raymond et al., 1990; Stanley and Powell, 2003).

In contrast to its diversification in the Early Carboniferous, *Isogramma* was sparse worldwide during the Bashkirian, with only two species and one uncertain species (Fig. 4). Of these, *I. licharevi* originated in the Donets Basin, Ukraine immediately after the mid-Carboniferous boundary event (Aisenverg, 1964), and both *I. millepunctata* and *I.* sp. occurred in the North American midcontinent (Sturgeon and Hoare, 1968) and the Donets Basin (Aisenverg, 1950) in the late Bashkirian, respectively. Following a diversity low in Bashkirian, *Isogramma* became abundant again in the Moscovian, with eight species spread over North America, China, Central Asia, Russia, Ukraine, South Europe and East Europe. Apart from *I. licharevi* and *I. millepunctata*, both being Bashkirian relicts, the remaining six species all originated in the Moscovian (Fig. 4). Species diversification of *Isogramma* continued into the Kasimovian, with 16 species (including five uncertain species) (Fig. 4). All but three forms (*I. millepunctata*, *I. davidsoni* and *I.* sp.) of these 16 species originated during this stage, or 81% in origination (Fig. 4). Clearly, the Kasimovian was characterised by the highest species diversity of all stages and a marked increase of species origination rate. Eleven of the 16 Kasimovian species (or 68.7%) persisted into the Gzhelian, which also saw the introduction of four new species (*I. renfrarum*, *I. coopi*, *I. vidriense* and *I. kahlerorum*) (Fig. 4). Although the Gzhelian remains considerably high species diversity (Fig. 4), its origination rate was relatively low, at only 26.7%.

Across the Carboniferous–Permian boundary, the species diversity of *Isogramma* started to decline, with a sharp drop to only five species at the beginning of the Permian (Asselian–Sakmarian) (Fig. 4). They include two Carboniferous relicts (*I. vidriense* and *I. paotechowensis*) and three newly originated species (*I. concavum*, *I. pokrowskiensis* and *I. permiana*). It is thus clear that *Isogramma* experienced another dramatic diversity drop, marked by the loss of 13 of the 15 Gzhelian species (about 86.7%). It is also notable that *I. heritschi* disappeared temporarily at the C–P boundary but re-appeared in the Wordian (Middle Permian).

The diversity of *Isogramma* remained low through the late Early Permian (Artinskian–Kungurian), with four species: *I. diabloense*, *I. lobatum*, *Isogramma* sp. 1 and *I.* (?) *carinata*, all of which are newly originated. In the Guadalupian (Middle Permian), *Isogramma* includes five species, all but one (*I. heritschi*) are new but uncertain taxa (Fig. 4). Except for *Isogramma* sp. 3 occurring in the Roadian, other species were confined to the Wordian and no species appeared in the Capitanian. Thus, all existing species of *Isogramma* disappeared prior to the end-Guadalupian. This fact indicates that the end-Guadalupian mass extinction event (Jin et al., 1994; Stanley and Yang, 1994) had little effect on *Isogramma* as most of its pre-Capitanian species had already become extinct before Capitanian. During the Lopingian, *Isogramma* was represented by only one species: *I. sinosa* (Jin et al., 1985). This species was confined to the Wuchiapingian and is herein considered to have given rise to *Schizopleuronia* Liao, 1983 in the late Wuchiapingian.

To sum up, *Isogramma* rapidly diversified once it originated in the middle Viséan. The genus achieved two species diversity peaks at the late Early Carboniferous and latest Carboniferous respectively; it also experienced two major diversity drops, at the Mississippian–Pennsylvanian and Carboniferous–Permian boundaries respectively (Fig. 4). Throughout the Permian, the diversity of *Isogramma* remained low and the genus finally became extinct by the end of Wuchiapingian.

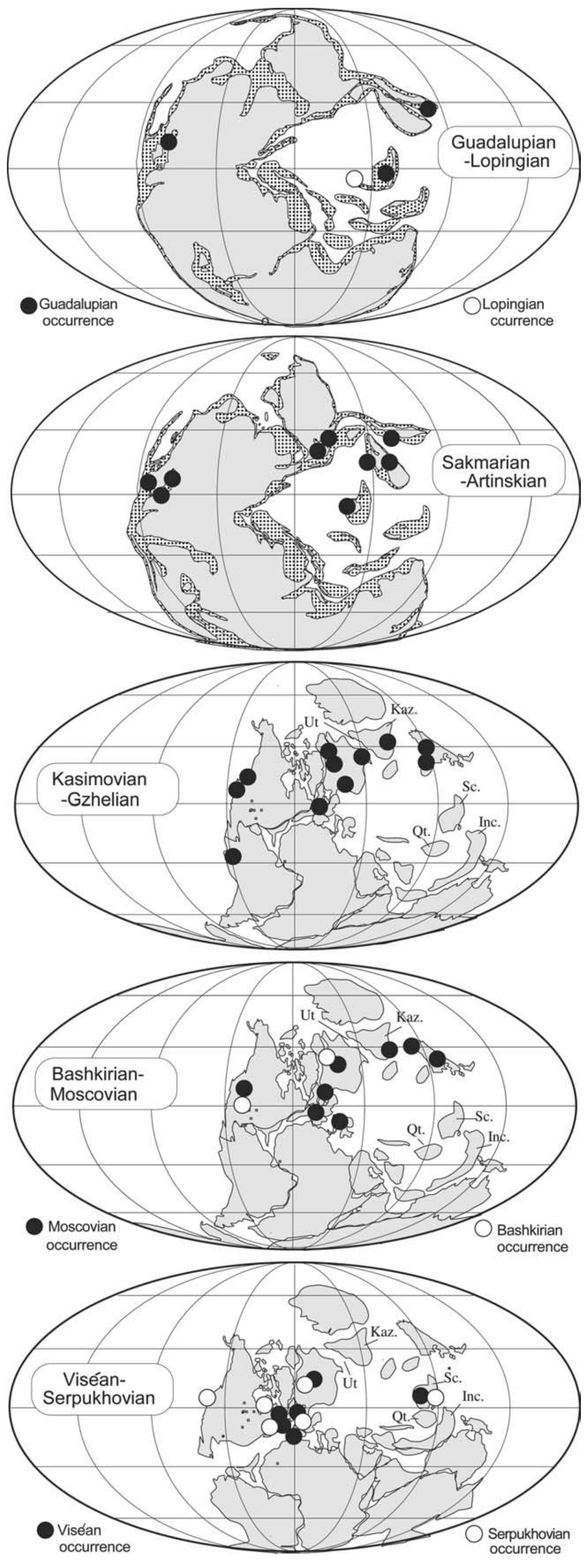

Fig. 6. Historical patterns of palaeobiographical migration of *Isogramma* through the Carboniferous and Permian times [the Carboniferous palaeogeographical maps modified from Winkler Prins (1989), Scotese and McKerrow (1990), and Chen (2004); the Permian palaeogeographical maps after Ziegler et al. (1997)].

6. Origin and spread of *Isogramma*

No *Isogramma* species are known in pre-Viséan strata around the world (Appendix). The oldest known *Isogramma* species occurs in the middle Viséan, including *I. chernyshevi*, *I. germanica* and *I. donbassica*, all from the lower Efremovsky (C_1^{ef}) (= middle Viséan; see also Table 1) of the Donets Basin, Ukraine. Slightly younger species, but still late Viséan in age, are widespread in Europe, South China and western USA (California). Thus it appears that the Donets Basin was the centre for the origin of *Isogramma*. After its origination in middle Viséan, *Isogramma* became extraordinarily proliferated in the Donets Basin and rapidly spread to western Europe (England, Ireland, Scotland) and southern Europe (southern Spain) via central Europe (Germany, Austria) in the late Viséan-Serpukhovian. The main evidence for this inference is the presence of Donets' species (*I. chernyshevi*, *I. germanica* and *I. donbassica*) in both western and central Europe (Brand, 1970).

