

Palaeobiogeographic affinities of Late Devonian brachiopods from Iran

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Abstract – A total of 34 Late Devonian brachiopod genera from north (Alborz Mountains), east (Tabas region) and central-southeast Iran were compared, using the Jaccard similarity index, with synchronous faunas from 28 localities spread across Gondwana, Euramerica, Siberia, Kazakhstan, and South China. The highest levels of similarity occur between brachiopod taxa from the three Iranian localities and terranes traditionally regarded as part of the northern margin of Gondwana (especially Afghanistan, Armenia, NW Pakistan, Libya, Cantabrian Mountains and Iberia). The distribution of benthic shelf faunas was probably strongly influenced by climatic (latitudinal) continuity, geographic proximity and open dispersal routes along the “North Gondwana Current”. Jaccard analysis also reveals some biogeographic links between Iran/Afghanistan and Euramerica throughout the Late Devonian, supporting the hypothesis that a narrow (< 1000 km) Prototethys Ocean separated the two super continents during this interval.

INTRODUCTION

There is general, but not universal agreement (cf. Soffel and Forster 1984), that the Iranian microcontinent(s), comprising central-east Iran and the Alborz Mountains was located near Saudi Arabia along the northern margin of Gondwana with numerous other ‘Asian’ and ‘European’ terranes (possibly forming an extensive “Cimmerian belt” of terranes according to Sengor and Hsu 1984) during the Devonian (Berberian and King 1981; Wensink 1983; Lensch *et al.* 1984; Talent *et al.* 1986; Belov 1986; Hussein 1991; Dastanpour 1996). Marine transgressions during the Late Devonian-Early Carboniferous deposited thick carbonate dominated sequences, replete with diverse shallow marine faunal assemblages, in north, east and central/SE Iran, consistent with the view that Iran (Figure 1), along with much of northern Gondwana, was positioned within the carbonate development zone, between 0° and 30° (Witzke and Heckel 1988; Dickens 1993) in the southern hemisphere (Eldridge *et al.* 1997; Figures 4–5). Some palaeogeographic reconstructions of the Late Devonian, especially those based on palaeomagnetic data, indicate that the northern margin of Gondwana was separated from the supercontinent of Euramerica, to the north, by a 4000+ km ocean basin, variously referred to as Prototethys or the Prehercynian Ocean (Morel and Irving 1978; Van der Voo 1988; Bachtadase *et al.* 1995; Metcalfe 1996, figure 13). If this were true, one could expect sharp provincial boundaries between coeval benthic faunas from Euramerica

and northern Gondwana. This is based on the fact that modern oceans act as formidable barriers to dispersal by shallow marine shelf benthic invertebrates, especially those organisms (the vast majority) that produce nonplanktotrophic larvae with relatively short lifespans (< 4 weeks), such as articulate brachiopods (Talent 1985; Talent *et al.* 1986; Gratsianova *et al.* 1988; Richardson 1997).

The aim of this study is to probe the biogeographic affinities of Late Devonian brachiopods from Iran by separately comparing Frasnian and Famennian faunas with a selection of synchronous faunas from Gondwana, Euramerica, Siberia, Kazakhstan and South China in an attempt to; 1) ascertain whether the faunas conform to patterns of ‘cosmopolitanism’ previously identified for the Late Devonian and, 2) constrain the position of the Iranian plate with respect to other Gondwanan and Euramerican terranes and test the validity of the claim that these two supercontinents were widely separated during the Frasnian-Famennian.

BIOSTRATIGRAPHY OF LATE DEVONIAN BRACHIOPODS FROM IRAN

Biostratigraphy of Devonian faunas from Iran has been recently reviewed by Dastanpour (1996), with additional refinements presented by various authors at the recent IGCP421 meeting held in Esfahan, Iran (e.g. Jafarian 1998; Brice *et al.* 1999). Late Devonian brachiopods from Iran are known from thick carbonate dominated sequences from

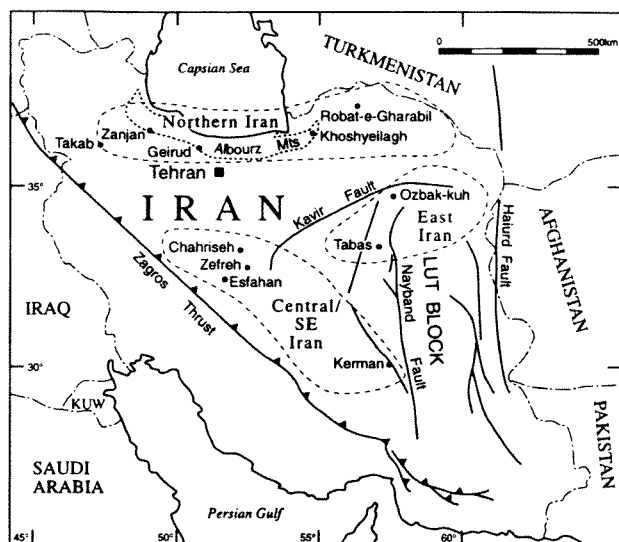


Figure 1 Map showing location of the three principal Late Devonian brachiopod bearing regions in Iran (modified after Hamedei *et al.* 1997).

three main regions (Figure 1). These faunas can be directly correlated with brachiopod biozones 6–12 erected by Brice (1977) for Late Devonian brachiopod faunas from Afghanistan. According to Brice's (1977) scheme brachiopod zones 6–8 are assigned a Frasnian age and zones 9–12 (part) are Famennian in age.

Northern Iran (Alborz Mountains and Robat-e-Gharabil)

The Khoshyielagh Formation consists of up to 1800 m of interbedded limestones, shales and sandstones outcropping extensively in the eastern Alborz Range (Dastanpour 1996) and the Robat-e-Gharabil region in northeastern Iran (Brice *et al.* 1974). The age of the base of the formation is in dispute. Brice *et al.* (1978) subdivided the formation into seven members and indicated the basal 560 m (members 1–4) could be assigned an Eifelian-Givetian age based on brachiopods, bryozoans, conodonts and corals. The presence of conodont species such as *Icriodus* aff. *obliquimarginatus*, *Polygnathus pseudofoliatus*, *P.* cf. *timorensis*, *P.* aff. *xylus* and *P. linguiformis linguiformis* provides strong evidence for a Middle Devonian age (Bultynck in Brice *et al.* 1978). A possible Emsian age for lowermost strata of the Khoshyielagh Formation has been suggested by Hamdi and Janvier (1981) based on conodont and vertebrate occurrences. However, Ghavidel-Syooki (1994, 1998) argues that the entire Khoshyielagh Formation is Late Devonian in age based on acritarch and spore evidence, and that "Lower and Middle Devonian strata are not present on the Iranian platform" (Ghavidel-Syooki 1998: 12). Late Devonian brachiopods have been recovered from strata 600 m above the base of the

Khoshyielagh Formation and these have been documented by Vandercammen (1967), Brice (1971), Brice *et al.* (1974, 1978) and Sartenaer and Plodowski (1975). The faunas are relatively diverse (Table 1) and broadly correlate with brachiopod zones 6–12 (Frasnian-Famennian) of Brice (1977).

The brachiopod fauna from the Geirud Formation (*sensu* Stepanov 1967) in the central Alborz Range (Figure 1) was documented by Gaetani (1965) with revisions of some taxa provided by Sartenaer (1966a). The Geirud Formation is up to 340 m thick and consists of fossiliferous calcarenite, marly limestone, shales and lithic sandstones. Diagnostic brachiopods from limestones near the base of the sequence include *Ripidiorhynchus elburzensis* and *Cyrtospirifer* cf. *syringothyrimiformis* equivalent to biozone 8 of Brice (1977) and indicative of an upper Frasnian age. The overlying *Centrorhynchus deltidialis* zone of Gaetani (1965) with *C. deltidialis*, *Gastrodetoechia iranica* and *Cyrtospirifer verneuili* has no direct biozone equivalent using Brice's (1977) scheme, but Brice *et al.* (1978: 22) indicate the *C. deltidialis* zone approximates a lower Famennian age. *Centrorhynchus* is a characteristic Famennian taxon (Sartenaer 1970).

Dastanpour (1996) reported the presence of Frasnian (*Ripidiorhynchus*) and unnamed Famennian brachiopods from limestones outcropping in the vicinity of Zanjan in the western Alborz Range (Figure 1), but these have not been formally described and are not included in the current analysis.

Eastern Iran

The Ozbak-Kuh Group, a 1500–1700 m thick sequence of Devonian-Carboniferous sediments, outcrops extensively in the Tabas area in the Ozbak-Kuh Mountains (Ruttner *et al.* 1991), the Shotori Range (Stocklin *et al.* 1965), and at Shirgesht (Ruttner *et al.* 1991). The Ozbak-Kuh Group is subdivided into four formations, with the principal Upper Devonian sequences being the Bahram and Shishtu formations. Detailed conodont biostratigraphy presented by Weddige (1984) for the Ozbak-Kuh area and by Yazdi (1996, 1997, 1998, 1999) for exposures in the Shotori Range indicate the Bahram Formation ranges in age from Givetian-Frasnian and, according to the latest work of Yazdi (1999), the conformably overlying Shishtu Formation spans an interval from Frasnian (Early *hassi* Zone or older) to latest Tournaisian (*anchorallatus* Zone). Brachiopods are known to occur in the Bahram and Shishtu formations from all three regions, but only a few taxa have been formally described.

