Palaeobiogeographic relationships and diversity of Upper Devonian ammonoids from Western Australia

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Abstract – Upper Devonian ammonoids from the Canning Basin of Western Australia represent one of the most diverse faunas globally known. It consists of cosmopolitan (pantropical), endemic and "spot" taxa (with disjunct distribution in few widely separated basin). Endemism is low at the generic but very significant (ca. 50%) at the species level. Linked with regional facies change and eustatic influences, there were alternating episodes with low-diverse, relatively highly endemic or with species-rich and rather cosmopolitan faunas. Faunal similarities both in the Frasnian and Famennian were closest with Germany, slightly less with North Africa, SW England, the Ardennes, and the Montagne Noire. Frasnian faunal links with the Timan and eastern North America were severed after the Frasnian-Famennian boundary whilst relationships with the Urals and Poland became closer. Faunal similarities were clearly more dependent on regional facies developments of plates than on their spatial distance. The regional diversity curve reflects both global extinctions and radiations as well as effects of Canning Basin structural evolution. Three major extinctions, the Bugle Gap, Lower Kellwasser and Upper Kellwasser Events occurred in the Frasnian. Not a single ammonoid species regionally survived the Frasnian-Famennian boundary and the basal Famennian lacked ammonoids all over Australia. The post-*Annulata* Event regression regionally initiated a strong final decline of ammonoid faunas.

INTRODUCTION

The spatial distribution patterns of Devonian ammonoids are still rather poorly studied although palaeobiogeographic differences of pelagic groups may give distinctive signals for routes of faunal exchange between open shelf areas of major crustal blocks. In the Devonian, the plate tectonic configuration of continents and of smaller crustal plates is still controversal if the world maps of Heckel and Witzke (1979), Scotese and McKerrow (1990), Kent and Van der Voo (1990), Bachtadse *et al.* (1995) and Metcalfe (1996) are compared. IGCP 421 intends to use consistent taxonomic and biogeographic data as well as regional event and extinction patterns to fingerprint former blocks of Northern Gondwana. Such signatures shall be compared with palaeomagnetic and tectonic data in order to revise the reconstruction of Mid-Palaeozoic plate movements. In this context, intensive work in recent years, jointly with M.R. House and W.T. Kirchgasser, will be used here for an analysis of ammonoid data from Western Australia. These hold important clues for the general understanding of Upper Devonian ammonoid biogeographies and for placing the famous Canning Basin reef complexes in a plate tectonic framework (Figure 1).

The interpretation of Mid-Palaeozoic ammonoid distribution data has to recognize their active nektonic lifestyle, either in the open water column or near to the seafloor, as well as the smaller significance of postmortem drift in comparison to Recent nautilids (House 1987). Ammonoid shells were flooded much faster and lived mostly in deeper quiet outer shelf settings lacking strong currents. Many taxa were pan(sub)tropical. In theory, both very shallow marine seaways and deep oceanic areas may have acted as barriers for Devonian ammonoids. This follows from palaeobiological constraints for maximum vertical migration to the food-bearing seafloor by maximum implosion depths (see Hewitt 1996) and from sensitiveness to high water agitation (e.g., by storms). Trends of endemic evolution in wide open seas, therefore, may be a more significant indication of plate tectonic isolation of regions than endemism in benthic and nearshore assemblages subject to larger influence of local environmental factors. However, in recent years, facies control on Devonian ammonoid distribution has become more and more evident. This study intends to investigate the importance of facies versus distance/barrier control on distribution patterns as it has been
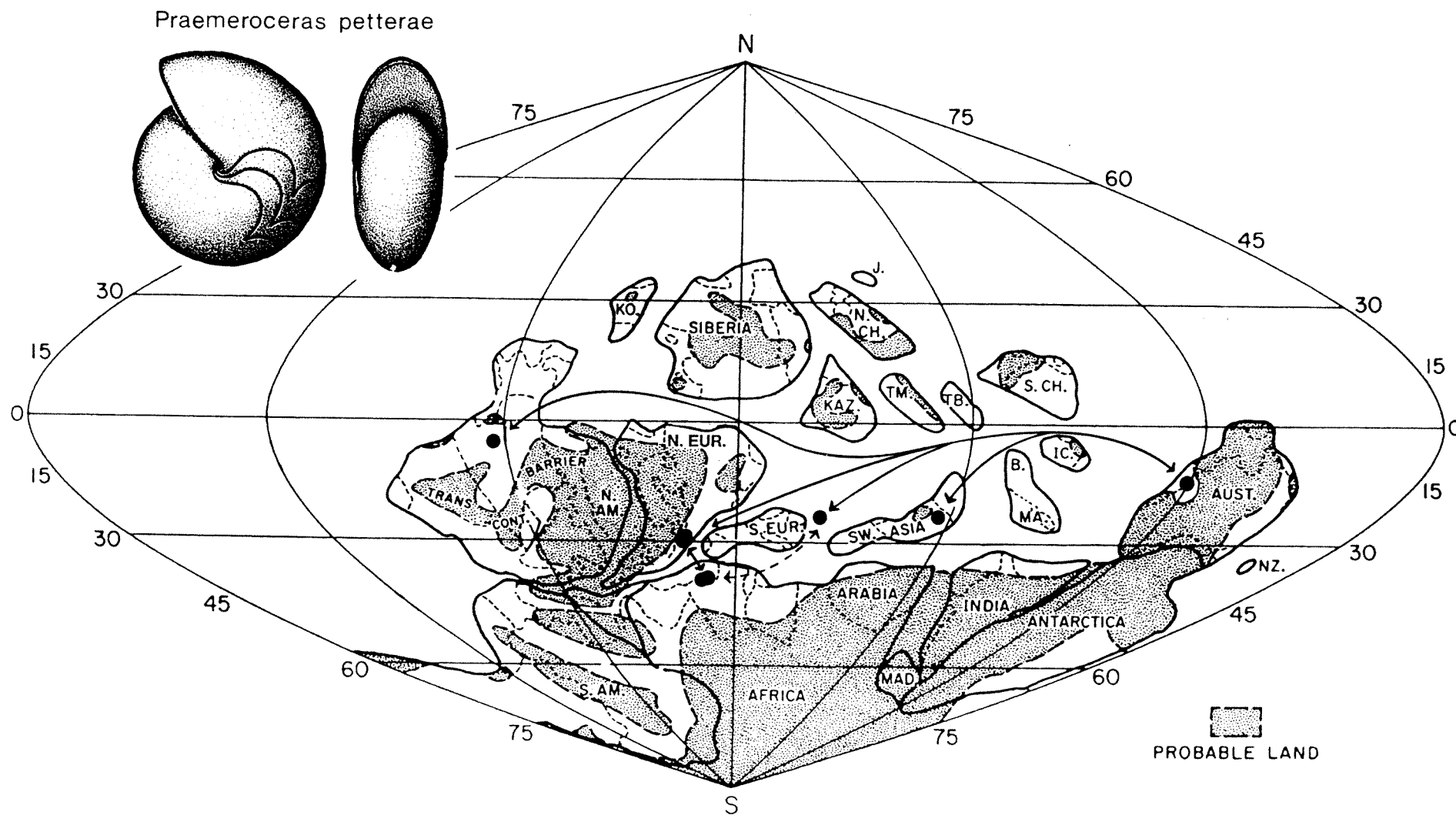
Figure 1 Global (pantropical) distribution of *Praemeroceras petterae* (Petersen) in UD II-E (*rhomboidea* Zone), originally only known from the Canning Basin. Slightly altered reconstruction from Heckel and Witzke (1979). NZ. = New Zealand, Ma. = Malaysia, B. = Burma, IC. = Indochina, S. CH. = South China, TB. = Tibet, TM. = Tarim, KAZ. = Kazakhstan, N. CH. = North China, J. = Japan, MAD. = Madagascar, KO. = Kolyma, N. EUR. = Northern Europe, S. EUR. = Southern Europe, N. AM. = North America, S. AM. = South America.

discussed for Frasnian conodonts by Klapper (1995). In addition, the detailed time resolution of ammonoid data gives prospects for a much refined history of palaeobiogeographical changes. Thus, the relative proportion of endemism has been analyzed zone by zone in Canning Basin faunas.