In addition, *Isogramma* had probably migrated to South China in the Palaeo-Tethyan region, and to the North American midcontinent in the late Viséan, because the genus appeared in these latter regions later in time than its origin in the Ukraine. Although the distant geographical separation of these two regions from Europe (Fig. 6) may weaken this interpretation, *Isogramma* could have migrated from Europe to both South China and North America if there were appropriate marine connections and the environmental conditions, including temperature conditions, were equitable during the middle–late Viséan. Another possible factor is the effect of the incompleteness of the fossil record on the present-day distribution patterns of *Isogramma*. The fact that there are no dispersal routes of *Isogramma* apparent between Europe, North America and South China in the Viséan palaeogeographical map (Fig. 6) could be due to lack of fossil records in the areas between these three regions.

The palaeobiogeographical pattern of *Isogramma* may have been affected by the possible mid-Carboniferous boundary mass extinction to some extent. During the Bashkirian, *Isogramma* disappeared in most places where it used to populate and proliferate, and the genus was restricted to the Donets Basin, Ukraine and North American midcontinent (Fig. 6). During the Moscovian, *Isogramma* proliferated and radiated globally. In Europe *Isogramma* spread over Ukraine and migrated to eastern Europe (Serbia), and the genus also re-occurred in northern Spain after its disappearance in the southern Spain during the mid-Carboniferous boundary event. In the eastern Palaeo-Tethys (Metcalfe, 1996), *Isogramma* migrated from South China apparently through two migratory pathways: northeasterly to northeastern China and northwesterly to the northern Xinjiang region of northwest China, respectively. In the eastern branch of the Panthalassan Ocean *Isogramma* re-occurred in the North American midcontinent.

The biogeographical distribution patterns of *Isogramma* are almost the same in both the Kasimovian and Gzhelian stages (Fig. 6). The genus inherited its proliferation in Ukraine and spread over the Moscow region of Russia and migrated eastwards to Central Asia. In Central–South Europe *Isogramma* spread over northern Spain and Asturian regions. In the eastern Palaeo-Tethys *Isogramma* spread over many areas of the North China Block. In the North American midcontinent *Isogramma* rapidly migrated, probably via the coastal zone of the Panthalasan Ocean, to northern South America and the northern margins of Gondwanaland (Winkler Prins, 1989; Scotese and McKerrow, 1990).

During the Asselian–Sakmarian (Early Permian) *Isogramma* proliferated widely in the North American midcontinent. The genus also occurred in South China. In contrast, *Isogramma* disappeared in vast regions of Europe and Central Asia, except for its sparse presence in the Ukraine. During the Artinskian–Kungurian, *Isogramma* was confined apparently to the eastern and western sides of the Panthalassan Ocean. The genus diversified in the North American midcontinent. In the Palaeo-Tethys *Isogramma* possibly moved from North China northwards to Transbaikalia in southern Siberia, which then was probably part of the 'Northern Transitional Zone' between the Palaeoequatorial and Boreal realms at that time (Shi et al., 1995; Shi and Grunt, 2000). In the Middle Permian, the global distribution of *Isogramma* was greatly restricted, being found only in the North American midcontinent and also sparsely in South China and northeastern Japan. After the end-Guadalupian mass extinction, *Isogramma* survived only in the Qiangtang Block, a mobile terrane in Palaeo-Tethys during the Permian (Ziegler et al., 1997).

An inspection of all the occurrence locations of *Isogramma* in the Carboniferous–Permian palaeogeographical reconstruction maps (Fig. 6) indicates that the genus was largely confined to the lower and middle palaeolatitude regions throughout the Late Palaeozoic, suggesting that *Isogramma* was adapted to the tropical warm-water to warm-temperate conditions.

7. Taxonomic notes

Order Dictyonellida Cooper, 1956
Superfamily Eichwaldioidea Schuchert, 1893
Family Isogrammidae Schuchert, 1929
Genus *Isogramma* Meek and Worthen, 1870

Type species. *Chonetes*? *millepunctata* Meek and Worthen, 1870, p. 35.

Isogramma manchoukuoensis Hatai and Omura, 1941
(Fig. 2)

1941 *Isogramma manchoukuoensis* Hatai and Omura, pp. 44–46, pl. 2, figs. 5–11

1983 *Isogramma paotechowensis* (Grabau and Chao); Zhang et al., p. 315, pl. 145, figs. 7–9.

1998 *Isogramma millepunctata* (Meek and Worthen); Wang and Yang, p. 66, pl. 24, fig. 3.

Description. Small *Isogramma*, about 7–10 mm long, 16–21 mm wide; outline transversely semicircular, nearly twice as wide as long; maximum shell width at hingeline. Ventral umbo slightly convex, grooved medially by a depressed collepax; interareas low, indistinct; collepax narrow, originating at beak, extending over a half shell length; its anterior portion usually covered by outer shell layers (Fig. 2F). Dorsal valve flat to slightly concave; umbo small, slightly convex. External surfaces ornamented with crowded concentric growth lines; about 7–8 occupying a length of 5 mm at midvalve. Numerous radiating muscle scars, serving as adductor scars, present on collepax; other ventral interior features not observed. Dorsal interior trifid cardinal process supported by a broad shaft; median septum united posteriorly with cardinal process shaft so that buttress plates indistinct; median septum thin, high, extending nearly to anterior margin; lateral ridges strong, extending anterolaterally and forming an angle of 5°–10° to posterior margins.

Remarks. When erecting the present species, Hatai and Omura (1941) neither described the collepax nor detailed its interior features. Our re-examination of the type specimens reveals that both collepax and dorsal interiors are fairly well preserved, as described above. As already discussed, the specimens figured by both Zhang et al. (1983) and Wang and Yang (1998) from the Moscovian Shiqiantan Formation of the Junggar Basin, Xinjiang, Northwest China are conspecific with the described specimens.

This Moscovian species is easily distinguished from the *I. paotechowensis,* a very common species in the Lower Permian of North China (Appendix), by its significantly smaller size, more transverse outline, lower interareas and the lateral ridges extending from posterior margins at slightly greater angles. Of the contemporaneous species (Appendix), *I. millepunctata*, widely distributed in the North American midcontinent, is much larger than the present species (Meek and Worthen, 1873); the little known *I. serbica* Stojanoviæ-Kuzenko (1968; see also Stojanovic-Kuzenko et al., 1995) possesses a similar size and shell outline to *I. manchoukuoensis*, from which it differs in having a more medially convex ventral valve and finer, more flattened concentric growth lines; *I. kesmensis* Ilkhovsky (1978) is poorly illustrated and it possesses a rather transverse and more convex ventral valve than the present species. The true *I. davidsoni* (Barrois, 1882, p. 326, pl. 16, fig. 6a–d) is less proportionally transverse and has finer concentric growth lines than *I. manchoukuoensis*. *I. scotica* Brand (1970) also approaches *I. manchoukuoensis* in many aspects, but it is much larger and has more regularly arranged growth lines than *I. manchoukuoensis*.

Isogramma aff. *paotechowensis* (Grabau and Chao in Chao, 1928)
(Fig. 3)

aff. 1928 *Aulacorhynchus paotechowensis* Grabau and Chao in Chao, p. 33, pl. 1, figs. 1–5.

aff. 1931 *Isogramma paotechowensis* (Grabau and Chao); Aigner and Heritsch, p. 307, pl. 2, figs. 32–36; pl. 3, figs. 37–44; pl. 4, figs. 45–51; pl. 5, figs. 52–53, 67, 71.

aff. 1936 *Isogramma paotechowensis* (Grabau and Chao); Metz, p. 171, pl. 5, fig. 7.

1955 *Isogramma paotechowensis* (Grabau and Chao); Minato, pp. 29–30, fig. 1.

1970 *Isogramma paotechowensis* (Grabau and Chao); Nakamura, p. 306, pl. 3, figs. 1–2; pl. 4, figs. 1–2.

Diagnosis. Large *Isogramma*; both valves nearly flat; ventral interarea high, broad, distinct; collepax broad, short, extending about two-fifth of shell length; concentric growth zones narrow, closely spaced; cardinal process strong, supported by broad shaft; median septum broad posteriorly, abruptly thinning anteriorly, extending over half shell length. Punctae conspicuous, densely arranged on inner surfaces of dorsal valve.