Sartenaer (1966b) described *Cyphoterorhynchus arpaensis*, *C. koraghensis* and *C. k. interpositus* from the Bahram and Shishtu formations at Ozbak-Kuh. *C. arpaensis* and *C. k. interpositus* also occur in the basal Shishtu Formation at Howz-e-Dorah (Yazdi

Late Devonian Brachiopod Genera	Localities	References
Atrypella (Fam-Carb)	Elbourz Mts N. IRAN	Gastani 1965; Sartenaer 1966b; Brice et al 1973, 1974; Vandercam. 1967; Sartenaer & Plodowski 1975
Athyris (Fam-Carb)	EAST IRAN	Sartenaer 1966a, 1968b; Legrand-Blain 1998
Avonia (Fam-Carb)	CENTRAL/SE IRAN	Djafarian & Brice 1973; Legrand-Blain 1998; Brice 1998; Brice et al. in press
Buxtonia (Fam-Carb)	AFGHANISTAN	Durkoop 1970; Brice 1971; Brice 1977; Brice & Farsan 1976; Farsan 1986
Centrotrichus (Fam-Carb)	ARMENIA	Abramian 1957 & 1974; Mambetov & Rzhon. 1985
Ctenolophora (Fam-Carb)	NW PAKISTAN	Sartenaer 1964; Morante 1989
Composita (Fam-Carb)	LIBYA	Mergl & Massa 1992; Legrand-Blain 1995
Cyrtonia (Fam-Carb)	MOROCCO	Brousseiche 1975; Drot 1982; Sartenaer 1985
Dichospira (Fam-Carb)	ALGERIA	Sartenaer 1975; Legrand-Blain 1995
Eobryozia (Fam-Carb)	Almaden SPAIN	Pardo & Garcia-Alcalde et al. 1984
Enatalia (Fam-Carb)	Seville SPAIN	Weyant et al. 1988
Magdalenotrypa (Fam-Carb)	Iberian Peninsula SPAIN	Oliveira et al. 1986
Mesopyca (Fam-Carb)	Cantabrian Mountains SPAIN	Garcia-Alcalde et al. 1985; Garcia-Alcalde & Menendez-Alvarez 1988
Schuchertella (Fam-Carb)	Franco-Belgium Basin FRANCE	Conil et al. 1986
Santostia (Fam-Carb)	Boulonnais FRANCE	Sartenaer 1966a; Brice & Meats 1971; Brice et al. 1976; Brice 1988
Torynietella (Fam-Carb)	BELGIUM	Sartenaer 1966a, 1968b; Vandercammen 1956, 1969
Unipapilla (Fam-Carb)	Bergischen Landes GERMANY	Jux & Krath 1974; Plodowski & Kononova 1994
Drynina (Fam)	Dubnik Anticline POLAND	Balnski 1979, 1995; Biernat 1971
Enchondrospirifer (Fam)	W. Lublin Basin POLAND	Kalis 1969; Matyja & Zbikowska 1974
Hambergella (Fam)	ENGLAND	Reed 1943; Butler 1981
Lapidoarctonichus (Fam)	KAZAKHSTAN	Martynova 1988; Litvinovich et al. 1975; Nasikanova 1975; Sidiachenko 1961
Parapaeobryonichus (Fam)	SIBERIA	Numerous sources
Stenaleobryonichus (Fam)	SOUTH CHINA	Chen Yuan-Ren 1984; Sartenaer 1985; Tan 1987; Hance et al. 1994
Sulcatospira (Fam)	JAPAN	Tachibana 1981
Aulocaria (Gv+Fam)	Iowa USA	Day 1988, 1995
Coelotrochonichus (Fam)	West Virginia USA	Carter & Kammer 1990
Cypriothronichus (Fam)	Idaho USA	Sartenaer & Sandberg 1974
Rapidithronichus (Fam)	NEW MEXICO	Cooper & Dutro 1982
Spinulocosta (Fam)	W. CANADA	Sartenaer 1969, 1975; Raasch 1988
Thomastaria (Fam-Carb)	WEST AUSTRALIA	Veevers 1959; Roberts 1971
Uchospira (Fam)	Queensland AUSTRALIA	Maxwell 1953, 1954; McKellar 1970
Whitfordella (Fam)		

Table 1 Distribution data for 34 Late Devonian 'core' genera used in the Jaccard analysis. Black square = present, white square = absent; source of data displayed.

1996; pers. observ.). Conodonts indicate a Frasnian age (older than Early *hassi* Zone) for this horizon. The presence of *C. arpaensis* and *C. koraghensis* equate with brachiopod zone 6 of Brice (1977) indicative of an early-mid Frasnian age. Sartenaer (1966b) also described *Coeloterorhynchus tabasensis* from the Shishtu Formation in the Kale Sardar area. Brice (1977) indicated *C. tabasensis* was diagnostic of the succeeding Frasnian brachiopod zone 7.

Description of Famennian brachiopod taxa from eastern Iran are limited to *Stenaulacorhynchus cheshmehshirensis* and *Pampoecilorhynchus arianus* from lower Famennian exposures (= zone 9 of Brice 1977) of the Shishtu Formation in the Ozbak-Kuh area (Sartenaer 1968a, b) and poorly preserved *Sentosia* sp. from late Famennian horizons of the Shishtu Formation in the Shotori Range (Legrand-Blain 1998). The presence of *Pampoecilorhynchus arianus* in the Khoshyielagh Formation, northern Iran (Brice *et al.* 1978) and Robot-e-Pai, Afghanistan (Brice 1971) provides a level of regional correlation for lower Famennian sequences (Brice 1977). Sartenaer (1985: Figure 1) indicated *Pampoecilorhynchus* and *Stenaulacorhynchus* are restricted to the lower Famennian *Palmatolepis triangularis* conodont Zone.

Central-SE Iran

Djafari and Brice (1973) documented four Famennian brachiopod zones from the Chahriseh area which broadly equate with zones 9–12 of Brice (1977), though exact correlation is difficult. Conodonts indicate the sequence at Chahriseh ranges from the mid-late Frasnian (*jamieae* and *linguiformis* zones) to early-late Famennian (*triangularis* to early *praesulcata* zones) (Gholamalian 1998). Common brachiopod taxa from this region include species of *Cyrtospirifer*, *Athyris*, *Cyrtiopsis*, *Cleiothyridina*, *Centrorhynchus*, *Megalopterorhynchus*, *Enchondrospirifer*, *Eobrachythyris* and *Toryniferella*. The presence of *Gastrodetoecia iranica* at Chahriseh provides a direct link with lower Famennian strata of the Geirud Formation in the central Alborz (Gaetani 1965).

Late Devonian brachiopods from the Soh area, NW of Chahriseh, have recently been listed by Brice *et al.* (1999). Frasnian taxa include *Ripidiorhynchus barroisi* (Rigaux) (biozone 6) and *R. kotalensis*, an index species of the Upper Frasnian (biozone 8). The Lower Famennian (biozone 9) is characterised by the presence of *Pampoecilorhynchus arianus* Sartenaer. Late Famennian taxa indicative of biozones 11–12 include species of *Araratella*, *Megalopterorhynchus*, *Eobrachythyris* and *Centrorhynchus*.

Brachiopods from the Kerman region reported by Brice (1998, 1999), Bassett and Dastanpour (1998), Legrand-Blain (1998) and Brice *et al.* (1999) are characteristic of brachiopod biozones 6, 8, 9, 10, 11.

Frasnian taxa include the rhynchonellides *Ripidiorhynchus* and *Ladogilina* and the spiriferids *Cyrtospirifer* and *Rigauxia*, whilst Famennian faunas include *Sulcatospirifer*, *Cyrtiorina* and the productids *Sinoproductella* (providing a link with South China) and *Nigerinoplica*.

MATERIALS AND METHODS

Talent *et al.* (1986) and Gratsianova *et al.* (1988) highlighted some of the problems associated with attaining a consistent taxonomic database for palaeobiogeographic studies using Devonian brachiopods. Some of the problems include differences in taxonomic style (lumping vs. splitting

FRASNIAN BRACHIOPOD DATA Jaccard Coefficient (% similarity)	NORTH IRAN (Alborz Mts) (10)	EAST IRAN	CENTRAL/SE IRAN	AFGHANISTAN
EAST IRAN (4)	40			
CENTRAL/SE IRAN (6)	45	67		
AFGHANISTAN (14)	26	29	43	
ARMENIA (10)	25	40	23	20
NW PAKISTAN (11)	24	15	13	9
LIBIYA (18)	17	16	14	10
MOROCCO (12)	10	14	20	13
ALGERIA	0	0	0	0
Almaden SPAIN (9)	12	18	15	10
Seville SPAIN	0	0	0	0
Iberian Peninsula SPAIN	0	0	0	0
Cantabrian Mts. SPAIN	0	0	0	0
Franco-Belgian Basin FRANCE (10)	11	0	14	9
Boulonnais FRANCE (21)	15	14	23	17
BELGIUM (22)	14	8	12	13
Bergischen Land GERMANY (1)	10	0	0	7
Debnik Anticline POLAND (28)	9	7	6	8
W. Lublin Basin POLAND	0	0	0	0
ENGLAND (3)	18	17	29	13
KAZAKHSTAN (40)	14	5	10	10
SIBERIA (40)	11	5	7	10
SOUTH CHINA (18)	12	16	20	14
JAPAN	0	0	0	0
Iowa USA (44)	6	0	4	5
West Virginia USA	0	0	0	0
Idaho USA	0	0	0	0
NEW MEXICO (29)	15	10	13	16
W. CANADA (6)	7	11	9	5
WEST AUSTRALIA (17)	4	5	5	3
Queensland AUSTRALIA (1)	10	0	0	0

Figure 2 Matrix displaying Jaccard Coefficients for Frasnian brachiopod genera from Iran and Afghanistan. Number in brackets after locality represents the total number of genera from that locality. Similarity index of 20% or more shaded.