A global diversity analysis of all Upper Devonian ammonoids at the generic level and based on the highest available time resolution has been conducted by Becker (1993a). This study gave clear relationships between eustatic changes and times of diversification and extinctions ("species area effect"). Major extinctions were associated with anoxic events and subsequent rapid regressions but ammonoids could flourish in times of long-lasting global sealevel lowstands. So far, there have been no published investigations at the species level and on regional scales, in order to elucidate differences between lower and major taxonomic levels, or to establish differences between regional and global diversity patterns. Of special interest are links between diversity changes and the degree of endemism since both were influenced by sealevel changes.

CANNING BASIN AMMONOID PALAEOBIOGEOGRAPHY

Previous work and data base

Principles of Devonian ammonoid palaeobiogeography have been established by House (1964, 1973, 1981). A recent review of general trends in the Devonian biogeographic history of the group was given by Becker (in Becker and Kullmann 1996). Palaeobiogeographic relationships of ammonoids from the Famennian of Western Australia (Canning Basin) were discussed by Teichert (1943) and Petersen (1975; see also Becker 1993b). They found strong similarities with other, widely separated regions that formed part of an Upper Devonian equatorial Prototethys (Figure 1). Based on the congruent evolution of Sporadoceratidae in widely distant regions, Petersen (1975: 11) postulated a permanent gene flow between European and Australian populations in the Famennian. But genetic isolation must have existed in other goniatite and clymenid groups at the same time and along the same route of potential faunal exchange. Differences in the degree of endemism of higher taxa may provide insights into palaeoecological aspects which enabled or restricted the formation of pantropical genepools.

Intensive new field work in the Canning Basin since 1989 has greatly expanded the knowledge of ammonoid taxonomy and stratigraphy of the region (Becker et al. 1993, Becker and House 1997). By now, it is the region with the most diverse and most detailed Upper Devonian ammonoid succession

known in the world, comprising a total of 165 species-level taxa (excluding ten species of bactritids) in the Frasnian (Upper Devonian = UD I-A/B) to middle part of the Famennian (UD IV-B). This forms the basis for a re-appraisal of faunal links with other regions as well as for a regional diversity analysis. An overview of Canning Basin ammonoid zones and their correlation with chronostratigraphic units and conodont zonations is given in Table 1.

Methodological aspects

Canning Basin ammonoid taxa fall into three categories concerning their spatial distribution: (a) taxa known from several to many widely separated areas (semicosmopolitan – cosmopolitan in the warm water biome = pantropical), (b) endemic taxa, and (c) "spot taxa" with patchy distribution in two or three widely separated regions, without evident intermediate occurrences. The latter are especially interesting for the establishment of faunal links and give evidence that an incomplete fossil record can artificially increase the number of supposed endemics. Westermann (2000) has recently proposed the term "didemic" for taxa with rather disjunct occurences but this includes only distribution in precisely two regions.

Many endemic taxa are also closely related to European, North African, or American forms and it is difficult to judge whether these were true allopatric species in a biological sense or morphologically distinctive regional morphotypes/ subspecies. Tests for genetic isolation by geographically intermediate populations are not available. For this reason, the current analysis does not distinguish between species and subspecies. Thus, for a cautious faunal comparison, closely related taxa are also taken into consideration (Table 2).

Many widespread Devonian ammonoid species are still the subject of detailed taxonomic revision and a number of species names used in the monographs by Glenister (1958) and Petersen (1975) will have to be changed due to the restudy of old type material. For example, Maeneceras biferum (Phillips) is a late Hembergian (UD IV) taxon and cannot be used any more as an Upper Nehdenian (UD II-G) zonal index, as shown by Becker (1993a, b) and Becker and House (1997). Updated faunal lists and range charts will be published elsewhere. Regardless of nomenclatoral aspects, the comparison of distant faunas is based on as consistent taxonomic concepts as possible. For some regions (e.g., North China, Algeria, Urals) published data had to be re-interpreted without the opportunity to examine type material. Comparison of most key regions, however, is based on recent detailed studies including the author (e.g., Becker 1992, 1993b, Becker and House 1993, 1994, House

CHRONOSTRAT.			AMMONOIDS	CONODONTS		EVENTS
FAMENNIAN	UD IV	B	Protoxyclymenia sp.		postera	Annulata
		A	Protactoclymenia eurylobica		postera	Annulata
	UD III	C	Protactoclymenia euryomphala		Upper trachytera	
		B2	Falcitornoceras n.sp. aff. bilobatum		Lower trachytera	
		B1	Pseudoclymenia australis		Lower trachytera	
		A3	Sporadoceras angustisellatum		Uppermost marginifera	
		A2	Pernoceras delepinei		Uppermost marginifera	
	UD II	A1	Protornoceras sp.		Upper marginifera	
		I2	Cycloclymenia n.sp.		Upper marginifera	
		I1	Dimeroceras n.sp. aff. padbergense		Upper marginifera	
		H	Sporadoceras teicherti		Upper marginifera	
		G2	Maeneceras latilobatum		Lower marginifera	"Enkeberg"
		G1	Maeneceras subvaricatum		Lower marginifera	
		F2	Acrimeroceras n.sp.		Lower marginifera	
		F1	Paratornoceras polonicum		Upper rhomboidea	
		E2	Praemeroceras primaevum		Upper rhomboidea	
		E1	Praemeroceras petterae		Upper rhomboidea	
		D	Oxytornoceras n.sp.		Lower rhomboidea / Uppermost crepida	Low. Condroz
		C	"Falcitornoceras" n.sp.		Upper crepida	
		A-B	no record		triangularis - M. crepida	
FRASNIAN	UD I	L2	Manticoceras sp.	13	lingui-formis	Upper Kellwasser
		L1b	Manticoceras guppyi	13	lingui-formis	
		L1a	Crickites lindneri	13	Upper rhenana	
		K	(Aulatornoceras n.sp.)		Upper rhenana	Lower Kellwasser
		J2	Virginoceras erraticum	12	Lower rhenana	
		J1	Maternoceras retorquatum	12	Lower rhenana	
		I2	Playfordites tripartitus	11	Lower rhenana	
		I1	Serramanticoceras serratum	11	jamieae	semichatovae
		H	Beloceras tenuistriatum	9 - 10	Upp. hassi	
		G2	Mesobeloceras thomasi	8	Lower hassi	
		G1	Naplesites housei	7	Lower hassi	Rhinestreet
		F3	Sphaeromanticoceras affine	6	punctata	
		F2	Gogoceras nicolli	6	punctata	
		F1	Prochorites alveolatus	6	punctata	
		E3	Manticoceras n.sp.	6	punctata	
		E2	Ponticeras discoidale	5	punctata	
		E1	Probeloceras lutheri lutheri	5	punctata	
		D	?no record	5	punctata	
		C2	Manticoceras sp.	4	transitans	
		C1	Timanites angustus	4	transitans	Timan
		B3	Koenenites n.sp.	3	falsi-ovalis	
		B2	"Protimanites" pons	2	falsi-ovalis	?Genundewa
		B1	Chutoceras n.sp.	2	falsi-ovalis	

Table 1   Regional ammonoid zonation of the Canning Basin and its correlation with conodont zones and chronostratigraphic units. UD = Upper Devonian.