Remarks. Our re-examination of the type specimens agrees almost with Nakamura's (1970) description of the species. Nakamura (1970) did not mention any details of the collepax and punctae, which are two most important morphologic characters, diagnostic for the genus. The collepax is not figured herein, but is clearly illustrated on the specimen (UHR 19042) of Nakamura (1970, pl. 4, fig. 2b). The prominent punctae are illustrated herein (Fig. 3A–B).

One of the authors (ZQC) also examined the type specimens of *I. paotechowensis*, described by Chao (1928) from the Lower Permian of North China and housed in the Nanjing Institute of Geology and Palaeontology. As a result of comparison between Kitakami and North Chinese materials, we consider that the Kitakami specimens are comparable with *I. paotechowensis* in many details. However, the Kitakami material differs clearly from the North Chinese specimens in having a much larger size, a much higher and more pronounced ventral interarea, a shorter collepax, a much broader cardinal process, and more conspicuous punctae in the inner surfaces of the shell. These differences suggest that the Kitakami specimens may represent a potential new species somewhat related to *I. paotechowensis*, but most of the specimens are too fragmental to erect a new species at the present. In addition, we agree with Nakamura (1970) that the smaller specimens from the Kitakami collection represent an independent species: *I. heritschi*, as they can be clearly distinguished from *I.* aff. *paotechowensis* in having a significantly smaller size, more transversely semicircular outline, a rather smaller cardinal process and a very thin median septum in the dorsal valve.

Acknowledgements

The senior author thanks Prof. J. Tazawa of Niigata University, Japan for his loan of the Japanese material included in this study, provision of literature and facilities when he visited Niigata in 2002–2003. Prof. K. Kaiho of Tohoku University, Japan is also thanked for his help when the senior author stayed in Tohoku in 2001–2003. We are grateful to both reviewers: Dr. C.H.C. Brunton of The Natural History Museum, London and Prof. M.L. Martínez-Chacón of the University of Oviedo, Spain for their constructive suggestions. Prof. M.L. Martínez-Chacón is particularly acknowledged for providing Spanish literature concerning *Isogramma* occurrences in Spain. This study is supported by a grant from the Japanese Society for Promotion of Sciences (JSPS P01103 to ZQC), a discovery grant from the Australian Research Council (DP0452296 to ZQC), and an ARC grant (LX0348047), two National Science Foundation of China grants (40321202, 40328003) and continuous support from Deakin University to GRS.

Appendix

Detailed stratigraphical and geographical distributions of *Isogramma* species

Species	References	Stratigraphical unit	Age	Loc. in Fig. 5
I. asymmetrica Yang	Yang et al. (1962, p. 91, pl. 1, figs. 16–17)	Xidagou Formation	Kasimovian	24
I. carinthiaca n. sp.	Aigner (1931, p. 73, pl. 1, fig. 10)	Lower Carboniferous	late Viséan-Serpukhovian	16
I. carinthiaca Aigner	Brand (1970, pl. 5, fig. 14)	Lower Carboniferous	late Viséan-Serpukhovian	16
I. (?) *carinata* Maslennikov	Maslennikov (1960, p. 343, pl. 82, fig. 10)	Lower Permian	Artinskian–Kungurian	12
I. coopi n. sp.	Wardlaw et al. (1987, p. 84, pl. 1, figs. 1–17)	Graham Formation	Virgilian	4
I. concavum n. sp.	Cooper and Grant (1974, p. 252, pl. 25, figs. 16–17)	Neal Ranch Formation	early Wolfcampian	4
I. concentrica (de Koninck)	Semenow (1854, p. 345, pl. 1, figs. 11–13)	Lower Carboniferous	late Viséan-Serpukhovian	16
I. concentrica (de Koninck)	de Koninck (1873, p. 41, pl. 2, fig. 3)	Lower Carboniferous	late Viséan-Serpukhovian	16
I. chernyshevi n. sp.	Aisenverg (1964, p. 147, pl. 1, figs. 3–4)	Elenovsky (C_1^{ef})	middle Viséan	8
I. davidsoni (Barrois)	Barrois (1882, p. 326, pl. 16, fig. 6a–d)	Upper Carboniferous	Moscovian–Kasimovian	18
I. davidsoni (Barrois)	Delépine (1943, p. 74); Leyva et al. (1985)	Upper Carboniferous	Moscovian	18
I. davidsoni (Barrois)	Winkler Prins (in Moore et al., 1971); Luque et al. (1985); Villa et al. (1988)	Upper Carboniferous	Moscovian	18
I. davidsoni (Barrois)	Wagner and Winkler Prins (1985)	Upper Carboniferous	Moscovian–Kasimovian	18
I. diabloense n. sp.	Cooper and Grant (1974, p. 252, pl. 25, fig. 15; pl. 26, figs. 5–15)	Bone Spring Formation	early Leonardian	4
I. donbassica Aisenverg	Aisenverg (1964, p. 149, pl. 1, figs. 7–18; pl. 2, figs. 19–25)	Elenovsky (C_1^{ef})	middle Viséan	8
I. donbassica Aisenverg	Aisenverg (1964, p. 149, pl. 1, figs. 7–18; pl. 2, figs. 19–25)	Prokhorovskaya (C_1^{sb})	early Serpukhovian	8
I. donbassica Aizenverg	Brand (1970, p. 71, pl. 6, figs. 1, 3; pl. 7, figs. 1–10)	Lower Limestone Group (P_2); Orchard Beds	late Viséan-Serpukhovian	13
I. expansa (Vinassa de Regny and Gortani)	Vinassa de Regny and Gortani (1905, p. 534, pl. 14, fig. 14)	Upper Carboniferous	Kasimovian-Gzhelian	16
I. expansa (Vinassa de Regny and Gortani)	Schmidt (1931, pl. 10, figs 1–10)	Uralian	Kasimovian-Gzhelian	16
I. expansa (Vinassa de Regny and Gortani)	Reichardt (1937, p. 976, pl. 2, fig. 10)	Uralian	Kasimovian-Gzhelian	16
I. expansa (Vinassa de Regny and Gortani)	Gauri (1965, p. 29, pl. 2, figs. 7–9; pl. 3, figs. 4–6)	Uralian	Kasimovian-Gzhelian	16
I. germanica n. sp.	Paeckelmann (1930, p. 211, pl. 15, figs. 1–4, no fig. 5)	Lower Carboniferous	late Viséan-Serpukhovian	17
I. germanica Paeckelmann	Semenow (1854, p. 345, pl. 5, fig. 1a–d)	Lower Carboniferous	late Viséan-Serpukhovian	17
I. germanica Paeckelmann	Dittmar (1872, p. 11, pl. 1, figs. 17–20)	Lower Carboniferous	late Viséan-Serpukhovian	17

(*continued on next page*)