taxonomic forms), identification of poorly preserved or inadequate material and misidentification of pivotal biostratigraphic forms. These types of taxonomic problems, when combined with imprecision in biostratigraphy and/or comparison of faunas from vastly different biofacies, can compromise the results of any palaeobiogeographic investigation. Talent (1985), Talent *et al.* (1986) and Gratsianova *et al.* (1988) recommended that before drawing any conclusions about the significance of similarities or dissimilarities of faunas relative to crustal blocks or terranes, 3 basic principles should be followed:

1.) Comparison should be made between faunas of

FAMENNIAN BRACHIOPOD DATA Jaccard Coefficient (% similarity)	NORTH IRAN (Alborz Mts) (23)	EAST IRAN	CENTRAL/SE IRAN	AFGHANISTAN
EAST IRAN (3)	4			
CENTRAL/SE IRAN (20)	56	0		
AFGHANISTAN (26)	78	0	48	
ARMENIA (27)	17	0	15	13
NW PAKISTAN	0	0	0	0
LIBIYA (13)	21	0	10	15
MOROCCO (11)	18	8	3	16
ALGERIA (14)	9	0	6	5
Almaden SPAIN	0	0	0	0
Seville SPAIN (9)	11	0	7	6
Iberian Peninsula SPAIN (8)	20	0	22	17
Cantabrian Mts. SPAIN (20)	50	0	29	44
Franco-Belgian Basin FRANCE (13)	21	0	14	15
Boulonnais FRANCE	0	0	0	0
BELGIUM (11)	14	0	15	12
Bergischen Land GERMANY (9)	24	0	21	21
Debnik Anticline POLAND (25)	15	4	15	13
W. Lublin Basin POLAND (16)	19	0	16	17
ENGLAND (13)	9	0	6	5
KAZAKHSTAN (55)	17	2	12	14
SIBERIA (37)	9	3	10	9
SOUTH CHINA (29)	11	3	7	10
JAPAN (23)	13	0	8	11
Iowa USA	0	0	0	0
West Virginia USA (11)	6	0	7	6
Idaho USA (10)	10	0	11	9
NEW MEXICO (28)	9	3	7	8
W. CANADA (31)	23	0	19	21
WEST AUSTRALIA (35)	19	3	10	17
Queensland AUSTRALIA (10)	14	8	11	9

Figure 3 Matrix displaying Jaccard Coefficients for Famennian brachiopod genera from Iran and Afghanistan. Number in brackets after locality represents the total number of genera from that locality. Similarity index of 20% or more shaded.

precisely the same age. As such, biostratigraphic underpinning using conodonts (and other microfossils) is of prime importance – usually requiring re-evaluation of accepted correlations.

In terms of the current investigation, only those Late Devonian faunas with at least some degree of biostratigraphic underpinning (utilising conodonts, ammonoids or palynological data) have been selected as part of the analysis. Frasnian and Famennian brachiopod occurrences were analysed separately (Figures 2, 3) so that only genera confidently assigned a Frasnian or Famennian age were included. In the case where a particular genus may have a stratigraphic range extending, for example, from the Famennian to the early Carboniferous (Table 1), only the confirmed Famennian occurrence is used in the analysis.

2.) Taxonomies of the faunas being compared should be consistent, preferably by the same worker or team. This is essential to avoid “the biogeographic phantoms” that arise from uncritical acceptance of the work of a diverse array of workers with differing taxonomic styles. Reappraisal of taxa described by past workers using current taxonomic methodology is usually required.

Only systematically described faunas are included in the analysis, and the assignment of each core genus used in the analysis has been (as far as is possible) evaluated based on the published illustrations and descriptions. Sources for faunal descriptions from all localities are listed in Table 1. The taxa reported (but not formally described) by Djafarian and Brice (1973) from the Chahriseh region of central Iran have been examined and evaluated by the senior author. The generic database intrinsically displays a high degree of taxonomic integrity, since many of the taxa, especially those from Iran, Afghanistan and parts of Euramerica have been documented by the same workers (mainly Drs D. Brice and P. Sartenaer). As far as possible the most modern, up-to-date, taxonomic works have been utilised for each of the localities.

3) Biogeographic data should be clearly differentiated from biofacies data. There is little point comparing faunas from contrasting sedimentary regimes. Ideally sampling should encompass the entire suite of palaeocommunities from a regional terrane. Failing this, meaningful comparison is best made between faunas from broadly equivalent lithologies.

As far as possible the various Late Devonian faunas have been selected from a broadly similar suite of carbonate dominated biofacies. The majority of faunas come from shallow shelf palaeocommunities broadly equivalent to benthic assemblages 3–5 of Boucot (1975). Since much of the “Cimmerian belt” was positioned along the northern margin of Gondwana within the carbonate development zone, a broadly similar suite of palaeoenvironments is not totally unexpected

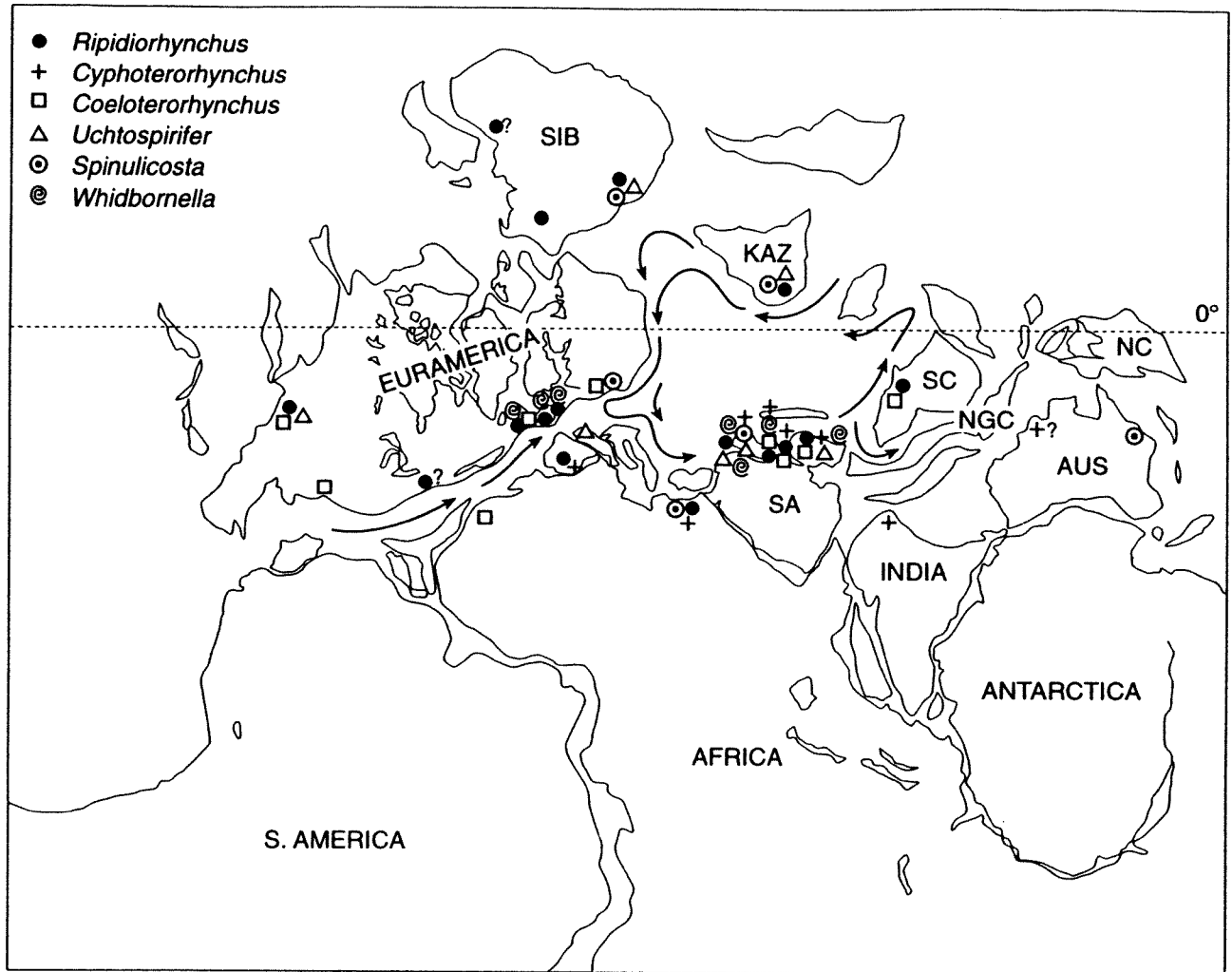


Figure 4 Global distribution of selected 'core' brachiopod genera during the Frasnian. SIB = Siberia, KAZ = Kazakhstan, SA = Saudi Arabia, SC = South China, NC = North China, AUS = Australia, NGC = "North Gondwana Current". Mercator base map modified from Eldridge *et al.* (1997).

(Dickins 1993). The majority of faunas included in the analysis also display comparable levels of preservation (mainly original shell and/or casts or moulds).

Described Frasnian faunas from Iran are characterised by the rhynchonellid genera *Coeloterorhynchus*, *Cyphoterorhynchus* and *Ripidiorhynchus*, the productids *Spinulicosta*, *Thomasaria* and *Whidbornella*, and the spiriferid *Uchtospirifer* (Figures 2, 4; Table 1). Famennian faunas are moderately more diverse and are characterised by taxa such as rhynchonellid genera *Centrorhynchus*, *Megalopterorhynchus*, *Leptocaryorhynchus*, *Pampecilorhynchus*, *Stenaulacorhynchus*, the spiriferids *Dichospirifer*, *Enchondrospirifer*, *Sulcatospirifer*, *Eobrachythyris*, and the productids *Ericiatia*, and *Sentosia* (Figures 3, 5; Table 1).