Table 2 Frasnian/Famennian faunal similarities between the Canning Basin and twenty other basins/crustal blocks, based on the number of identical species and on the number of additional closely related species.

Region	Frasnian: identical species	Frasnian: related species	Frasnian: "total similarity"	Famennian: identical species	Famennian: related species	Famennian: "total similarity"
NW Canada	-	2	2	3	2	5
W. United States	1	-	1	-	3	3
E. United States	18	9	27	2	0	2
SW England	12	6	18	3	-	3
Armorican Massif	1	-	1	3	-	3
Ardennes	16	1	17	5	-	5
Germany	32	19	51	27	14	41
Montagne Noire	15	5	20	11	2	13
Kantabrian Mts.	6	-	6	5	1	6
North Africa	14	8	24	22	5	27
Poland	4	3	7	21	9	30
Ural	9	3	12	18	7	25
Timan	11	7	18	1	-	1
Novaya Zemlya	4	5	9	6	3	9
Chios, Greece	-	-	-	6	1	7
Kazakhstan	-	-	-	6	-	6
Turkestan	-	-	-	2	-	2
Rudnyi Altai	7	1	8	-	-	-
North China	-	-	-	8	1	9
South China	5	3	8	1	-	1
Canning Basin			99			69

and Kirchgasser 1993, Becker *et al.* 1997, 2000, unpublished work in Morocco, North America, Germany and other regions).

Faunal comparisons have been made with twenty other regions (Table 2) which include some blocks with rather limited scientific investigation (e.g., Chios, North China, Turkestan, Rudnyi Altai, Novaya Zemlya, Urals: Bashkiria) or with rather poor faunas in terms of abundance and diversity (e.g., Frasnian of Poland and western United States; Canada, South China; early to middle Famennian of the Ardennes Shelf, of England and of Kazakhstan). No distinction has been made between German regions south (Saxothuringia) and north (Rhenish Massif/Harz Mountains) of a supposed "Rheic Ocean", since no intra-German biogeographic differences have been recognized at all in the Upper Devonian. The restricted Kazakhstan data base excludes the prolongation of the Urals into the western part (Aktyubinsk region/Mugodzhar Mountains) of the country and leaves the Karaganda Basin and Semipalatinsk regions as one entity. Records from other regions are so incomplete and sporadic that they were omitted. These include the Frasnian of Kolyma (NE Siberia), of the Kuznetsk Basin, and of Kirgisia as well as the Famennian records from Bohemia, Moravia, Bolivia, the Caucasus, and Taimyr. Faunas from the Carnic Alps and Iran are under current detailed study and interpretations have to await the forthcoming results.

Qualitative analysis: "Spot Taxa" and other indicators

Frasnian

Typical Frasnian cosmopolitan species are *Manticoceras cordatum* (Sandberger and Sandberger), *M. lamed* (Sandberger and Sandberger), *Aulatornoceras auris* (Quenstedt), and *Tornoceras typum* (Sandberger and Sandberger). The latter is commonly but wrongly quoted in the literature as *T. simplex* (v. Buch), which represents a Middle Devonian *nomen dubium*, probably a holzapfeloceratid (Becker 1993b). The listed taxa seem to be both very widespread and rather bradytelic but future taxonomic revision may show that populations from various regions and strata can also be separated. Species of *Manticoceras* (in a wider sense), especially *M. intumescens* (Beyrich), have been frequently misidentified.

Significant Frasnian "spot taxa" of the Canning Basin are *Prochorites alveolatus* (Glenister) and *Probeloceras lutheri* (Clarke) (suggesting a link to New York State), the *Costamanticoceras koeneni* (Roemer) and *"Maternoceras" prumiense* (Steininger) Groups (link to the Rhenish Massif), *Manticoceras evolutum* Petter (link to North Africa), and rare *M. latisellatum* Yanishewsky and *M. solnzevi* Bogoslovskiy (link to the Timan). *Ponticeras discoidale* described by Glenister (1958) from Western Australia was reported by Gatley (1983) to occur also in the Ardennes (Belgium). Much richer
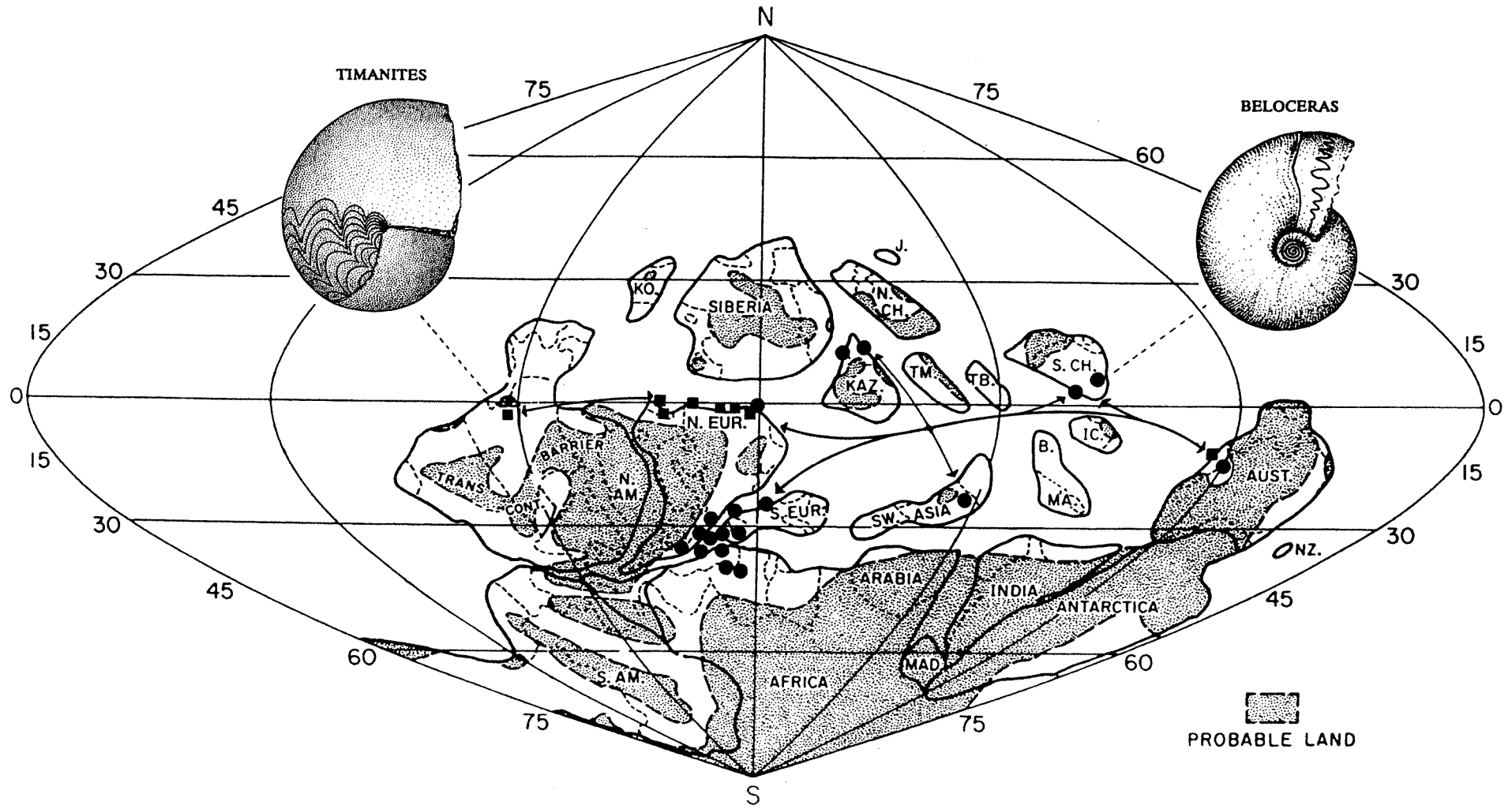
Figure 2 Frasnian distribution of lower Frasnian *Timanites* (squares) and of middle to upper Frasnian *Beloceras* (dots) showing significant differences in their distribution patterns. *Timanites* is lacking in the western Prototethys region, *Beloceras* along the equatorial Transarctic Route.