Species	References	Stratigraphical unit	Age	Loc. in Fig. 5
I. germanica Paeckelmann	Aigner and Heritsch (1931, p. 312, pl. 1, figs. 11–17; pl. 5, figs. 55, 58)	Lower Carboniferous	late Viséan-Serpukhovian	17
I. germanica Paeckelmann	Sarycheva and Sokolskaya (1952, p. 60, pl. 3, fig. 51)	Alexinsky (C_1^{al}), Mikhailovsky (C_1^{mkh})	late Viséan	11
I. germanica Paeckelmann	Aisenverg (1964, p. 146, pl. 1, figs. 1–2)	Efremovsky (C_1^{ef})	middle Viséan	8
I. germanica Paeckelmann	Aisenverg (1964, p. 146, pl. 1, figs. 1–2)	Prokhorovskaya (C_1^{sb})	Serpukhovian	8
I. germanica Paeckelmann	Brand (1970, p. 72, pl. 6, figs. 10–11)	Lower Carboniferous	late Viséan-Serpukhovian	17
I. cf. *germanica* Paeckelmann	Brand (1970, p. 72, pl. 6, figs. 8–9)	Hotwells Limestone (D_2)	late Viséan	14
I. heritschi n. sp.	Nakamura (1970, p. 308, pl. 4, figs. 3–7)	lower Kanokura Series	Wordian	31
I. heritschi Nakamura	Aigner and Heritsch (1931, pl. 5, figs. 52)	Cora Formation	Kasimovian-Gzhelian	16
I. kahlerorum n. sp.	Gauri (1965, p. 30, pl. 4, figs. 1–4)	uppermost Uralian	Gzhelian	16
I. kesmensis Ilkhovsky	Ilkhovsky (1978, p. 201, fig. 1a)	Kashirian Horizon	Moscovian	11
I. licharevi n. sp.	Aisenverg (1964, p. 151, pl. 2, figs. 26–32)	topmost Voznesenskaya	earliest Bashkirian	8
I. licharevi n. sp.	Aisenverg (1964, p. 151, pl. 2, figs. 26–32)	C_2^{Am} Suite	Moscovian	8
I. licharevi Aizenverg	Sarycheva (1968, p. 66, pl. 3, fig. 9a–b)	Keregetasskaya Suite	Bashkirian–Moscovian	22
I. lobatum n. sp.	Cooper and Grant (1974, p. 253, pl. 24, figs. 1–4; pl. 25, figs. 3–10)	Cathedral Mountain Fm.	late Leonardian	4
I. manchoukuoensis n. sp.	Hatai and Omura (1941, p. 44, pl. 2, figs. 5–11)	Benchi Formation	Moscovian	28
I. manchoukuoensis Hatai and Omura	Zhang et al. (1983, p. 315, pl. 145, figs. 7–9)	Shiqiantan Formation	Moscovian	25
I. manchoukuoensis Hatai and Omura	Wang and Yang (1998, p. 66, pl. 24, fig. 3)	Shiqiantan Formation	Moscovian	254
I. manchoukuoensis Hatai and Omura	This study	Benchi Formation	Moscovian	28
I. millepunctata n. sp.	Meek and Worthen (1870, pp. 35–36)	Coal Measure	Missourian	1
I. millepunctata Meek and Worth	Meek and Worthen (1873, p. 566, pl. 25, fig. 3)	Coal Measure	Missourian	1
I. millepunctata Meek and Worth	Hall and Clarke (1894, p. 311, pl. 83, figs. 14–15)	Coal Measure	Missourian	1
I. millepunctata Meek and Worth	Morningstar (1922, p. 180, pl. 7, fig. 12)	Coal Measure	Missourian	4
I. millepunctata Meek and Worth	Aigner and Heritsch (1931, pl. 1, figs. 23–27)	Coal Measure	Missourian	1
I. millepunctata Meek and Worth	Dunbar and Condra (1932, p. 282, pl. 42, figs. 18–20)	Douglas Group	Missourian	3
I. millepunctata Meek and Worth	Licharew (1936, pl. B, figs. 4)	Upper Carboniferous	Kasimovian-Gzhelian	21
I. millepunctata Meek and Worth	Hatai and Omura (1941, pl. 2, fig. 4)	Coal Measure	Missourian	1
I. millepunctata Meek and Worth	Volgin (1957, p. 37, pl. 1, figs. 1–7; 1960, p. 41, pl. 2, figs. 3–5)	Uchbulak and Dastarsky Horizons	Kasimovian-Gzhelian	20
I. millepunctata Meek and Worth	Terriere (1960, p. 7)	Graham Formation	Virgilian	4
I. millepunctata Meek and Worth	Sturgeon and Hoare (1968, p. 25, pl. 2, figs. 15–16)	Pottsvrlle and Conemangh Groups	Morrowan-Desmornesian, Missourian	2
I. cf. *millepunctata* Meek and Worth	Licharew (1936, pl. B, figs. 2–3)	Upper Carboniferous	Kasimovian-Gzhelian	21
I. pachti (Dittmar)	Dittmar (1872, p. 2–6, pl. 1, figs. 1–13)	Steshevsky Horizon (C_1^{st})	Serpukhovian	11

Species	References	Stratigraphical unit	Age	Loc. in Fig. 5
I. pachti (Dittmar)	Aigner and Heritsch (1931, pl. 1, figs. 1–8)	Steshevsky Horizon (C_1^{st})	Serpukhovian	11
I. pachti (Dittmar)	Sarycheva and Sokolskaya (1952, p. 60, pl. 3, fig. 52)	Steshevsky Horizon (C_1^{st})	Serpukhovian	11
I. pachti (Dittmar)	Brand (1970, p. 72, pl. 5, figs. 1–6; pl. 6, figs. 2, 4)	Upper Limestone Group (E_2); Passage Group (R_1)	Serpukhovian	13
I. cf. *pachti* (Dittmar)	Dutro (1955, p. 921, fig. 1)	Baird Formation	late Mississippian	6
I. cf. *pachti* (Dittmar)	Brand (1970, p. 73)	Upper Limestone Group (E_2);	early Serpukhovian	15
I. paeckelmanni n. sp.	Aigner and Heritsch (1931, p. 313, pl. 5, figs. 54, 56, 59–66)	Lower Carboniferous	late Viséan-Serpukhovian	16
I. paeckelmanni Aigner and Heritsch	Koninck (1873, p. 41, pl. 2, fig. 3)	Lower Carboniferous	late Viséan–Serpukhovian	16
I. paeckelmanni Aigner and Heritsch	Paeckelmann (1930, p. 211, pl. 15, fig. 5)	Lower Carboniferous	late Viséan–Serpukhovian	17
I. paeckelmanni Aigner and Heritsch	Aisenverg (1964, p. 148, pl. 1, fig. 6)	Ustiluzhskaya Suite	late Viséan-Serpukhovian	9
I. paotechowensis (Grabau and Chao)	Chao (1928, p. 33, pl. 1, fig. 27; pl. 4, figs. 1–5)	Taiyuan Formation	Asselian–Sakmarian	23
I. paotechowensis (Grabau and Chao)	Aigner and Heritsch (1931, p. 307, pl. 2, figs. 32–36; pl. 3, figs. 37–44; pl. 4, figs. 45–51; pl. 5, figs. 53, 67, 71)	Cora Formation	Kasimovian-Gzhelian	16
I. paotechowensis (Grabau and Chao)	Metz (1936, p. 171, pl. 5, fig. 17)	Cora Formation	Kasimovian-Gzhelian	16
I. paotechowensis (Grabau and Chao)	Licharew (1936, pl. 13, fig. 1)	Topmost Carboniferous	Kasimovian-Gzhelian	21
I. paotechowensis (Grabau and Chao)	Licharew (1939, p. 83, pl. 17, figs. 1–2)	Topmost Carboniferous	Kasimovian-Gzhelian	21
I. paotechowensis (Grabau and Chao)	Aisenverg (1950, p. 106, pl. 1, figs. 1–6; pl. 2, figs. 7–11)	Kasimovian/Gzhelian boundary beds	Kasimovian-Gzhelian	8
I. paotechowensis (Grabau and Chao)	Wang (1957, p. 160, pl. 92, fig. 14)	Taiyuan Formation	Asselian–Sakmarian	23
I. paotechowensis (Grabau and Chao)	Volgin (1957, p. 39, pl. 1, figs. 8–9; 1960, p. 41, pl. 2, fig. 6)	Uchbulak and Dastarsky Horizons	Kasimovian-Gzhelian	21
I. paotechowensis (Grabau and Chao)	Wang et al. (1964, p. 354, pl. 37, fig. 38)	Taiyuan Formation	Asselian–Sakmarian	23
I. paotechowensis (Grabau and Chao)	Sergun'kova and Zhizhlo (1975, p. 68, pl. 12, figs. 1–3)	Uchbulak and Dastarsky Horizons	Kasimovian-Gzhelian	21
I. paotechowensis (Grabau and Chao)	Lee and Duan (1985, p. 239, pl. 66, figs. 14–15, 23)	Taiyuan Formation	Asselian–Sakmarian	23
I. aff. *paotechowensis* (Grabau and Chao)	Minato (1955, p. 29, fig. 1)	Kanokura Series	Wordian	31
I. aff. *paotechowensis* (Grabau and Chao)	Nakamura (1970, p. 306, pl. 3, figs. 1–2; pl. 4, figs. 1–2)	Kanokura Series	Wordian	31
I. aff. *paotechowensis* (Grabau and Chao)	This study	Kanokura Series	Wordian	31
I. aff. *paotechowensis* (Grabau and Chao)	Sánchez de Posada et al. (1999, 2002)	Cantabrian	Kasimovian	18
I. permiana Ding	Ding and Qi (1983, p. 298, pl. 102, fig. 9)	Shuixiakou Formation	Asselian–Sakmarian	27
I. pokrowskiensis Menshagin	Menshagin (1936, p. 51, figs. 1–2)	Dolomite Series	Asselian–Sakmarian	10
I. renfrarum n. sp.	Cooper (1952, p. 114, pl. 21, figs. 1–3; pl. 22, fig. 1; pl. 23, fig. 1)	Gonzales Shale; Strawn Sandstone	Virgilian	4
I. vidriense n. sp.	Cooper and Grant (1974, p. 253–254, pl. 25, figs. 13–14)	Gaptank and Neal Ranch Formations	Virgilian; Wolfcampian	4
I. vidriense Cooper and Grant	King (1931, p. 65, pl. 10, fig. 8)	Wolfcamp Formation	early Wolfcampian	4
I. salteri n. sp.	Brand (1970, p. 73, pl. 5, figs. 7–13, 15)	Hotwells Limestone (D_2); Upper Limestone Group	late Viséan-Serpukhovian	14