The 34 "core" Frasnian and Famennian genera identified from the three main brachiopod bearing regions in Iran (Figure 1) were compared to described faunas from 28 separate localities

situated on crustal blocks associated with North Gondwana, Euramerica, Siberia, Kazakhstan, South China and Australia (Table 1, Figures 2–5) using the Jaccard Similarity Coefficient. As noted by Talent and Mawson (1979: 90) discussions "of the deficiencies of similarity/dissimilarity coefficients used in palaeobiogeography have become almost routine". Detailed review of the advantages and disadvantages of the numerous statistical equations used in palaeobiogeographic studies is beyond the scope of this paper. For review and discussion of the various quantitative methods employed in palaeobiogeographic investigations see Raup and Crick (1979), Talent and Mawson (1979), Shi (1993, 1995). The Jaccard Coefficient, one of the more robust binary measures of similarity (Shi 1993), has been chosen as the main statistical measure of similarity for palaeobiogeographical studies associated with IGCP 421. To facilitate future comparison between different invertebrate groups the brachiopod

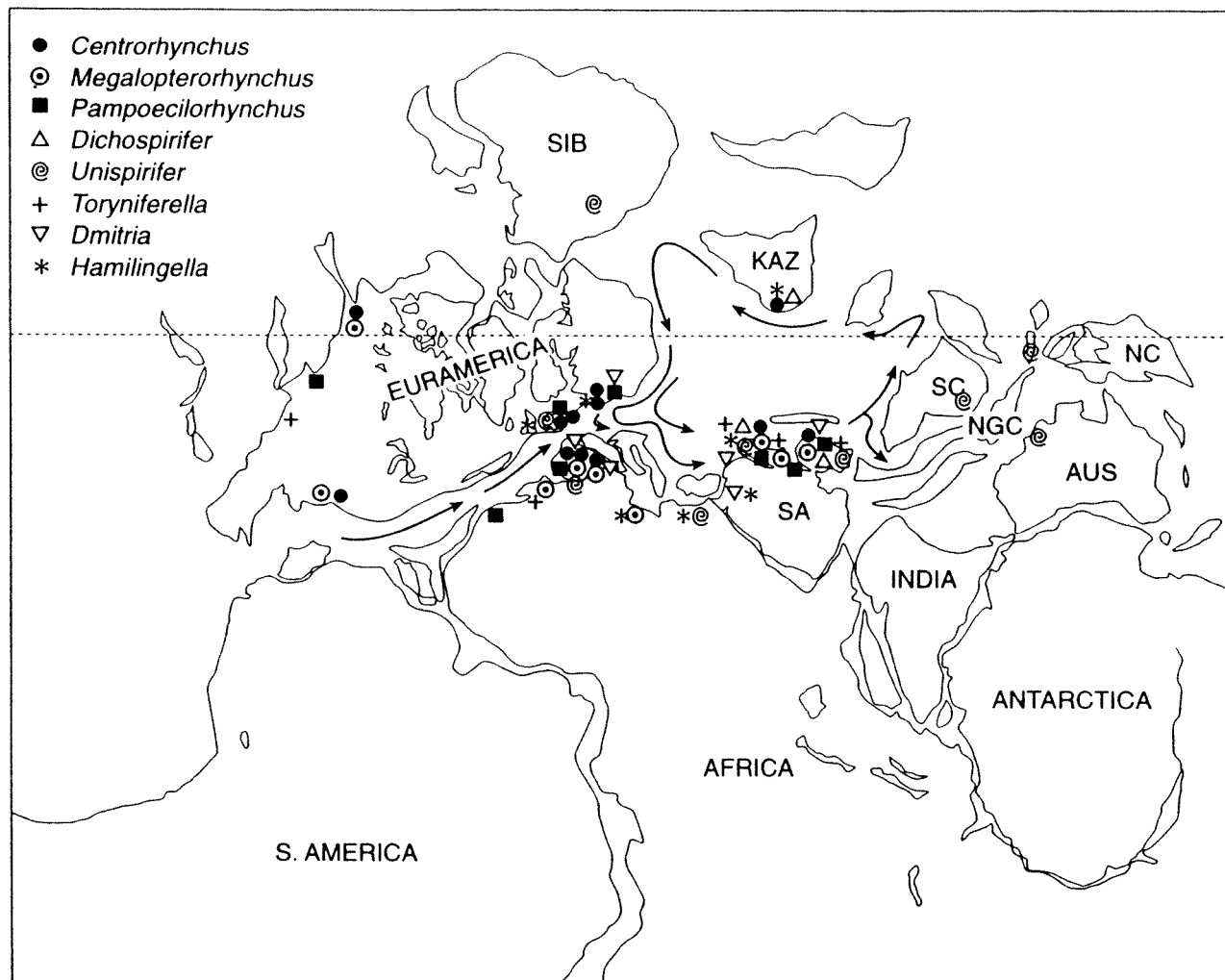


Figure 5 Global distribution of selected 'core' brachiopod genera during the Famennian. For abbreviations see Figure 4. Mercator base map modified from Eldridge *et al.* (1997).

dataset was analysed using the Jaccard Coefficient (JC),

$$JC = c / a + b - c \times 100$$

Where *a* is the number of genera from locality A, *b* is the number of genera from locality B, and *c* is the number of genera shared by localities A and B. The equation is multiplied by 100 to provide a percentage similarity. Future analyses will focus on species comparisons (once faunas are adequately described) using binary and probabilistic methods. Cosmopolitan taxa, such as *Cyrtospirifer*, *Productella*, *Schizophoria* and many of the Frasnian atrypids with little or no biogeographic signature were omitted from the analysis.

RESULTS

Frasnian brachiopod indices (Figure 2)

Alborz Range

During the Frasnian, brachiopod faunas from the

Alborz Mountains display greatest similarity with those from East Iran (40%) and central-southeast Iran (45%) (Figure 2). The degree of similarity is not unexpected given that a widespread transgressive episode at the beginning of the Frasnian resulted in the development of an extensive shallow water carbonate platform that covered much of central Iran from the northeast Alborz to the Faraghan Mountains, south of Kerman (Dastanpour 1996: figure 6). Despite the fact that each of the Iranian localities has a relatively small total number of genera for analysis (Figure 2) the Jaccard Coefficient still reflects a moderate level of generic overlap. Indeed, each of the localities has a significant number of species in common (Gaetani 1965; Djafarian and Brice 1973; Brice *et al.* 1978). Moderate levels of similarity occur with regions known to have been associated with the northern margin of Gondwana, including Afghanistan (26%), Armenia (25%), and NW Pakistan (24%), based mainly on the co-occurrence of *Coeloterorhynchus*, *Cyphoterorhynchus* and the more cosmopolitan *Spinatrypina*

(Table 1). Though the levels of similarity are relatively low, there is also some evidence of links with Euramerica, including England (18%), Boulonnais, France (15%), Belgium (14%), and New Mexico (15%). Links with Kazakhstan (14%) are also recorded.

East Iran

Taxa from East Iran show greatest similarity with central/SE Iran (67%), northern Iran (40%), Afghanistan (29%) and Armenia (40%). There is also some weak links with other regions from north Gondwana, including NW Pakistan (15%) Libya (16%), Morocco (14%) and southern Spain (18%). Links with Euramerica include Boulonnais, France (14%), England (17%), New Mexico (10%) and western Canada (11%).

Central-southeast Iran

Apart from moderate similarity with the Alborz Range and east Iran, the greatest similarity for central/SE Iran occurs with Afghanistan (43%), Armenia (23%), Morocco (20%), and with the Euramerican localities Boulonnais, France (23%), England (29%), South China (20%), New Mexico (13%) and western Canada (11%). The similarity index for England is artificially inflated because there are two shared genera from a total of only 6 genera. Description of diverse faunas from the Late Devonian of Kerman (Brice, 1999) not included in the present analysis will undoubtedly decrease this index. Unlike the faunas from the Alborz Range and east Iran, the faunas from central/SE Iran show a higher level of similarity with South China (20%), but this is mainly based on the shared occurrence of the widely distributed taxa *Ripidiorhynchus*, *Aulacella* and *Spinatrypina*.

Famennian brachiopod indices (Figure 3)

Alborz Range

Famennian faunas from the Alborz Range display significant levels of similarity with central-southeast Iran (56%), but only one genus (*Pampoecilorhynchus*) is shared with East Iran. This is mainly due to the fact that Famennian faunas from East Iran, though not diverse, have not been formally described. The presence of *Sentosia* (Legrand-Blain 1998) and other undescribed genera from sections in the Shotori Range (Brock *et al.* in prep.) indicates that future investigations will probably boost the degree of similarity between these regions. Within Gondwana, the Alborz faunas display highest similarity with Cantabrian Mountains (50%), Libya (21%), Bergischen Landes (24%), and Iberia (20%). Again, though the biogeographic signal is weak, there are some links with Euramerica, especially with the Franco-Belgium Basin (21%) and Western Canada (23%). Famennian taxa from the Alborz

Range also show linkages to regions such as Poland (up to 19%), Japan (13%) Idaho (10%) and Australia (up to 19%).