middle Frasnian *Ponticeras* assemblages occur in the Timan. Southern Chinese species of *Mesobeloceras*, *Beloceras*, and *Sphaeromanticoceras* were partly described under different generic names but are very close, if not conspecific, with members of the genera from the Canning Basin, Germany, and North Africa.

Conclusive is the distribution of early Frasnian (UD I-C) *Timanites* (Figure 2), which was spread along the equator from the Canning Basin via the Urals (Bashkiria, Tartar Republic, western slope of Middle Ural), Timan, Polar Ural and Novaya Zemlya to Western Canada (Transarctic Route of House 1973 and Becker 1993a, b). For unknown reasons, and neglecting false records of homoeomorphic late Givetian Eobeloceratidae (see Becker and House 1993), the genus did not inhabit the Western European, North African, and eastern North American regions. The late middle to upper Frasnian *Beloceras* shows a partly reverse distribution excluding the Transarctic Route and New York but with wide distribution on North Gondwanan crustal blocks such as North Africa (South Morocco, Southwest Algeria and eastern Moroccan Meseta), the Montagne Noire, Pyrenees, Cantabrian Mountains, West Iberia, Carnic Alps, Eastern Iran, and South China (Guangxi, Yunnan) as well as in the surrounding of the "Rheic Ocean" including SW England, Belgium/Northern France, and Germany (Rhenish Massif, Harz Mountains, Thuringia). Another branch of distribution led around Kazakhstan to the Rudnyi Altai and to the Kusnetsk Basin. The westerly restricted *Beloceras* distribution is even more remarkable in the light of the fact that ancestral members of its lineage (*Naplesites*, *Mesobeloceras*) occur in New York State and on Novaya Zemlya (also in Poland). *Beloceras williamsi* Wells of New York was re-assigned by House and Kirchgasser (1993) to the triainoceratid genus *Wellsites*. An indication that *Beloceras* ranged into the eastern part of the Ural seaway is based on an unconfirmed note in Tiasheva (1961: 99) that the genus co-occurs with *Manticoceras* faunas in Bashkiria.

Famennian

Early Famennian (UD II) goniatites have been intensively revised by Becker (1993b), which allows a detailed evaluation of Canning Basin cheiloceratid, tornoceratid, dimeroceratid and sporadoceratid faunas. *Praemeroceras petterae*, originally described by Petersen (1975) as an endemic form of Western Australia, turned out to be globally widespread (Becker 1993b). It was previously illustrated under different names or was subsequently reported from Poland, Germany, Morocco, Chios (eastern Greek Ägäis), the Canadian Rocky Mountains and (new record herein) from Eastern Iran (Figure 1). This example

confirms the necessity for a rigorous and consistent taxonomy and the suspicion that true endemism was perhaps somewhat lower than is apparent from current data.

Famennian examples of "spot taxa" are *Tornia* n.sp. and the *Cheiloceras postinversum-semiinversum* Group (indicating links to Poland), *Protactoclymenia krasnopolski* (Tschernyscheff) (link to the Urals), *Karaclymenia* n.sp. juv. (link to Polar Russia), and *Maeneceras milleri* (Famennian link to New York; Figure 3). The last, however, is related to *M. acutolaterale* (Sandberger and Sandberger) and *M. sedgwicki* Wedekind from Germany and Iran. The late middle Famennian (UD IV) *Raymondiceras* is rare but occurs as widely separated as in the Canning Basin (*R. inceptum* Petersen), Southern Urals (*R. aktubense* Bogoslovskiy), and in Montana (*R. simplex* (Raymond)). Pseudoclymeniidae can be very common in lower Hembergian (UD III-B) beds, but show a patchy distribution in Germany, the Urals and Western Australia. Similar irregular patterns were recognized in the Prolobitidae but new records of endemic genera from Morocco and the Canning Basin expand our palaeobiogeographical knowledge of the family considerably.

Simple quantitative analysis

There are strong biogeographic differences between taxonomic levels. Australia has no endemic Devonian ammonoid family and at the generic level the relative rate of endemism is also low (around 5% of all genera). At the species level, endemism is significant and lies around 50% and over, both in the Frasnian and in the Famennian. Analyzed zone by zone, the average rate of endemism is around 40% in both stages. This rather high rate seems to reflect the wide spatial distance between eastern and western parts of the Prototethys (Figures 1–2). Since investigations of Canning Basin faunas have proceeded much farther than in other regions, it can, however, be expected that some Australian supposed endemics will eventually be discovered elsewhere, as has happened in the past (see above: *Praemeroceras petterae* and *Ponticeras discoidale*). Despite the high number of endemic species-level taxa it is not suggested that Canning Basin faunas belong to a clearly defined eastern Gondwana province but subprovince status (see Westermann 2000; chorotype = Canning Basin, chronotype = Famennian) may be granted. The low-level distinction is based on the fact that there are no endemic genera in the studied faunas which are common as well as very distinctive.