(*continued on next page*)

Species	References	Stratigraphical unit	Age	Loc. in Fig. 5
I. scotica n. sp.	Brand (1970, p. 75, pl. 8, figs. 1–4)	Lower Limestone Group (P_2)	Briganitian (late Viséan)	13
I. scotica Brand	Davidson (1863, p. 278, pl. 55, fig. 13; 1884, p. 283)	Lower Limestone Group	late Viséan	13
I. scotica Brand	Hatai and Omura (1941, pl. 2, fig. 3)	Lower Limestone Group	late Viséan	13
I. scotica Brand	Wright (1981, pl. 63, fig. 4)	Lower Limestone Group	late Viséan	13
I. cf. *scotica* Brand	Brand (1970, pl. 8, fig. 5)	Lower Limestone Group	late Viséan	13
I. serbica n. sp.	Stojanoviæ-Kuzenko (1968, pl. 1, figs. 8–9; pl. 2, fig. 1)	Stojkovici Formation	Vereian (Moscovian)	20
I. serbica Stojanoviæ-Kuzenko	Stojanoviæ-Kuzenko et al. (1995, pl. 65, figs. 6, 6a)	Stojkovici Formation	Vereian (Moscovian)	20
I. sinosa Jin and Shi	Jin et al. (1985, p. 188, pl. 9, fig. 10)	Chidantan Group	Wuchiapingian	26
I. texanum n. sp.	Cooper (1952, p. 115, pl. 21, figs. 4–5; pl. 22, figs. 2–4)	Gaptank Formation	Virgilian	4
I. texanum Cooper	Dunbar and Condra (1932, pl. 42, fig. 21)	Douglas Group	Virgilian	4
I. ussensis (Dittmar)	Dittmar (1872, p. 12, pl. 1, figs. 14–16)	Upper Carboniferous	Kasimovian-Gzhelian	11
I. ussensis (Dittmar)	Aigner and Heritsch (1931, pl. 1, figs. 9–10)	Upper Carboniferous	Kasimovian-Gzhelian	11
I. ussensis (Dittmar)	Ilkhovsky (1978, p. 202, fig. 1b–d)	Dorogomilovian Horizon	Kasimovian	11
I. zoellnerensis n. sp.	Gauri (1965, p. 29, pl. 3, figs. 1–3)	Uralian	Kasimovian-Gzhelian	16
I. sp. 1	Aisenverg (1964, p. 148, pl. 1, fig. 5)	Ustiluzhskaya Suite	late Viséan	9
I. sp. A	Brand (1970, p. 76, pl. 7, fig. 13); Wilson (1989, p. 101)	Dinwoodie Beds (D_1)	early late Viséan	13
I. sp. B	Brand (1970, p. 76, pl. 7, figs. 11–12)	Upper Limestone Group (E_2)	Serpukhovian	13
I. sp. C	Brand (1970, p. 77, pl. 6, fig. 7)	Lower Limestone Group (P_2)	late Viséan	13
I. sp.	Liñán Guijarro (1978, p. 91)	Viseense Superior	late Viséan	19
I. sp.	Martínez-Chacón and Winkler Prins (1985, p. 437); Río García (1998); Sánchez de Posada et al. (1999, 2002)	Westphalian D-Cantabrian	Moscovian–Kasimovian	18
I. sp.	Gauri (1965, p. 31, pl. 4, figs. 5–6)	Uralian	Kasimovian-Gzhelian	16
I. sp.	Yang et al. (1977, p. 314, pl. 131, fig. 11)	Zimenqiao Formation	late Viséan-Serpukhovian	29
I. sp.	Zhu (1990, p. 84, pl. 17, fig. 5)	Tongtzyen Formation	Wordian	30
I. sp.	Sutherland and Harlow (1973, p. 19, pl. 1, fig. 15)	LaPasada Formation	early Desmoinesian	5
I. sp.	Aisenverg (1950, p. 108, pl. 2, fig. 12)	I_8 horizon	late Bashkirian	8
I. sp.	Branisa (1965, pl. 23, fig. 1)	lower Copacabana Group	Kasimovian-Gzhelian	7
I. sp.	Ishibashi and Fujikawa (1999, pl. 1, figs. 4–8); Fujikawa et al. (2003, p. 20, fig. 4.1–4.4)	lower Copacabana Group	Kasimovian-Gzhelian	7
I. sp. indet.	Aisenverg (1950, p. 109, pl. 2, fig. 13)	$C_{3\,8}^{N}$ horizon	Kasimovian	8
I. sp. 1	Cooper and Grant (1974, p. 254, pl. 24, figs. 5–6)	Skiner Ranch Formation	Kungurian	4
I. sp. 2	Cooper and Grant (1974, p. 254, pl. 25, figs. 1–2)	Cherry Canyon Formation	middle Wordian	4
I. sp. 3	Cooper and Grant (1974, p. 254, pl. 25, figs. 11–12)	Road Canyon Formation	Roadian	4

References

Aigner, G., 1931. Die Brachiopoden des Karbons von Notsch. II. Naturwissenschaftliche Verein für Steiermark. Mitteilungen 68, 3–15. 1 pl.

Aigner, G., Heritsch, F., 1931. Das Genus *Isogramma* im Carbon der Südalpen. Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse. Denkschriften 102, 303–316. 5 pls.

Aisenverg, D.E., 1950. *Isogramma* Meek & Worthen verkhnego karbona Donetskogo basseina. In: Materialy po stratigrafii i paleontologii Donetskogo basseina. Ugletekhizdat, Kharkov, pp. 104–112.

Aisenverg, D.E., 1964. Predstaviteli roda *Isogramma* Meek & Worthen iz nizhnego karbona Donetskogo basseina i drugikh raionov Ukrainy. Akademiia Nauk Ukrainskoi RSR, Instytut Geologicheskikh Nauk, Seriia Stratigrafii i Paleontologii, Trudy 48, pp. 144–153, 2 pls.

Aisenverg, D.E., Brazhnikova, N.E., Vassilyuk, N.P., Vdovenko, M.V., Gorak, S.V., Dunaeva, N.N., Zernetskaya, N.V., Poletaev, V.I., Potievskaya, P.D., Rotai, A.P., Sergeeva, M.T., 1979. The Carboniferous sequence of the Donetz Basin: a standard section for the carboniferous. In: Wagner, E.H., Higgins, A.C., Meyen, S.V. (Eds.), The Carboniferous of the USSR Yorkshire Geological Society Occasional Publication 4, pp. 197–224.

Barrois, C.H., 1882. Recherches sur les terrains anciens des Asturias et de la Galice. Societé géologique du Nord. Mémoires 2 (1), 1–630. 20 pls.

Bensh, F.R., Rumiantseva, Z.S., Sergunkova, O.I., 1996. Tianshan and Pamirs. In: Martinez Diaz, C., Wagner, R.H., Winkler Prins, C.F., Granados, L.F. (Eds.), The Carboniferous of the World III, The former USSR, Mongolia, Middle eastern Platform, Afghanistan and Iran. IUGS Publication. Instituto Tecnologico, GeoMinero de Espana, 33, pp. 122–153.