East Iran

Brachiopod diversity is relatively low in Famennian sequences from East Iran, with only *Pampoecilorhynchus*, *Stenaulacorhynchus*, and *Sentosia* formally described (Sartenaer 1966b, 1968a, b; Legrand-Blain 1998). *Stenaulacorhynchus* is only known from East Iran (Sartenaer 1985) and Seville, Spain (Weyant *et al.* 1988). Other cosmopolitan taxa such as *Cyrtospirifer*, "*Productella*", and *Cyrtiopsis* have been reported from East Iran (see Ruttner *et al.* 1991), but these require formal systematic treatment (Brock *et al.* in prep.). The lack of formal taxonomy from this region precludes meaningful comparison with other regions.

Central-southeast Iran

Strongest links are with Afghanistan (48%), the Cantabrian Mountains (29%), and Iberian Peninsula (22%) along the periphery of Gondwana. Compared with the Alborz faunas, faunal links between central/SE Iran and Euramerica are not as strong. The highest levels of similarity are with Poland (16%), Belgium (15%) and western Canada (19%).

DISCUSSION

The Late Devonian is acknowledged as a time interval represented by high levels of faunal and floral cosmopolitanism, in both the marine and terrestrial realms (Boucot *et al.* 1969; Oliver 1977; Talent 1984; Young 1987; Boucot 1988). The relatively low levels of faunal and floral provinciality during the Late Devonian is generally considered to be the result of continental or terrane amalgamation, favourable oceanic circulation patterns, and warm climatic conditions (Dickins 1993) that permitted interchange of once isolated faunas. On a global scale, the distribution of Late Devonian brachiopods (at least at generic level) tends to fit this pattern of weak provinciality (Boucot 1988). However, comparison of Frasnian (Figure 2) and Famennian (Figure 3) data indicates that Frasnian brachiopods from Iran appear to be more provincial than Famennian faunas. This is in accord with more detailed comparisons, such as those reported by Talent *et al.* (1986: 106), for Late Devonian brachiopod species from Western Australia, central and southwestern Kazakhstan and South China which reveals such low levels of species similarity, that by modern standards, these regions would be placed in separate zoogeographic provinces and regions. Talent and Mawson (1979: 4) also documented strong "provincial heterogeneity" of Frasnian brachiopod faunas from Pakistan, Siberia, Kazakhstan, Vietnam and

Afghanistan consistent with reproductive isolation associated with the existence of oceanic waters between the various blocks. Soja (1992) has also recorded high levels of endemism in Famennian faunas from eastern North America. These records of unusually high levels of provinciality for the Late Devonian, imply significant geographic separation and isolation of faunas, at least for these regions (Figures 4 and 5). Whilst it is true that Late Devonian faunas are not as markedly provincial as Early Devonian faunas, it is clear that regional differences were apparent during the Late Devonian and the suggestion that *all* Frasnian-Famennian brachiopod faunas were uniformly cosmopolitan is a gross oversimplification.

In terms of Iranian faunas, previous authors such as Gaetani (1965, 1968), Brice (1971) and Brice *et al.* (1973; 1999) have commented on the remarkable similarity between Late Devonian brachiopod faunas from Iran and synchronous faunas from Afghanistan, Armenia and Pakistan, with Brice *et al.* (1978) suggesting the probable existence of an Irano-Afghan platform during this interval. The quantitative data presented herein strongly supports these conclusions (Figures 2, 3). Frasnian and Famennian genera from Iran display strongest links with faunas on terranes situated at a similar latitude along the northern margin of Gondwana (Figures 4, 5).

Though the palaeobiogeographic signal is not as strong, there is also clear evidence of some links with Euramerica (Figures 2-5; Table 1). Within Euramerica, Brice *et al.* (1994) documented faunal links between Frasnian faunas from Boulonnais, North France and eastern North America. Detailed evaluation of biostratigraphy and location of first occurrences of corals, brachiopods, crinoids and ostracods from these areas led Brice *et al.* (1994) to suggest an easterly migration route along the southern margin of Euramerica from eastern North America to Boulonnais. However, Oczlon (1990: figure 1) used palaeocurrent evidence to suggest that the southern margin of Euramerica was probably dominated by strong westerly directed "South Equatorial Current" during the Middle Devonian that swept down to North Africa to eventually form the easterly directed "North Gondwana Current" along the southern margin of Prototethys. Heckel and Witzke (1979) suggested similar current directions in their palaeoclimatic reconstructions for the Devonian. If Oczlon's (1990) interpretation is accepted, it seems more likely that the larvae of North American taxa would be more likely to have dispersed along the northern margin of Gondwana following the dominant current direction (Figures 4, 5). The presence of congeneric (in some cases conspecific) brachiopods in Frasnian-Famennian sequences in eastern Euramerica (western Europe) and Northern Gondwana is

strongly suggestive that, at least for some taxa, dispersal was occurring between these regions.

If the same range of biological (short larval life span, substrate selection) and physical (temperature, substrate, salinity) factors known to limit the distribution of modern articulate brachiopods (Richardson 1997) also prevailed during the Palaeozoic, then this distribution pattern can only be adequately explained if the shallow marine shelves of Euramerica and North Gondwana were close enough to allow larval dispersal and some degree of faunal mixing (Brice *et al.* 1994; 1999). Support for this interpretation is provided by Galle *et al.* (1995: 233) who presented detailed biogeographic data on Middle Devonian (Eifelian-Givetian) brachiopods and corals from the Czech Republic that indicated the northern Gondwanan margin "approached closely to southern Laurussia" (=Euramerica) during the Devonian.

The suggestion that the Iran-Afghan microcontinent may have been situated midway between Euramerica and Gondwana in a 2000 km + wide ocean and acted as a staging post for trans-oceanic dispersal of brachiopods and other marine invertebrates cannot be totally ruled out, especially if the subtropical latitude for the entire region is accepted. Jaccard Coefficients presented here show that Late Devonian brachiopods from Iran and Afghanistan had much stronger ties to Gondwana than to Euramerica, though this may simply reflect prevailing oceanic current patterns.

Talent and Mawson (1979: figure 5) have presented results of a Jaccard analysis of Frasnian brachiopod faunas from Pakistan. Though no direct comparison was made with Iranian brachiopod faunas, links are recorded with western (29%) and eastern (17%) Afghanistan. Comparison of Frasnian faunas from NW Pakistan and Afghanistan presented herein record a Jaccard Coefficient of 9% (Figure 2), though this may be due to an increase in knowledge of faunas from both regions.

Young (1987, 1990, 1995, 1998) provided comprehensive palaeobiogeographical analyses of global mid Palaeozoic vertebrate faunas and concluded that there was gradual convergence between Euramerica and Gondwana throughout the Devonian leading to eventual "collision and exchange of continental floras and faunas at or near the Frasnian-Famennian boundary" (Young 1987: 299). However, Talent (1984) has pointed out that if such a connection took place at the Frasnian-Famennian boundary, the resultant isolation of shelf faunas either side of the collision zone should have generated increased provinciality in Famennian and early Carboniferous marine faunas. In terms of the brachiopod data presented herein there is no evidence of such provinciality. Indeed the presence of taxa such as *Centrorhynchus*, *Megalopterorhynchus*

and *Toryniferella* in eastern North America and Northern Gondwana (Figure 5) during the Famennian indicates that some sort of latitudinal seaway must have been open between the two supercontinents. Becker (1998: 5) has also presented evidence suggesting migration of Late Devonian ammonoids took place along the northern margin of Gondwana via the "Rhenohercynian" seaway. It seems more likely, given the increase in provincialism of marine faunas globally after the Visean, that the collision of Euramerica and North Africa coincided with the Variscan orogeny (Oczlon 1992), sometime during the Visean (Ross 1979; Talent 1984).

A few interesting examples of disjunct distribution are apparent in the Famennian data presented (Figures 3, 5; Table 1), possibly reflecting rising cosmopolitanism. The genus *Sulcatospirifer* originally described from the lower Famennian of the Mount Morgan district, Queensland is only otherwise documented from the Chahriseh area of central Iran (Brice *et al.* 1999). Similarly, the productoid *Sentosia* recorded from the Shotori Range, eastern Iran (Legrand-Blain 1998) is also known from widely separated regions such as Western Australia and Queensland, New Mexico, Siberia, Kazakhstan and South China (Table 1). Legrand-Blain (1998) notes the presence of *Sinoproductella* and *Nigerinoplica* from the Famennian of the Kerman region providing direct links with South China. These taxa were not included in the current analysis due to a lack of formal description at the time of analysis.

CONCLUSIONS

The moderate-high levels of similarity between brachiopod taxa from the three Iranian localities, Afghanistan and terranes traditionally regarded as being part of Gondwana, strongly indicate that the Iranian microcontinent was part of the "Cimmerian belt" of terranes stretching along the northern rim of Gondwana during the Late Devonian. Frasnian brachiopod faunas from Iran tend to be more provincial than Famennian faunas. Though details of the chronology of pre-Hercynian plate movements are still controversial, the identification of weak palaeobiogeographic links between elements of Euramerica and northern Gondwana (Figures 2–5; Table 1) supports previous faunal, lithologic, and tectonic evidence indicating a relatively narrow oceanic vestige separated these two supercontinents (Kent *et al.* 1984; Young 1987; Zeigler 1988; Morzadec *et al.* 1988; Blicek *et al.* 1988; Witzke and Heckel 1988; Galle *et al.* 1995). This interpretation contrasts significantly with previous reconstructions based on palaeomagnetic data advocating an extensive (up to 4500 km wide) Prototethys Ocean separating Euramerica and

northern Gondwana during the Late Devonian (e.g. Morel and Irving 1978; Van der Voo 1988; Bachtadse *et al.* 1995; Metcalfe 1996, figure 13).