The comparison of the Canning Basin with twenty other regions (Table 2) gives a clear picture of faunal similarities that bears no easy correlation with estimated distances between crustal blocks or with their postulated spatial configuration. There is
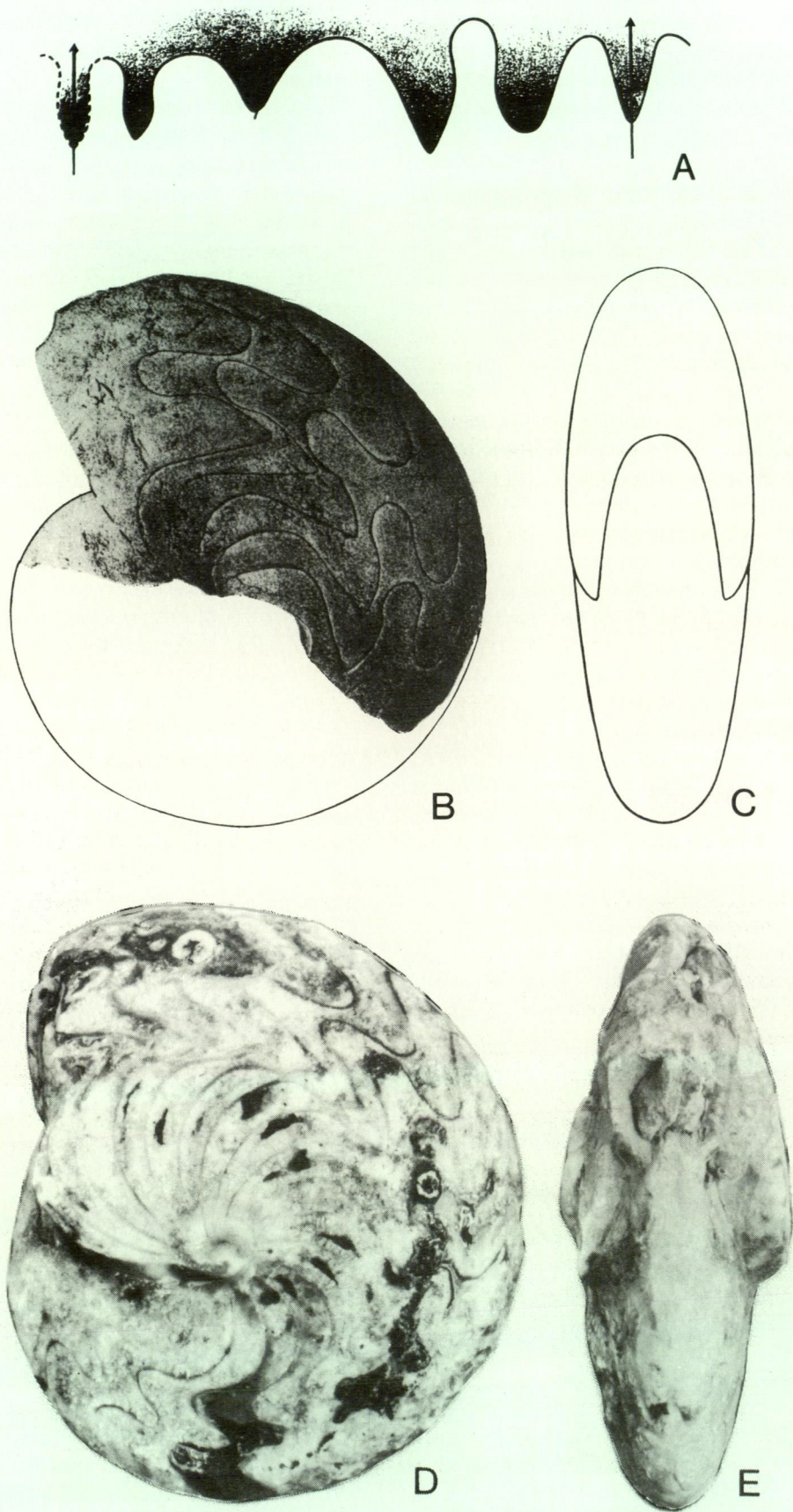
Figure 3 *Maeneceras milleri* (Flower and Caster), a typical "spot taxon" known from a single specimen in eastern North America (3A–C, natural size, from Miller 1938: Pl. 37, Figures 5–7) and abundantly from the late UD II of the Canning Basin (D–E; GSWA 109145/A1, "Syncline Gully", Bed K, Mt. Pierre area, natural size).

also no fundamental palaeobiogeographic difference between the two Upper Devonian stages. The global Kellwasser Crisis at the end of the Frasnian had no lasting effect on principle faunal exchange although there are some interesting trends in detail.

The greatest faunal similarities during all of the investigated time-span are with the classical faunas from Germany. In the Frasnian there are 32 common species (33%) and further 19 similar taxa, giving a "total similarity" of more than 50%. In the Famennian there are 27 common species (39%) and the wider similarity is close to 60% (41 taxa). Frasnian ammonoids show also clear relationships ("total similarity" between 20 and 30%) with the Timan, North Africa, the Montagne Noire, the Ardennes Shelf, SW England, and with Eastern North America (mostly New York State). These regions all formed one larger realm within or adjacent to the western Prototethys. Close affinities with the Canning Basin emphasize that there was no general biogeographic barrier, neither too deep oceanic nor too shallow, between eastern and western Prototethys regions plus the Uralian-Transarctic seaway. This important conclusion is in some conflict with the plate tectonic reconstructions of Scotese and McKerrow (1991) which shows an extensive central Prototethys ocean that should at least have produced a clearer separation of Russian faunas. Migrations from and to Europe and North Africa could have taken place along the equatorial northern margin of Gondwana but this is contradicted by the absence of Frasnian intermediate faunas from Tibet, Pakistan, Afghanistan, Iran or Turkey and by the lack of *Timanites* in the western Prototethys. In the Scotese and McKerrow reconstruction, *Beloceras* faunas from the Rudnyi Altai and Kusnetsk Basin also would be completely isolated. The Devonian reconstruction of Kent and Van der Voo (1990) shows an even wider ocean without intermediate plates between Australia and Europe and is anyway dismissed here because of the highly unlikely wide ocean separating North Africa and Europe.

Crustal blocks positioned in the neighbourhood of northwest Australia, especially former parts of Western Indonesia-Malaysia-Thailand, Vietnam-Laos-Cambodia, Burma, and Tibet have no recorded Upper Devonian ammonoid faunas at all; ammonoid facies never developed there or did not occupy significant areas. Southeast Asian blocks seem to have had a different shelf-facies history. If placed just west of Australia, as in the reconstruction of Metcalfe (1996) and to a lesser extent (W/NW) also in Scotese and McKerrow (1990), these plates (Figure 4) would have restricted the faunal exchange to the west more than evident from the data. The reconstruction of Heckel and Witzke (1979) leaves more space between South

East Asian plates to account both for pantropical genepools of pelagic forms and for diverging outer shelf facies differences.

Assemblages from South China (Hunan, Guangxi, Guizhou, and the Baoshan region of Yunnan) are also rather rare and of low-diversity although typical cephalopod facies were present in some depressions between wide reefal platforms. The poor affinities between the Canning Basin and Southeast Asian regions is again thought to reflect mostly differences in shelf facies rather than the presence of biogeographical barriers. It is possible that detailed future work will produce richer Frasnian faunas from South China. A few unpublished goniatites have been seen by the author in regional museum collections at Guilin and Nanning.