Brand, P.J., 1970. British Carboniferous Isogrammidae, Geological Survey of Great Britain. Bulletin 33, 67–83. 4 pls.

Branisa, L., 1965. Los fósiles guías de Bolivia. I. Paleozoico. Servicio Geologico de Bolivia Ex-departamento Nacional de Geologia. Boletin 6, 1–282. 80 pls.

Chao, Y.T., 1928. Productidae of China. Part II: Chonetinae, Productinae and Richthofeninae. Palaeontologica, Sinica, Series B 81, p. 6 pls.

Chen, Z.Q., 2004. Devonian–Carboniferous brachiopod zonation of the Tarim Basin, Northwest China: implications for biostratigraphy and biogeography. Geological Journal 39, 431–458.

Cooper, G.A., 1952. Unusual specimens of the brachiopod family Isogrammidae. Journal of Paleontology 26 (1), 113–119.

Cooper, G.A., 1956. Chazyan and related brachiopods. Smithsonian Miscellaneous Collections 127, 1–1245.

Cooper, G.A., Grant, R.E., 1974. Permian brachiopods of West Texas, II. Smithsonian Contributions to Paleobiology 15, 233–793. 167 pls.

Davidson, T., 1863. A monograph of the British fossil Brachiopoda (Volume 2, Part 5, No. 5: the Fossil Brachiopoda–Carboniferous). Monograph of the Palaeontographical Society 14, 211–280 pls. 48–55.

Davidson, T., 1884. A monograph of the British fossil Brachiopoda (Volume 5, Part 3: Appendix to supplement, general summary, with catalogue and index of the British species). Monograph of the Palaeontographical Society 38, 243–476 pls. 18–21.

de Koninck, L.G., 1873. Monographie des Fossiles Carbonifères de Bleiberg en Carinthie. In: Récherches Sur les Animaux Fossiles. F. Hayez, Bruxelles, 114 pp., 4 pls.

Delépine, G., 1943. Les faunes marines du Carbonifère des Asturias (Espagne). Academie des Sciences, Mémoires, Series 2, 66 (3), 1–122 pls. 1–6.

Ding, P.Z., Qi, G., 1983. Brachiopoda (Carboniferous and Permian Parts). In: Paleontological Atlas of Northwest China (Shaanxi- Gansu-Ningxia Provinces Volume), Part II Upper Paleozoic. Geological Publishing House, Beijing, pp. 244–425, pls. 88–143.

Dittmar, A., 1872. Palaeontologische notizen. Uber ein neues Brachiopoden-Geschichte aus dem Bergkalk. Russische-Kaiserliche mineralogische Gesellschaft, Verhandlungen 2 (7), 1–14.

Dunbar, C.O., Condra, G.E., 1932. Brachiopoda of the Pennsylvanian System in Nebraska. Nebraska Geological Survey Bulletin, Series 2 5, 1–377. 44 pls.

Dutro Jr., J.T., 1955. Occurrence of the brachiopod *Isogramma* in the Baird Formation of California. Journal of Paleontology 29 (5), 920–922.

Fujikawa, M., Ishibashi, T., Tazawa, J., 2003. *Isogramma* (Brachiopoda) from the lower Copacabana Group of the Lake Titicaca region, Bolivia. Science Reports of Niigata University, Series E (Geology) 18, 17–24.

Gauri, K.L., 1965. Uralian stratigraphy, trilobites and brachiopods of the western Carnic Alps (Austria). Geologische Bundesanstalt, Jahrbuch 11, 1–94. 17 pls.

George, T.N., Johnson, G.A.L., Mitchell, M., Prentice, J.E., Ramsbottom, W.H.C., Sevastopulo, G.D., Wilson, R.B., 1976. A correlation of Dinantian rocks in the British Isles. Geological Society of London, Special Report 7, 1–87.

Hall, J., Clarke, J.M., 1894. An introduction to the study of the genera of Palaeozoic Brachiopoda. New York Geological Survey, Palaeontology 8 (1), 311–312.

Hatai, K.M., Omura, T., 1941. On a species of *Isogramma* (Brachiopoda) from Manchoukuo. Geological Society of Japan, Journal 48 (568), 43–46 pl. 2.

Holmer, L.E., 2000. Dictyonellida. In: Williams, A., Brunton, C.H.C., Carlson, S.J. (Eds.), 44 others (revised), Treatise on Invertebrate Palaeontology, Part H, Brachiopoda, vol. 2–3. Geological Society of America, University of Kansas Press, Lawrence, pp. 196–200.

Ilkhovsky, R.A., 1978. Middle and Late Carboniferous brachiopods of the genus *Isogramma* from the Moscow Basin. Paleontological Journal 12 (2), 201–205.

Ishibashi, T., Fujikawa, M., 1999. Permian fauna of the Copacabana Group distributed around the Lake Titicaca in the Central Andes. Journal of Geography 108 (3), 321–327.

Jin, Y.G., Wang, Y., Sun, D.L., Shi, Q., 1985. Late Paleozoic and Triassic brachiopods from the East of the Qinghai-Xizang Plateau. In: Stratigraphy and Palaeontology in western Sichuan and eastern Xizang, China, Part 3. Sichuan Science and Technology Publishing House, Chengdu, pp. 182–249, 20 pls.

Jin, Y.G., Zhang, J., Shang, Q.H., 1994. Two phases of the end-Permian mass extinction. Canadian Society of Petroleum Geologists, Memoir 17, 813–822.

King, R.E., 1931. The Geology of the Glass Mountains, Texas, Part II: faunal summary and correlation of the Permian formations with description of Brachiopoda. University of Texas. Bulletin 3042, 1–245. 44 pls.

Kotlyar, G.V., Popeko, L.I., 1967. Biostratigraphy, bryozoans and brachiopods of the Upper Palaeozoic of Zabaikal. In: Obrycheva, V.A. (Ed.), Zapinski Zabaikal'skogo filiala geolograficheskogo obtshestva SSSR vypuski 28, Trudy Otdeleniiya Geologii In V.A. Obrycheva, 5, 323 pp., 57 pls.

Kotlyar, G.V., Kurilenko, A.V., Biakov, A.S., Popeko, L.I., 2002. Permian system. In: Oleinikov, A.N. (Ed.), Atlas of Palaeozoic–Mesozoic fauna and flora in the Transbaikal region. Nauka, Novosibirk, pp. 134–271.

Lane, H.R., Brenckle, P.L., Baesemenn, J.F., Richards, B., 1999. IUGS The boundary in the middle of the Carboniferous: Arrow Canyon, Nevada, USA. Episodes 22, 272–283.

Lee, L., Duan, C.H., 1985. Brachiopoda. In: Paleontological Atlas of northern China, Paleozoic Era, vol. 1. Geological Publishing House, Beijing, pp. 209–260, pls. 62–85.

Leyva, F., Granados, L.F., Solovieva, M.N., Laveine, J.P., Lys, M., Loboziak, S., Martínez-Díaz, C., Brousmiche, C., Candelier, A.M., García, A., Esnaola, J.M., 1985. La estratigrafía del Carbonífero Medio en la zona de Campo de Caso-Tanes (sector central de la region de Mantos). C.R. X Congres International de Stratigraphie et de Géologie du Carbonifère, Madrid, 1983 1, 249–268.

Liao, Z.T., 1983. Two new genera of Brachiopoda from the Heshan Formation (Upper Permian) of Guangxi. Acta Palaeontologica Sinica 22 (6), 637–641.

Licharew, B.K., 1936. O nekotorykh predstaviteliakh redkikh verkhnepaleozoiskikh brakhiopod. Biulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdelenie Geologicheskii 14 (2), 133–158 pls. A–C.

Licharew, B.K., 1939. Klass Brakhiopody. In: Gorsky, I. (Ed.), Atlas Rukovodiashchikh Form Iskopaemykh Faun SSSR, Tome V. Srednii i Verkhnii Karbon. Nauk, Moscow, pp. 79–113 pls. 16–28.

Liñán Guijarro, E., 1978. Bioestratigrafía de la Sierra de Córdoba. Tesis Doctorales de la Universidad de Granada 191, 1–211, 17 pls.