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REFERENCES

- Abramian, M.S. (1957). Brachiopody verkhnefamenskikh i etrenskikh otlozhenii jugo-zapadnoi Armenii. *Izdatelstvo AN Armianskoi SSR*, Erevan: 1–142.
- Abramian, M.S. (1974). Brachiopods of the Devonian. In *Atlas Iskopaemoi Fauny*: 48–64, Armianskoi SSR, Erevan.
- Bachtadse, V., Torsvik, T.H., Tait, J.A. and Soffel, H.C. (1995). Paleomagnetic constraints on the paleogeographic evolution of Europe during the Paleozoic. In Dallmeyer *et al.* (eds), *Pre-Permian geology of central and eastern Europe*: 567–578.
- Balinski, A. (1979). Brachiopods and conodonts from the Frasnian of the Debnik Anticline, Southern Poland. *Palaeontologia Polonica* 39: 3–95.
- Balinski, A. (1995). Brachiopods and conodonts from the Famennian of the Debnik Anticline, Southern Poland. *Palaeontologia Polonica* 54: 3–88.
- Bassett, M. and Dastanpour, M. (1998). Frasnian-Famennian brachiopod faunas from south-east Iran: documentation of major extinction, re-diversification and sea level changes. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*: 4.
- Becker, T. (1998). Biogeographic studies of Late Devonian ammonoid faunas. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*: 5.
- Belov, A.A. (1986). The Paleozoic of the Caucasus and the problem of Paleo-Tethys. *Geotectonics* 20: 230–236.
- Berberian, M. and King, G.C.P. (1981). Towards a paleogeography and tectonic evolution of Iran. *Canadian Journal of Earth Science* 18: 210–265.
- Biernat, G. (1971). The brachiopods from the Kadzielnia Limestone (Frasnian) of the Holy Cross Mts. *Acta Geologica Polonica* 21: 137–163.
- Blicek, A., Brice, D., Feist, R., Guillot, F., Majeste-Menjoulas, C. and Meilliez, F. (1988). The Devonian of France and Belgium. In McMillan, N.J., Embry, A.F. and Glass, D.J. (eds), *Devonian of the World*,

- Canadian Society of Petroleum Geologists, Memoir* **14**(1): 359–400.
- Boucot, A.J. (1975). *Evolution and Extinction rate controls*: 1–427, Elsevier, Amsterdam.
- Boucot, A.J. (1988). Devonian biogeography: an update. In McMillan, N.J., Embry, A.F. and Glass, D.J. (eds), *Devonian of the World, Canadian Society of Petroleum Geologists, Memoir* **14**(3): 211–227.
- Boucot, A.J., Johnson, J.G. and Talent, J.A. (1969). Early Devonian brachiopod zoogeography. *Geological Society of America, Special Paper* **119**: 1–113.
- Brice, D. (1971). Etude paléontologie et stratigraphie du Dévonien d'Afghanistan. *Notes et Mémoires sur le Moyen-Orient* **11**: 1–364.
- Brice, D. (1977). Biostratigraphie du Dévonien d'Afghanistan. *Mémoires hors série Société géologique de France* **8**: 267–276.
- Brice, D. (1998). Rhynchonellid and spiriferid brachiopod faunas from Silurian and Devonian of central and east-central Iran. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*: 5–6.
- Brice, D. (1999). New Upper Devonian rhynchonellid and spiriferid brachiopod taxa from eastern Iran (Kerman Province) and central Iran (Soh region). *Annales de la Société géologique du Nord (2nd série)* **7**(1–2): 71–78.
- Brice, D., Bultynck, P.L., Colbeaux, J.P., Lethiers, F., Mistiaen, B., Rohart, J.C. and Bigey, F. (1976). Une nouvelle coupe dans le Dévonien de Ferques (Boulonnais, France). *Annales de la Société géologique du Nord* **96**: 135–155.
- Brice, D. and Farsan, M. (1976). Brachiopods from the Upper Devonian of Robat-e-Pai (Afghanistan). Discovery of the genera *Ladogia* Nalivkin, 1941 and *Eoparaphorhynchus* Sartenaer, 1961 (Rhynchonellida). *Annales de la Société géologique du Nord* **96**: 225–232.
- Brice, D., Jenny, J., Stampfli, G. and Bigey, F. (1978). Le Dévonien de l'Elbourz oriental: Stratigraphie, paléontologie (brachiopodes et bryozoaires), paléogéographie. *Rivista Italiana di Paleontologia e Stratigrafia* **84**: 1–56.
- Brice, D., Lafuste, J., Lapparent, A.F. de., Pillet, J. and Yassini, I. (1973). Etude de deux gisements paléozoïques (Silurien et Dévonien) de l'Elbourz oriental (Iran). *Annales de la Société géologique du Nord* **93**: 177–218.
- Brice, D. and Meats, P. (1971). Le genre *Ripidiorhynchus* Sartenaer 1966 (Rhynchonellida–Brachiopodes) dans le Dévonien de Ferques (Boulonnais-France). *Annales de la Société géologique du Nord* **91**: 215–228.
- Brice, D., Milhau, B. and Mistiaen, B. (1994). Affinités nord-américaines de taxons Dévoniens (Givétien-Frasnien) du Boulonnais, nord de la France. Migrations et diachronismes. *Bulletins de la Société géologique de France* **165**: 291–306.
- Brice, D., Mistiaen, B. and Rohart, J.-C. (1999). New data on distribution of brachiopods, rugose corals and stromatoporoids in Upper Devonian of central and eastern Iran. Palaeobiogeographical implications. *Annales de la Société géologique du Nord (2nd série)* **7**(1–2): 21–32.
- Brock, G.A., Yazdi, M. and Kebriaei, M. (in prep). Late Devonian brachiopods from eastern and central Iran.
- Brousmiche, C. (1975). Etude de quelques Productida (Brachiopoda) du Maroc présaharien. *Annales de Paléontologie, Invertébrés (Paris)* **61**: 119–163.
- Butler, D.E. (1981). Marine Faunas from concealed Devonian rocks of southern England and their reflection of the Frasnian Transgression. *Geological Magazine* **118**: 679–697.
- Carter, J.L. and Kammer, T.W. (1990). Late Devonian and Early Carboniferous brachiopoda (Brachiopoda, Articulata) from the Price Formation of West Virginia and adjacent areas of Pennsylvania and Maryland. *Carnegie Museum, Annals* **59**: 77–103.
- Chen, Yuan-Ren (1984). Brachiopods from the Upper Devonian Tuqiaozi Member of the Longmenshan Area (Sichuan, China). *Palaeontographica Abteilung A* **184**: 95–166.
- Conil, R., Dreesen, R., Lentz, M.-A., Lys, M. and Plodowski, G. (1986). The Devonian-Carboniferous transition in the Franco-Belgian Basin with reference to foraminifera and brachiopods. *Société géologique de Belgique, Annales (Liège)* **109**: 19–26.
- Cooper, G.A. and Dutro, J.T. (1982). Devonian brachiopods of New Mexico. *Bulletin of American Paleontological Association* **82–83**: 1–215.
- Dastanpour, M. (1996). The Devonian System in Iran: a review. *Geological Magazine*, **133**: 159–170.
- Day, J.E. (1988). The brachiopod succession of the Late Givetian-Frasnian of Iowa. In McMillan, N.J., Embry, A.F. and Glass, D.J. (eds), *Devonian of the World, Canadian Society of Petroleum Geologists, Memoir* **14**(3): 303–325.
- Day, J.E. (1995). Biostratigraphic and taxonomic significance of the Upper Devonian (Late Frasnian) brachiopod fauna from new exposures of the Amana Beds of eastern Iowa. *Geological Society of America, Abstracts with programs* **27**: 46.
- Dickins, J.M. (1993). Climate of the Late Devonian to Triassic. *Palaeogeography, Palaeoclimatology, Palaeoecology* **100**: 89–94.
- Djafarian, M. and Brice, D. (1973). Biostratigraphie des brachiopodes dans le Famennien supérieur de la région d'Ispahan (Iran Central). Mise en évidence de la zone d'Etroeungt. *Compte Rendus Hebdomadaires de Sciences de l'Académie des Sciences, Paris* **276D**: 2125–2128.
- Drot, J. (1982). Brachiopods near the Givetian-Frasnian boundary in Tafilalet and Ma'Der (southern Morocco). In Sartenaer, P. (ed.), *Papers on the Frasnian/Givetian Boundary*. International Union of Geological Sciences (IUGS), Subcommittee on Devonian Stratigraphy, Publication: 70–84.
- Dürkoop, A. (1970). Brachiopoden aus dem Silur, Devon und Karbon in Afghanistan. *Palaeontographica Abteilung A* **134**: 153–225.
- Eldridge, J., Walsh, D. and Scotese, C.R. (1997). *Plate Tracker for Windows* 95 version 1. CD-Rom.
- Farsan, N.M. (1986). Faunenwandel oder Faunenkrise? Faunistische Untersuchung der Grenze Frasnium/Famennium im mittleren Südasien. *Newsletter on Stratigraphy* **16**: 113–131.
- Gaetani, M. (1965). The geology of the Upper Djadjerud and Lar Valleys (North Iran) II. *Palaeontology*.