The Famennian picture differs insofar that ammonoid faunal similarities with North America and the Timan were lost. This is not based on differences in faunal composition but, again, on the simple fact that early to middle Famennian ammonoids are almost lacking in the two regions. After the Upper Kellwasser Event, typical ammonoid biofacies did not re-develop for a long period. The influence of regional structural and facies evolution was the dominant factor controlling a restricted ammonoid distribution, not increased spatial distance or the establishment of migrational barriers. A reverse process can explain the increased Famennian faunal similarity between the Canning Basin, the Urals (18 common species) and the Holy Cross Mountains (21 common species). At the same time poorly studied faunas appeared in regions lacking Frasnian goniatites completely: Greek Ägäis, North China (Great Khingan), Caucasus, Turkestan, and Kazakhstan. Transgression produced new regions hospitable for ammonoids but spreading events, such as the one associated with the global *Annulata* Event (Becker and Kullmann 1996: Figure 4), did not reach all basins.

The ammonoid analyses seems to contradict to some extent palaeogeographic results obtained from the study of Asian and Australian vertebrates. Rich and Young (1996) observed that fish faunas of both regions became more similar at some stage in the Upper Devonian and suggested a narrowing of the marine barriere between both crustal units, fitting the Metcalfe (1996) reconstruction. Palaeomagnetic data (Zhao *et al.* 1996), however, indicate that Chinese blocks were pulling away from the western part of Australia as early as between the Early Silurian and Middle Devonian. Furthermore, Johanson and Ritchie (1999) recently pointed out that latest Devonian fish faunal similarities between South China and eastern Australia were not as close as originally thought and during most of the Upper Devonian there were close affinities with Euramerica. Stratigraphical data in Rich and Young
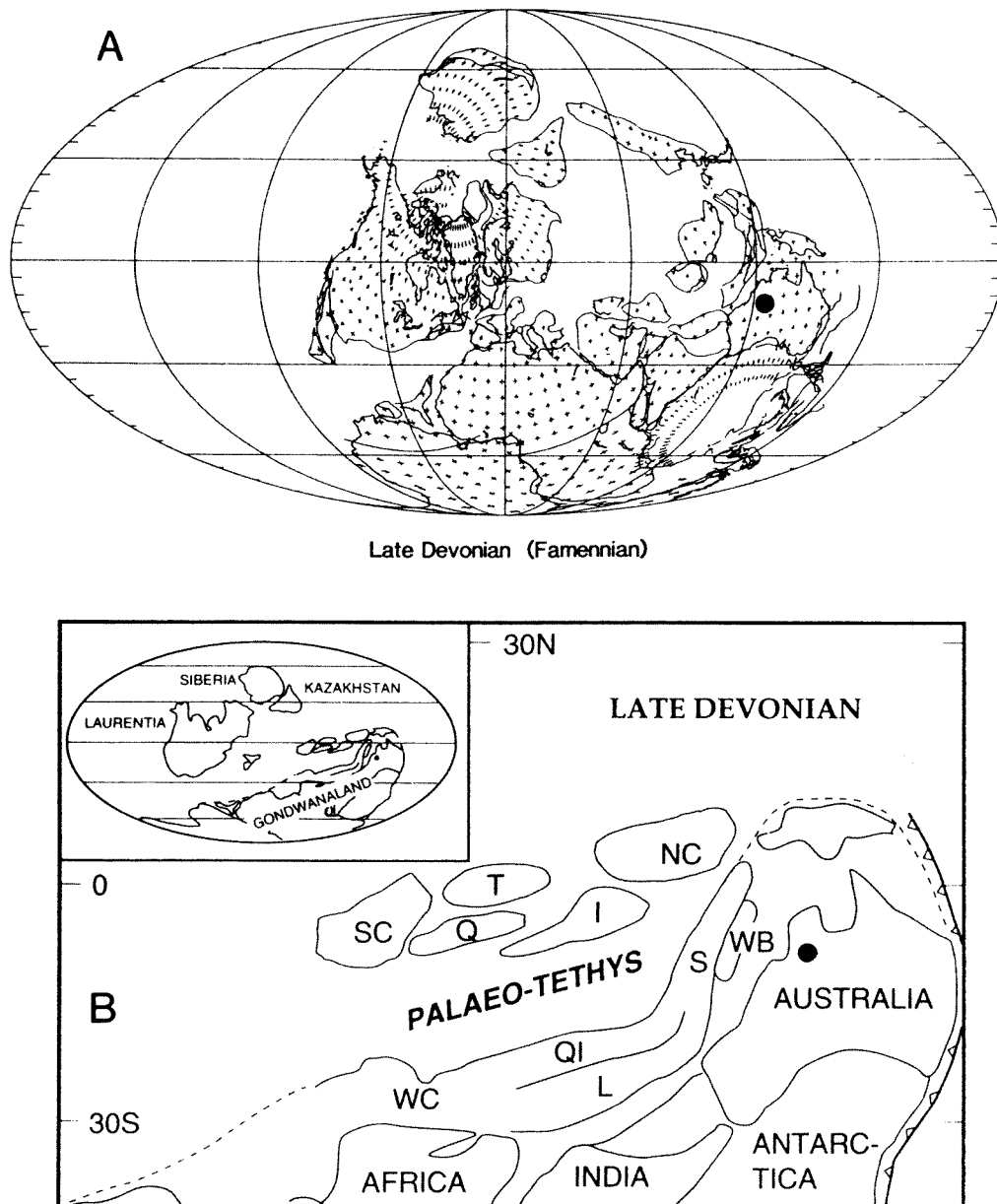
Late Devonian (Famennian)

Figure 4 Rejected plate tectonic reconstructions for the Upper Devonian by (A) Scotese and McKerrow (1990) and by (B) Metcalfe (1996) showing too wide a central Prototethys ("Palaeotethys") and blocking of the Canning Basin (black dots) by an array of Southeast Asian crustal blocks. WB = West Burma, S = Sibumasu (parts of Indonesia, Malaysia and Thailand), L = Lhasa, QI = Qiangtang, WC = Western Cimmerian Continent (ca. Turkey to Pakistan), NC = North China, I = Indochina (parts of Vietnam, Laos/Cambodia), T = Tarim, Q = Qaidam, SC = South China. The Scotese and McKerrow reconstruction is especially in conflict with the Transarctic and Kazakhstan distribution of *Timanites* and *Beloceras* (Figure 2).

(1996: Figure 2) show that faunal links between eastern Australia and China appeared late in the Famennian when they were no more ammonoids in Western Australia.

"Intra-Australian" relationships

In Famennian II and IV, the Canning Basin and New South Wales have not a single species in common. Eastern Australian ammonoid source areas are part of terranes which were attached later to the craton. There was certainly again a facies influence on different faunal composition since

Canning Basin UD IV-assemblages (Piker Hills) were found in a rather unusual hemi-pelagic shallow black shale facies with many gastropods, brachiopods, and plant remains. New South Wales faunas (Jenkins 1966, 1968) contain both endemic species (e.g., *"Genuclymenia" keepitensis*) and forms known from Western Europe and North Africa (*Erfoudites, Platyclymenia*). Generally, western and eastern Australian Devonian ammonoid faunas represent completely disjunct basins and subprovinces that both had some permanent faunal exchange with western parts of the Prototethys.

Migration from Eastern Australia via the Protopacific (Panthalassia) is ruled out because of the lack of similar faunas in western North America.