Luque, C., Gervilla, M., Sáenz de Santa María, J.A., Leyva, F., Laveine, J.P., Loboziak, S., Martínez-Chacón, M.L., 1985. Características sedimentológicas y paleontológicas de los paquetes productivos en el corte de La Inverniza-El Cabo (Cuenca Central Austuriana). C.R. X Congres International de Stratigraphie et de Géologie du Carbonifère, Madrid 1, 281–302.

Martínez-Chacón, M.L., Winkler Prins, C.F., 1985. Upper Carboniferous (Kasimovian) brachiopods from Asturias (N. Spain). 10th International Congress on Carboniferous Stratigraphy and Geology, Madrid, Sept. 12–17, 1983, Compte Rendu 2, 435–448, 4 pls.

Maslennikov, D.F., 1960. Novyi vid permskikh izogrammid Zabaikal'ia. In: Markowskii, B.P. (Ed.), Novye Vidy Drevnikh Rastenii i Bespozvonochnykh SSSR. Part 1. VSEGEI, Moscow, pp. 343–344.

Meek, F.B., Worthen, A.H., 1870. Descriptions of new species and genera of fossils from the Paleozoic rocks of the Western States. Academy of Natural Sciences of Philadelphia, Proceedings, Series 2 22, 22–56.

Meek, F.B., Worthen, A.H., 1873. Paleontology: descriptions of invertebrates from Carboniferous system. Geological Survey of Illinois 5 (2), 323–619 pls. 5–32.

Menshagin, N.V., 1936. On the occurrence of a representative of the genus *Isogramma* Meek and Worthen in the Dolomite Series of Bachmut Trough of the Donets Basin. Leningradskyi Obshchestva Estestvoispytatelei, Otdelenie Geologii i Mineralogie, Trudy 65 (1), 51–54.

Metcalfe, I., 1996. Gondwanaland dispersion, Asian accretion and evolution of eastern Tethys. Australian Journal of Earth Sciences 43, 605–620.

Metz, K., 1936. Eine fauna aus den untersten Schichten des Obercarbons der Karnischen Alpen (Waideggerfauna). Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B 75 (1), 163–188 pls. 5–7.

Minato, M., 1955. *Isogramma paotechowensis* (Grabau et Chao) from the Permian of Japan. Palaeontological Society of Japan, Transactions and Proceedings 18, 29–30.

Moore, L.R., Neves, R., Wagner, R.H., Wagener-Gentis, C.H.T., 1971. The stratigraphy of Namurian and Westphalian rocks in the Villamanín area of northern León, N.W. Spain. Trabajos de Geología, Universidade de Oviedo 3, 307–363, 8 pls.

Morningstar, H., 1922. The Pottsville fauna of Ohio. Geological Survey of Ohio, Bulletin 25, 1–312.

Nakamura, K., 1970. *Isogramma* from the Permian Kanokura Series of the Kitakami Mountains Japan. Journal of the Hokkaido University, Faculty of Science (Geology and Mineralogy), Series 4 14 (3), 301–311. 2 pls.

Noda, M., 1939. Stratigraphical studies on the Carboniferous and Permian formations of southern Manchoukuo. Bulletin of Central National Museum of Manchoukuo 7, 7–70.

Paeckelmann, W., 1930. Die Fauna des deutschen Unterkarbons. 1. Teil. Die Brachiopoden, 1. Teil: Die Orthiden, Strophomeniden und Choneten des mittleren und oberen Unterkarbons. Königliche-Preussiche geologische Landesanstalt, Abhandlungen 122, 143–326, pls. 9–24.

Poletaev, V.I., Brazhnikova, N.E., Vasilyuk, N.P., Vdovenko, M.V., 1990. Local zones and major Lower Carboniferous biostratigraphic boundaries of the Donets Basin (Donbass), Ukraine, USSR. In: Brenckle, P.L., Manger, W.L. (Eds.), Intercontinental Correlation and Division of the Carboniferous System. Courier Forschungsinstitut Senckenberg, vol. 130, pp. 47–59.

Ramsbottom, W.H.C., Calver, M.A., Eagar, R.M.C., Hodson, F., Holliday, D.W., Stubblefield, C.J., Wilson, R.B., 1978. A correlation of Silesian rocks in the British Isles. Geological Society of London, Special Report 10, 1–82.

Raymond, A., Kelley, P.H., Lutken, C.B., 1990. Dead by degrees: articulate brachiopods, paleoclimate and the mid-Carboniferous extinction event. Palaios 5 (2), 111–123.

Reichardt, W., 1937. Die Ostalpinen Nassfeldschichten- Eine Brucke zweischen Mitteleuropa und Russland. Compte Rendu du Deuxième Congres pour l'Avancement des Etudes de Stratigraphie Carbonifère 2, 919–1055, pls. 100–105.

Reitlinger, E.A., Vdovenko, M.V., Gubareva, V.S., Shcherbakov, O.A., 1996. Lower Carboniferous. In: Martinez Diaz, C., Wagner, R.H., Winkler Prins, C.F., Granados, L.F. (Eds.), The Carboniferous of the World III, The Former USSR, Mongolia, Middle eastern Platform, Afghanistan and Iran IUGS Publication No. 33. Instituto Tecnologico, GeoMinero de Espana, pp. 23–55.

Río García, L.M., 1998. Asociaciones de braquiopods en los paquetes improductivos de la Cuenca Carbonífera Central de Asturias. Trabajos de Geología, Universidad de Oviedo 20, 157–166.

Rowell, A.J., 1965. Family Isogrammidae. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Brachiopoda, Part H, vol. 1. Geological Society of America and University of Kansas Press, Lawrence, p. 361.

Sánchez de Posada, L.C., Villa, E., Martínez-Chacón, M.L., Rodríguez, R.M., Rodríguez, S., Coquel, R., 1999. Contenido paleontológico y edad de la sucesión de Demués (Carbonífero, Zona Cantábrica). Trabajos de Geología, Universidade de Oviedo 21, 339–352.

Sánchez de Posada, L.C., Villa, E., Rodríguez, R.M., Martínez-Chacón, M.L., Rodríguez, S., Coquel, R., 2002. Paleontological content of the Demues section (Upper Carboniferous, Cantabrian Mountains, Spain) and its significance for correlation. In: Hills, L.V., Henderson, C.M., Bamber, E.W. (Eds.), Carboniferous and Permian of the World Canadian Society of Petroleum Geologists, Memoir, 19, pp. 588–595.

Sarycheva, T.G. (Ed.), 1968. Brakhiopody verkhnego paleozoia vostochnogo Kazakhstana. Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy 121, 1–212, 23 pls.

Sarycheva, T.G., Sokolskaya, A.N., 1952. Opredelitel' paleozoiskikh brakhiopod podmoskovnoi kotloviny. Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy 38, 1–307, 71 pls.

Schmidt, H., 1931. Bau und Anjeftungsweise des Brachiopoden *Isogramma* aus dem Oberkarbon Karntes. Paläontologisch Zeitschrift 13 (4), 278–283, pl. 10.

Schuchert, C., 1893. Classification of the Brachiopoda. American Geologist 11, 141–167.

Schuchert, C., 1929. Classification of brachiopod genera, fossil and recent. In: Schuchert, C., Le Vene, C.M. (Eds.), Brachiopoda (generum et genotyporum index et bibliographia), Fossilium Catalogus I: Animalia, Pars 42. W. Junk, Berlin, pp. 10–25.

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, pp. 1–21.

Semenow, P., 1854. Fauna des schlesischen Kohlenkalkes. Zeitschrift der Deutschen geologischen Gesellschaft 6, 317–404.

Sergun'kova, O.I., Zhizhlo, O.R., 1975. Brakhiopody srednogo karbona, verkhnego karbona i nizhnei permi Fergany. In: Sikstel', T.A. (Ed.), Biostratigrafiia verkhnego paleozoia gornogo obramleniia iuzhnoi Fergany. Tashkent, pp. 54–77 pls. 7–20.

Sheng, J.Z., 1958. Fusulinidae from the Benchi Series of the Taitz River region. Palaeontologica Sinica, New Series B B 7, 1–219. 18 pls.