- Brachiopods and molluscs from Geirud Formation, Member A (Upper Devonian and Tournaisian). *Rivista Italiana di Paleontologia e Stratigrafia* **71**: 679–770.
- Gaetani, M. (1968). Devonian of northern and eastern Iran, northern Afghanistan and northern Pakistan. *International Symposium on the Devonian System, Alberta Society of Petroleum Geologists* **1**: 519–527.
- Galle, A., Hladil, J. and Isaacson, P.E. (1995). Middle Devonian biogeography of closing south Laurussia-North Gondwana Variscides: examples from the Bohemian Massif (Czech Republic), with emphasis on Horni Benešov. *Palaios* **10**: 221–239.
- García-Alcalde, J.L., Menéndez-Alvarez, J.R., García-López, S. and Soto, F. (1985). El Devónico superior y el Carbonífero inferior del Sinclinal de Berberino (Pola de Gordon, León, de Espana). *International Congress on Carboniferous stratigraphy and geology, Madrid, Sept, 12–17, 1983. Compte Rendus* **10**: 375–386.
- García-Alcalde, J.L. and Menéndez-Alvarez, J.R. (1988). The Devonian-Carboniferous boundary in the Asturo-Leonese Domain (Cantabrian Mountains, NW Spain). *Courier Forschungsinstitut Senckenberg* **100**: 21–37.
- Ghavidel-Syooki, M. (1994). Biostratigraphy and paleobiogeography of some Paleozoic rocks at Zagros and Alborz Mountains. *Treatise on the Geology of Iran* **18**: 1–168.
- Ghavidel-Syooki, M. (1998). Palynostratigraphy and palaeobiogeography of Padeha and Khoshyeilagh Formation in Kuh-e-ozom at northeastern Alborz Range (Kopet Dag region) of Iran. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*, 12.
- Gholamalian, H. (1998). Biostratigraphy of the Late Devonian sediments based on conodont species in the Chahriseh area, north-east of Esfahan. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*, 13.
- Gratsianova, R.T., Talent, J.A. and Yolkin, E.A. (1988). Devonian brachiopod zonal schemes, provinciality and crustal blocks in the Asia-Australia hemisphere. In McMillan, N.J., Embry, A.F. and Glass, D.J. (eds), *Devonian of the World, Canadian Society of Petroleum Geologists, Memoir* **14**: 295–301.
- Hamdi, B. and Janvier, P. (1981). Some conodonts and fish remains from Lower Devonian (lower part of the Khoshyeylaq (sic) Formation) northeast of Shahrud, Iran. *Geological Survey of Iran, Report* **49**: 195–210.
- Hance, L., Muechez, P., Coen, M., Fang, X-S, Groessens, E., Hou, H., Poty, E., Steemans, P., Streel, M., Tan, Z., Tourneur, F., Steenwinkel, M. van. and Xu, S-C. (1994). Biostratigraphy and sequence stratigraphy at the Devonian-Carboniferous transition in southern China (Hunan Province). Comparison with southern Belgium. *Société géologique de Belgique, Annales (Liège)* **116**: 359–378.
- Hamedi, M.A., Wright, A.J., Aldridge, R.J., Boucot, A.J., Brunton, D.L., Chatterton, B.D.E., Jones, P., Nicoll, R.S., Rickards, R.B. and Ross, J.P.R. (1997). Cambrian to Silurian of East-Central Iran: new biostratigraphic and biogeographic data. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1997(7)**: 412–424.
- Heckel, P.H. and Witzke, B.J. (1979). Devonian world palaeogeography determined from distribution of carbonates and related lithic palaeoclimatic indicators. In House, M.R., Scrutton, C.T. and Bassett, M.G. (eds), *The Devonian System, Special Papers in Palaeontology* **23**: 99–123.
- Husseini, M.I. (1991). Tectonic and depositional model of the Arabian and adjoining plates during the Silurian-Devonian. *American Association of Petroleum Geologists, Bulletin* **75**: 108–120.
- Jafarian [Djafarian], M.A. (1998). Biostratigraphical correlation of Late Devonian Brachiopoda in Iran. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*: 16.
- Jux, U. and Krath, J. (1974). Die fauna aus dem mittleren Oberdevon (Nehden-Stufe) des Südwestlichen Bergischen Landes (Rheinisches Schiefergebirge). *Palaeontographica Abteilung A* **147**: 115–168.
- Kalis, J. (1969). Wstepna stratygrafia serii górnodewonskiej z niektórych wiercen zachodniej czesci niecki lubelskiej. *Acta Geologica Polonica* **19**: 805–821.
- Kent, D.V., Dia, O. and Sougy, J.M.A. (1984). Paleomagnetism of Lower-Middle Devonian and Upper Proterozoic-Cambrian (?) rocks from Mejeira (Mauritania, West Africa). In Van der Voo, R., Scotese, C. and Bonhommet, N. (eds), *Plate reconstruction from Paleozoic Paleomagnetism (Geodynamics 12)*: 99–115, American Geophysical Union, Washington D.C.
- Legrand-Blain, M. (1995). Les brachiopodes Productida au passage Dévonien-Carbonifère sur le craton Nord-Saharien. In Arbey, F. and Lorenz, J. (eds), *Basins sédimentaires africains. Géodynamique et géologie séquentielle Biominéralisation, Sédimentation et organismes*: 425–444, Paris.
- Legrand-Blain, M. (1998). Famennian (Strunian) Productida (brachiopods) from central and east-central Iran. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*: 18–20.
- Lensch, G., Schmidt, K. and Davoudzadeh, M. (1984). Introduction to the Geology of Iran. *Neues Jahrbuch für Geologie Paläontologie, Abhandlungen* **168**: 155–164.
- Litvinovich, N.V., Aksenova, G.G. and Martynova, M.V. (1975). Brachiopody. In Fauna pograničnykh otloženii devona i karbona Tsentral'nogo Kazakhstana, *Materialy po Geologii Tsentral'nogo Kazakhstan (Moscow)* **18**: 50–96.
- Mambetov, A.B. and Rzhonsnitskaya, M.A. (1985). Devonian of the South Transcaucasus Zonal subdivision, boundaries of series and stages, correlation. *Courier Forschungsinstitut Senckenberg* **75**: 135–156.
- Martynova, M.V. (1988). Novye brachiopody iz devona Tsentral'nogo Kazakhstana. *Paleontologicheskii Zhurnal* **1988(3)**: 39–44.
- Matyja, H. and Zbikowski, B. (1974). Stratygrafia dewonu gornego profilu wiercenia Minkowice 1 (basen lubelski). *Acta Geologica Polonica* **24**: 663–694.
- Maxwell, W.G.H. (1953). Upper Palaeozoic formations in the Mt. Morgan District – Stratigraphy and structure. *University of Queensland, Department of Geology, Papers* **4(4)**: 1–14.
- Maxwell, W.G.H. (1954). Upper Palaeozoic formations in

- the Mt. Morgan District – Faunas. *University of Queensland, Department of Geology, Papers* 4(5): 1–69
- McKellar, R.G. (1970). The Devonian productoid brachiopod faunas of Queensland. *Geological Survey of Queensland, Publications* 342: 1–40.
- Mergl, M. and Massa, D. (1992). Devonian and Lower Carboniferous brachiopods and bivalves from western Libya. *Biostratigraphie du Paléozoïque* 12: 1–115.
- Metcalfe, I. (1996). Gondwanaland dispersion, Asian accretion and evolution of eastern Tethys. *Australian Journal of Earth Sciences* 43: 605–623.
- Morante, R.J. (1989). *Late Middle and Early Upper Devonian (Givetian-Frasnian) brachiopods from the Shogran Formation, Kuragh Spur, Chitral, Northwest Pakistan*. Unpublished MSc. Thesis, Macquarie University, Sydney.
- Morel, P. and Irving, E. (1978). Tentative paleocontinent maps for the Early Phanerozoic and Proterozoic. *Journal of Geology* 86: 535–561.
- Morzadec, P., Paris, F., Plusquellec, Y., Racheboeuf, P. and Weyant, M. (1988). Devonian stratigraphy and palaeogeography of the Armorican massif (western France). In McMillan, N.J., Embry, A.F. and Glass, D.J. (eds), *Devonian of the World, Canadian Society of Petroleum Geologists, Memoir* 14: 401–420.
- Nasikanova, O.N. (1975). Biostratigraphical foundation of the Devonian-Carboniferous Boundary in Kazakhstan. *International Congress on Carboniferous Stratigraphy and Geology, Moscow, Abstracts* 8: 194–195.
- Oczlon, M.S. (1990). Ocean currents and unconformities: The North Gondwana Middle Devonian. *Geology* 18: 509–512.
- Oczlon, M.S. (1992). Gondwana and Laurussia before and during the Variscan orogeny in Europe and related areas. *Heidelberger Geowissenschaftliche Abhandlungen* 53: 1–56.
- Oliver, W.A. (1977). Biogeography of Late Silurian and Devonian rugose corals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 25: 85–135.
- Oliveria, J.T., Garcia-Alcalde, J.L., Linan, E. and Truyols, J. (1986). The Famennian of the Iberian Peninsula. *Société géologique de Belgique, Annales (Liège)* 109: 159–174.
- Pardo, M.V. and Garcia-Alcalde, J.L. (1984). Biostratigrafía del Devonico de la region de Almaden (Ciudad Real, Espana). *Trabajos de Geología* 14: 79–120.
- Plodowski, G. and Kononova, L.I. (1994). *Dichospirifer Brice, 1970, eine Leit-Gattung im höchsten Oberdevon.. Courier Forschungsinstitut Senckenberg* 169: 17–27.
- Raasch, G.O. (1988). Famennian faunal zones in Western Canada. In McMillan, N.J., Embry, A.F. and Glass, D.J. (eds), *Devonian of the World, Canadian Society of Petroleum Geologists, Memoir* 14: 619–632.
- Raup, D.M. and Crick, R.E. (1979). Measurement of faunal similarity on paleontology. *Journal of Paleontology* 53: 1213–1227.
- Reed, F.R.C. (1943). Notes on certain Upper Devonian brachiopods figured by Whidborne, Part 1. *Geological Magazine* 80: 69–78; 95–106; 132–138.
- Richardson, J. (1997). Biogeography of articulated brachiopods. In Kaesler, R.L. (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised)* 1: 463–472. Geological Society of America and University of Kansas.
- Roberts, J. (1971). Devonian and Carboniferous brachiopods from the Bonaparte Gulf Basin, northwestern Australia. *Bureau of Mineral Resources Bulletin of Australian Geology and Geophysics* 122: 1–319.
- Ross, C.A. (1979). Carboniferous. In Teichert *et al.* (eds), *Treatise on Invertebrate Paleontology, Part A, Introduction*: 254–290. Geological Society of America, Boulder and University of Kansas, Lawrence.
- Ruttner, A., Nabavi, M.H. and Hajian, J. (1991). Geology of the Shirgesht Area (Tabas area, East Iran). *Geological Survey of Iran, Report* 4: 1–133.
- Sartenaer, P. (1964). Rynchonelloidea de Shogran et Kuragh (Chitral). In *Italian Expeditions to the Karakorum (K2) and Hindu Kush, Scientific Reports* 4: 51–62.
- Sartenaer, P. (1966a). *Ripidiorhynchus*, nouveau genre de brachiopode Rhynchonellide du Frasnien. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 42: 1–15.
- Sartenaer, P. (1966b). Frasnian Rhynchonellida from the Ozbak-Kuh and Tabas regions (East Iran). *Geological Survey of Iran, Report* 6: 25–53.
- Sartenaer, P. (1968a). *Stenaulacorhynchus*, nouveau genre de brachiopode Rhynchonellide de Famennien inférieur de l'Iran Oriental. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 44(30): 1–14.
- Sartenaer, P. (1968b). De l'importance stratigraphique des rhynchonelles famenniennes situées sous la zone a *Ptychomaletoechia omaliusi* zone; 6, *Pampocilorhynchus* n. gen. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 44(43): 1–36.
- Sartenaer, P. (1969). Late Upper Devonian (Famennian) rhynchonellid brachiopods from Western Canada. *Geological Survey of Canada, Bulletin* 169: 1–269.
- Sartenaer, P. (1970). Nouveaux genres rhynchonellidés (Brachiopodes) du Paléozoïque. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 46(32): 1–32.
- Sartenaer, P. (1975). Rhynchonellides du Famennien supérieur du Sahara occidental (Algérie). *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 51(5): 1–12.
- Sartenaer, P. (1985). The stratigraphic significance of rhynchonellid genera at the Frasnian-Famennian boundary. *Courier Forschungsinstitut Senckenberg* 75: 319–330.
- Sartenaer, P. and Plodowski, G. (1975). Importance stratigraphique et répartition géographique de genre rhynchonellide *Araratella* n. gen. du Famennien supérieur. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 51(8): 1–34.
- Sartenaer, P. and Sandberg, C.A. (1974). New North American species of Upper Famennian rhynchonellid genus *Megalopterorhynchus* from Lost River Range, Idaho. *Journal of Paleontology* 48: 756–765.
- Sengor, A.M.C. and Hsu, K.J. (1984). The Cimmerides of Eastern Asia: history of the eastern end of Paleo-Tethys. *Mémoires Société géologique de France* 147: 139–167.