Level of endemism in taxonomic groups

All Canning Basin species-level taxa were sorted according to their family affinity. Representatives of the Anarcestidae (*Archoceras*), Praeglyphioceratidae (*Lagowites*), Kosmoclymeniidae (*Protoxyclymenia*) and Carinoclymeniidae (*Karaclymenia*) are so rare that they were not considered. The Phenacoceratidae (*Cycloclymenia*), Prolobitidae (with a new genus) and Posttornoceratidae are only represented by single endemic species. The high endemism within the Prolobitidae was probably related to their demersal (suprabenthonic) lifestyle in conjunction with a global sealevel lowstand (Becker 1993a, Becker and Kullmann 1996) in the UD III-C (*Prolobites delphinus* Zone). The same may apply to the "spot genus" *Cycloclymenia* which was previously only known in UD II and UD V of Germany. *Posttornoceras glenisteri* (Petersen) is very close to *P. contiguum* (Münster) from Germany. All six species of the Koenenitidae are restricted to northwestern Australia. These forms compose early Frasnian very low diverse assemblages which were obviously more isolated in shallow hypoxic interreefal basins than faunas from later in the Frasnian when the sealevel was much higher. *Timanites angustus* (Glenister) is very close to the Russian *T. keyserlingi* (Miller) and to the northwest Canadian *T. occidentalis* (Miller and Warren).

High numbers of endemic species (between 50 and 70%) can be found in the Tornoceratidae, Pseudoclymeniidae, Dimeroceratidae, Acanthoclymeniidae and in the Beloceratidae. These groups represent a wide range of morphotypes that cannot be assigned to a single type of lifestyle. The Famennian tornoceratid endemism is rather special since the majority of species is regarded as typical pelagic forms of the open sea (Becker 1995).

Lower numbers (between 30 and 50%) of endemic species are found in early Famennian Cheiloceratidae, in the Frasnian Gephuroceratidae, and in the regionally low-diverse middle Famennian Platyclymeniidae. The dominance of the *Cheiloceras* (*Puncticeras*) *postinversum-semiinversum* Group, however, gives a unique structure to cheiloceratid assemblages. The highest degree of cosmopolitanism is apparent in the Sporadoceratidae (see Teichert 1943 and Petersen 1975) and in the Cyrtoclymeniidae. Again, there is no easy correlation between morphology, assumed lifestyle and wide distribution. Dispersal or genetic isolation was more influenced by episodes of facies changes and eustatic movements than by general

types of morphology and paleoecology. Only a more general study might clarify whether representatives of certain morphotypes tend to be more endemic or cosmopolitan than others.

Outer shelf synecology and palaeobiogeography

In Canning Basin marginal slope and intereefal environments, ammonoids are frequently associated with a range of other fossil groups, especially with conodonts, nautiloids, rhynchonellids, trilobites, crinoids, bivalves, gastropods, solitary rugose corals, sponges, and fish remains. Only some of these groups have been studied sufficiently in detail to allow palaeobiogeographic comparisons. It remains an interesting question which parts of buried assemblages display similar or different patterns of endemism. Almost nothing is known at present about changes in Devonian "pelagic communities" with distance or latitude. For example, the complete lack of trilobites in pelagic assemblages of the Timan and of Eastern North America is well-known but not understood. Klapper (1995) compared Frasnian conodonts and found high levels of endemism (up to 1/3) at the species level; this group was previously regarded as cosmopolitan at that time. Even higher endemism seems to apply to many Canning Basin benthic groups of the Gogo and Virgin Hills Formations: Frasnian and Famennian crinoids (Jell and Jell 1999), sponges (Rigby 1986) and rhynchonellids. By contrast, buchiolinid bivalves (Grimm 1998) show close relationships with European taxa. This suggests an interesting difference in the spatial gene flow between faunal groups living in the same environment. But, anyway, a range of faunal groups can be used to define a biogeographic Canning Basin Subprovince in the Upper Devonian.

Regional diversity analysis

Canning Basin extinction and diversification phases

The Canning Basin taxonomic diversity is higher in the Frasnian (36 genera/subgenera with 99 species/subspecies) than in the Famennian II-IV (32 genera with 69 species/subspecies). The average diversity of Frasnian zones lies at ca. 9.5 species but only at ca. 7 species in Famennian zones. These figures are based on real occurrences and do not include regional "Lazarus episodes" (record gaps) of taxa. These often do not reflect sampling gaps of rare taxa but episodic and facies-controlled absence of taxa from the studied sections. Bactritids have been omitted since their record is strongly biased by preservational aspects (easy species identification is only possible in haematitic faunas). Generally, faunas from individual levels of the Canning Basin inter-reefal deposits are not as diverse as
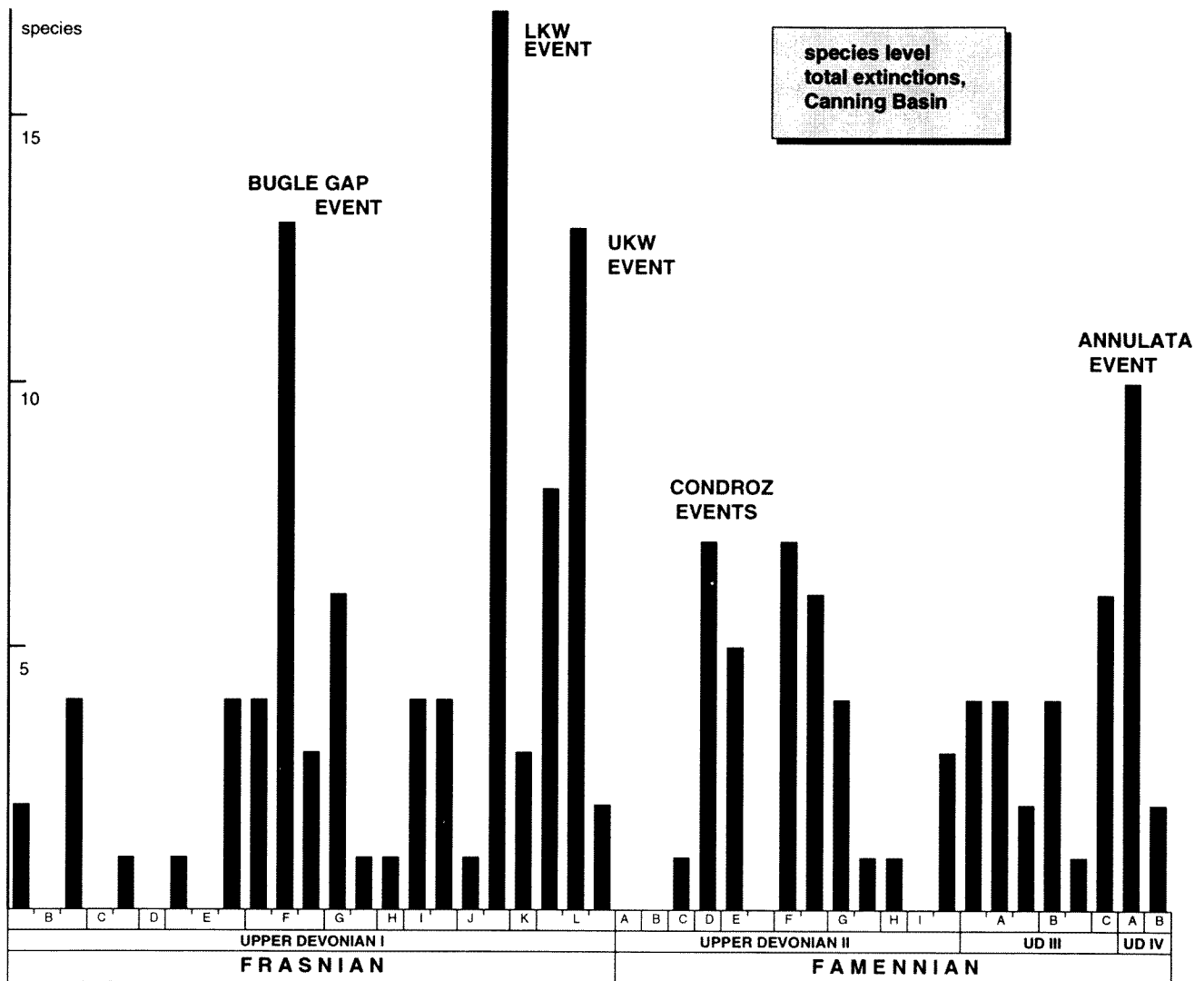
Figure 5 Species level total extinctions in the Upper Devonian of the Canning Basin showing three major Frasnian extinctions (Bugle Gap, Lower Kellwasser and Upper Kellwasser Events) and some Famennian phases of high faunal overturn (Condroz Events, UD II-F/G, extinction subsequent to the *Annulata* Event).