Shi, G.R., Chen, Z.Q., 2003. Global review of Permian Tyloplecta Muir-Wood and Cooper, 1960 (Brachiopoda): morphology, palaeobiogeographic and palaeogeographical implications. Gondwana Research 6, 777–790.

Shi, G.R., Grunt, T.A., 2000. Permian Gondwanan–Boreal antitropicality with special reference to brachiopod faunas. Palaeogeography, Palaeoclimatology, Palaeoecology 155, 239–263.

Shi, G.R., Tazawa, J., 2001. *Rhynchopora* and *Blasispirifer* (Brachiopoda) from the Middle Permian of the Hinda Gaien Belt, central Japan, and their paleobiogeographical significance. Journal of the Geological Society of Japan 107, 755–761.

Shi, G.R., Archbold, N.W., Zhan, L.P., 1995. Distribution and characteristics of mixed (transitional) mid-Permian (Late Artinskian-Ufimian) marine faunas in Asia and their palaeogeographical implications. Palaeogeography, Palaeoclimatology, Palaeoecology 114, 241–271.

Stanley, S.M., Powell, M.G., 2003. Depressed rates of origination and extinction during the late Paleozoic ice age: a new state for the global marine ecosystem. Geology 31 (10), 877–880.

Stanley, S.M., Yang, X.N., 1994. A double mass extinction at the end of the Paleozoic Era. Science 266, 1340–1344.

Stojanovic-Kuzenko, S., 1968. Biostratigraphy of the Middle Carboniferous of western Serbia and its correlation with that in northwestern Bosnia, part of Velebit, and Stanisic (Montenegro). Bulletin of the Institute for Geological and Geophysical Research, Series A 24–25 (1966/67), 201–237.

Stojanovic-Kuzenko, S., Pajic, V., Archbold, N.W., 1995. Biostratigrafija. In: Filipovic, I. (Ed.), The Carboniferous of Northwestern Serbia Mémoires du Service Géologique GEMINI, pp. 22–69.

Sturgeon, M.T., Hoare, R.D., 1968. Pennsylvanian brachiopods of Ohio. Geological Survey of Ohio, Bulletin 63, 95 pp., 22 pls.

Sutherland, P.K., Harlow, F.H., 1973. Pennsylvanian brachiopods and biostratigraphy in southern Sangre de Cristo Mountains, New Mexico. New Mexico Bureau of Mines and Mineral Resources, Memoir 27, 1–173, 18 pls.

Tazawa, J., Ibaraki, Y., 2001. Middle Permian brachiopods from Setamai, the type locality of the Kanokura Formation, southern Kitakami Mountains, northeastern Japan. Science reports of the Faculty of Science, Niigata University, Series E (Geology) 16, 1–33.

Terriere, R.T., 1960. Geology of the Grosvenor Quadrangle Brown and Coleman Counties, Texas. Pennsylvanian and Lower Permian Stratigraphy between the Brazos and Colorado Rivers, North-Central Texas. United States Geological Survey Bulletin 1096, 1–35.

Villa, E., Horvath, V., Martínez-Chacón, M.L., Sánchez de Posada, L.C., 1988. Datos paleontológicos y edad de la sección de Villamanín (Carbonífero, C. Cantábrica, España). II Congreso Geologico de España, Communicaciones 1, 337–341.

Vinassa de Regny, P., Gortani, M., 1905. Fossili Carboniferi del M. Pizzul e del Piano di Lanza nella Alpi Carniche. Societa Geologica Italiana, Bollettino 24, 461–605, pls. 12–15.

Volgin, V.I., 1957. Izogrammidy iuzhnoi Fergany. Vestnik Leningradskogo Gosudarstvennogo Universiteta (LGU), Seriia Geologia i Geografia 18 (3), 34–42, 1 pl.

Volgin, V.I., 1960. Brakhiopody verkhnekamennougol'nykh i nizhnepermskikh otlozhenii iuzhnoi Fergany. Leningrad: Leningradskii Gosudarstvennyi Universitet, 202 pp., 18 pls.

Wagner, R.H., Winkler Prins, C.F., 1985. The Cantabrian and Barruelian stratotypes: a summary of basin development and biostratigraphic information. Anais da Faculdade de Ciências. Universidade do Porto, Supplement to Volume 64, 359–410.

Wagner, R.H.I., Sanchez de Posada, L.C., Martínez-Chacón, M.L., Winkler Prins, C.F., 2002. The Asturian stage: a preliminary proposal for the definition of a substitute for Westphalian. In: Hills, L.V., Henderson, C.M., Bamber, E.W. (Eds.), Carboniferous and Permian of the World Canadian Society of Petroleum Geologists, Memoir 19, pp. 832–850.

Wang, Y., 1957. Brachiopoda. In: Yang, K., Wang, Y. (Eds.), Index Fossils of China, Invertebrate, Part 2. Geological Publishing House, Beijing, pp. 109–171.

Wang, Z.J., 1990. The Carboniferous System of China. Stratigraphy of China, vol. 8. Geological Publishing House, Beijing. 419 pp., 22 pls.

Wang, R.L., 2000a. Penchi Formation. In: Compiling Group of Chinese Stratigraphy (Ed.), Stratigraphy of China. Carboniferous System. Geological Publishing House, Beijing, pp. 29–30.

Wang, R.L., 2000b. Taiyuan Formation. In: Compiling Group of Chinese Stratigraphy (Ed.), Stratigraphy of China. Carboniferous System. Geological Publishing House, Beijing, pp. 85–87.

Wang, C.W., Yang, S.P., 1998. Late Carboniferous to Early Permian Brachiopod Faunas and Biostratigraphy of the Middle Parts of Xinjiang. Geological Publishing House, Beijing. 156 pp., 24 pls.

Wang, Y., Jin, Y.G., Feng, D.W., 1964. Brachiopod Fossils of China. Science Press, Beijing. 777 pp.

Wardlaw, B.R., Schindel, D.E., Yochelson, E.L., 1987. A new species of *Isogramma* (Brachiopoda) from the Pennsylvanian of North-Central Texas. United States Geological Survey Bulletin 1, 81–85. 1 pl.

Williams, A., Brunton, C.H.C., 1997. Morphological and anatomical terms applied to brachiopods. In: Williams, A., Brunton, C.H.C., Carlson, S.J. (Eds.), Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised) 1, Introduction. The Geological Society of America and the University of Kansas Press, Lawrence, pp. 421–440.

Wilson, R.B., 1989. A study of the Dinantian marine macrofossils of central Scotland. Royal Society of Edinburgh, Transactions, Earth Sciences 80 (2), 91–126.

Winkler Prins, C.F., 1989. Brachiopod distributions and the palaeogeographic reconstructions for the Carboniferous. Onzième Congrès International de Stratigraphie et Géologie du Carbonifère Beijing, 1987, Comptes Rendus 2, 382–390.

Wright, A.D., 1981. The external surface of *Dictyonella* and of other pitted brachiopods. Palaeontology 24 (3), 443–482, pls. 62–71.

Yang, T.Y., Ting, P.C., Yin, H.F., Chang, S., Fang, C., 1962. The brachiopod fauna of Carboniferous, Permian, and Triassic in the Chilianshan Region. Monograph on the Geology of the Chilianshan Mountains 4 (4), 1–134, 48 pls.

Yang, D.L., Ni, S.Z., Chang, M.L., Zhao, R.X., 1977. Brachiopods. In: Palaeontological Atlas of Central–South China 2, Geological Publishing House, Beijing, pp. 306–470, pls. 129–188.

Zhang, Z., Zhang, F.M., Zhang, Z.X., Wang, Z., 1983. Brachiopoda. In: Palaeontological atlas of northwestern China (Xinjiang Part), Paleozoic Part 2.Geological Publishing House, Beijing, pp. 262–386, pls. 86–145.

Zhu, T., 1990. The Permian coal-bearing strata and palaeobiocoenosis of Fujian. Geological Publishing House, Beijing, 127 pp., 47 pls.

Ziegler, A.M., Michael, L.H., Rowley, D.B., 1997. Permian world topography and climate. In: Martini, I.P. (Ed.), Glacial and Post-Glacial Environmental Changes: Pleistocene, Permo-Carboniferous, Proterozoic. Oxford University Press, New York, pp. 11–146.