- Shi, G. R. (1993). A comparative study of 39 binary similarity coefficients. *Memoir of the Association of Australasian Palaeontologists* 15: 329–421.
- Shi, G.R. (1995). Spatial aspects of palaeobiogeographical data and multivariate analysis. *Memoir of the Association of Australasian Palaeontologists* 18: 179–188.
- Sidiachenko, A.I. (1961). Verkhnedevonskii polrod tsirtospiriferid Dmitria. *Paleontologicheskii Zhurnal* 1961: 80–85.
- Soffel, H.C. and Förster, H.G. (1984). Polar wander path of the central-east-Iran microplate including new results. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 168: 165–172.
- Soja, C. (1992). Potential contributions of ancient oceanic islands to evolutionary theory. *Journal of Geology* 100: 125–134.
- Stepanov, D.L. (1967). Carboniferous stratigraphy of Iran. *6th International Congress on Carboniferous Stratigraphy and Geology (Sheffield, 1967)* 4: 1505–1518.
- Stocklin, J., Eftekhar-Nezhad, J. and Hushmand-Zadeh, A. (1965). Geology of the Sotori Range (Tabas area, East Iran). *Geological Survey of Iran, Report* 3: 1–69.
- Tachibana, K. (1981). Some species of late Upper Devonian and lowest Carboniferous brachiopods from the Higashiyama District, Iwate Prefecture, North Japan. *Annual Report of the Faculty of Education, Iwate University* 41: 59–73.
- Talent, J.A. (1984). Australian biogeography past and present: determinants and implications. In Veevers, J.J. (ed.), *Phanerozoic Earth history of Australia*: 57–92, Clarendon Press.
- Talent, J.A. (1985). Provintzializm i raskhozhgenie kontinental'nykh blokov v proshlom. In Simakov, K.V. (ed.), *Ekostatigrafiya, paleobiogeografiya i stratigraficheskie granitsy*: 54–90. Akademia Nauk, Magadan.
- Talent, J.A., Gratsianova, R.T. and Yolkin, E.A. (1986). Prototethys: Fact or phantom? Palaeobiogeography in relation to the crustal mosaic for the Asia-Australia hemisphere in Devonian-Early Carboniferous times. In *Proceedings of the 2nd Conference Shallow Tethys*: 87–111. A.A. Balkema Press.
- Talent, J.A. and Mawson, R. (1979). Palaeozoic-Mesozoic biostratigraphy of Pakistan in relation to biogeography and the coalescence of Asia. In Farah, A. and De Jong, K.A. (eds), *Geodynamics of Pakistan*: 81–102. Geological Survey of Pakistan, Quetta.
- Tan, Zheng-Xiu (1987). Brachiopods. In *The Late Devonian and Early Carboniferous Strata and Palaeobiocoenosis of Hunan*: 111–133, Geological Publishing House, Beijing.
- Vandercammen, A. (1956). Revision des Ambocoeliinae du Dévonien de la Belgique. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 32(43): 1–51.
- Vandercammen, A. (1967). Les Spiriferida de la collection Hommaire de Hell *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 43(17): 1–20.
- Vandercammen, A. (1969). Le genre *Dmitria* dans le Frasnien de Belgique *Bulletin de l'Institut royal des Sciences Naturelles de Belgique* 45(1): 1–7.
- Van der Voo, R. (1988). Paleozoic paleogeography of North America, Gondwana and displaced terranes: comparisons of paleomagnetism with paleoclimatology and biogeographical patterns. *Geological Society of America, Bulletin* 100: 311–324.
- Veevers, J.J. (1959). Devonian and Carboniferous brachiopods from North-Western Australia. *Bureau of Mineral Resources Bulletin of Australian Geology and Geophysics* 55: 1–34.
- Weddige, K. (1984). Zur Stratigraphie und Paläogeographie des Devons und Karbons von NE-Iran. *Senckenbergiana lethaea* 65: 179–223.
- Wensink, H. (1983). Paleomagnetism of red beds of Early Devonian age from Central Iran. *Earth and Planetary Sciences Letters* 63: 325–334.
- Weyant, M., Brice, D., Racheboeuf, P.R., Babin, C. and Robardet, M. (1988). Le Dévonien supérieur du synclinal du Valle (Province de Séville, Espagne). *Revue de Paléobiologie* 7: 233–260.
- Witzke, B.J. and Heckel, P.H. (1988). Paleoclimatic indicators and inferred Devonian paleolatitudes of Euramerica. In McMillan, N.J., Embry, A.F. and Glass, D.J. (eds), *Devonian of the World, Canadian Society of Petroleum Geologists, Memoir* 14: 49–63.
- Yazdi, M. (1996). *Late Devonian-Carboniferous conodont biostratigraphy of the Tabas area, Eastern Iran*. Unpublished Ph.D. thesis: 1–200, Macquarie University, Sydney, Australia.
- Yazdi, M. (1997). Ironstone facies throughout the Frasnian-Famennian in Central Iran: a Gondwana key in East Iran. *Palaeobiogeography of Australasian Faunas and Floras. Geological Society of Australia, Abstracts* 48: 1–116.
- Yazdi, M. (1998). Late Devonian-Carboniferous conodonts from Eastern Iran. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*, 41.
- Yazdi (1999). Late Devonian-Carboniferous conodonts from Eastern Iran. *Rivista Italiana di Paleontologia e Stratigrafia* 105: 167–200.
- Young, G.C. (1987). Devonian palaeontological data and the Armorica problem. *Palaeogeography, Palaeoclimatology, Palaeoecology* 60: 283–304.
- Young, G.C. (1990). Devonian vertebrate distribution patterns, and cladistic analysis of palaeobiogeographic hypotheses. In McKerrow, W.S. and Scotese, C.R. (eds), *Palaeozoic biogeography and palaeogeography. Geological Society of London, Memoir* 12: 243–255.
- Young, G.C. (1995). Early vertebrates and palaeogeographic models. *Geobios, Mémoire spécial* 19: 129–134.
- Young, G.C. (1998). North Gondwana mid-Palaeozoic connections with Euramerica and Asia; Devonian vertebrate evidence. *UNESCO-IGCP Project 421, Isfahan Meeting, Abstracts*: 44–45.
- Ziegler, P.A. (1988). Laurussia – the old red continent. In McMillan, N.J., Embry, A.F. and Glass, D.J. (eds), *Devonian of the World, Canadian Society of Petroleum Geologists, Memoir* 14: 15–48.