those from German or Polish submarine seamount sections positioned in deeper parts of shelf margin basins. Several diversity peaks clearly correlate with transgressive episodes, but not all eustatic rises (see Becker and House 1997) allowed diversification or the spread of more species into the Canning Basin. This indicates a significant influence of regional structural evolution. The maximum diversity with 31 species/subspecies was reached in the *Virginoceras erraticum* Zone (UD I-J$_2$). Plots of total species level diversity and of total extinctions (Figures 5–6) give the following stages of diversity development (for event sequence and terminology see Becker *et al.* 1993 and Becker and House 1997):

a) Early Frasnian (UD I-B/C) immigration and speciation of low-diverse faunas, probably corresponding with the international transgressive episodes associated with the Genundewa and Timan Events.

b) Small scale extinction at the end of UD I-C corresponding with the global Koenenitidae decline near the end of MN Zone 4 (= *transitans* Zone).

c) Important regional diversification, with a peak in UD I-F$_2$ (*Gogoceras nicolli* Zone; ca. MN Zone 6 = upper part of *punctata* Zone), correlating with the regional main development of hypoxic goniatite shales.

d) **Bugle Gap Event** (named herewith): Significant regional extinction associated with a retreat of hypoxic facies and regression at the end of UD I-F$_2$ (within MN Zone 6) in the Bugle Gap area. This event may be an important and characteristic regional signature of the Canning Basin.
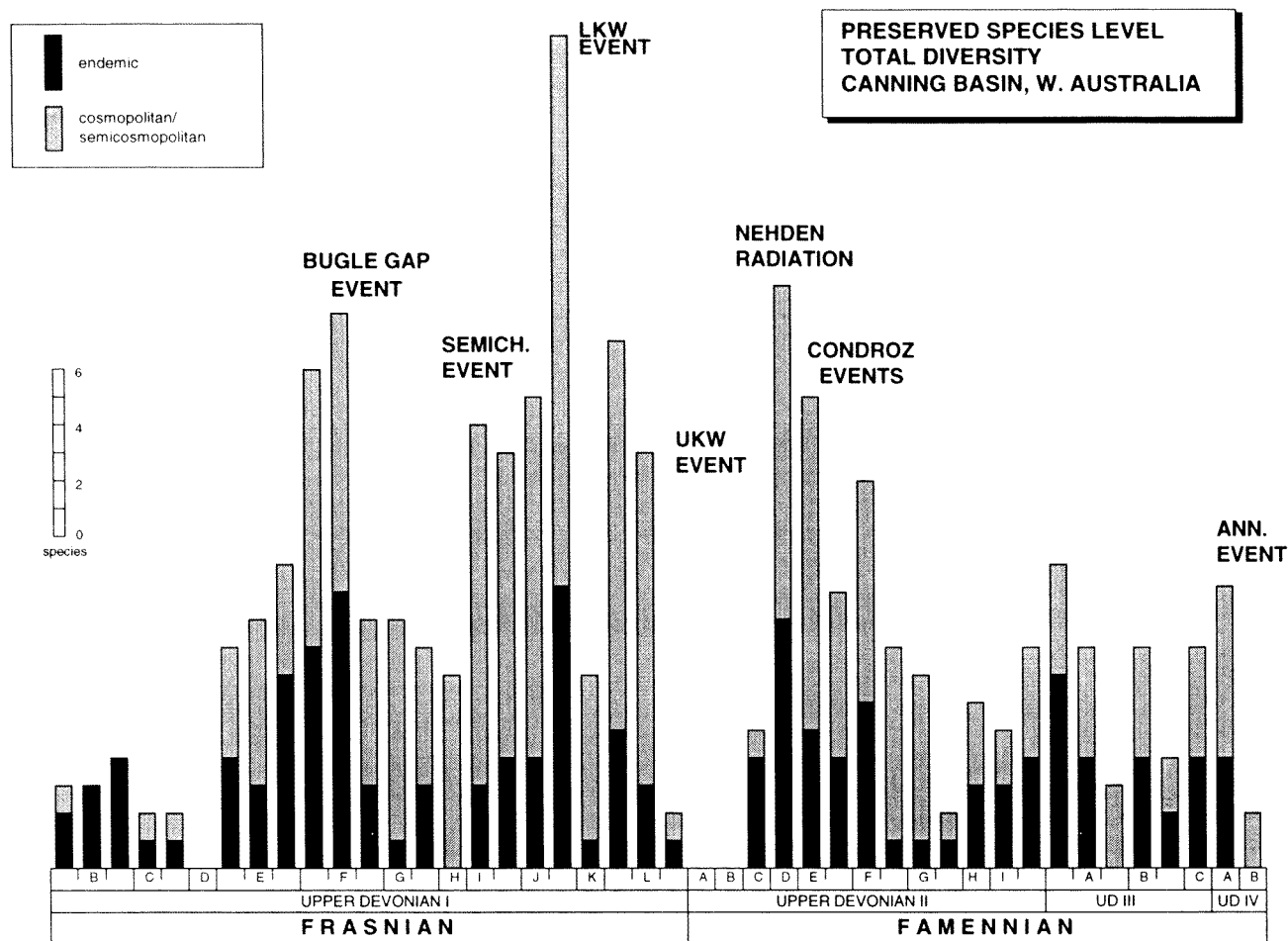
Figure 6 Preserved species level total diversity in the Upper Devonian of the Canning Basin and the total number of endemic species. Diversifications occurred in the early middle Frasnian (UD I-E/F), with the *semichatovae* Transgression, in the upper Frasnian, lower Famennian (Nehden Radiation), early in UD III and with the global *Annulata* Event.

e) Stable and moderately low diversity in UD I-G/H (MN Zones 7–10, = ca. *hassi* Zones).

f) Important wave of immigration and speciation at the base of UD I-I corresponding with the international "*semichatovae* Transgression" (early MN Zone 11, = *jamieae* Zone to lowest part of Early *rhenana* Zone).

g) Stable high diversity in UD I-I_2 and I-J_1 (MN Zones 11–12, = Early *rhenana* Zone), in agreement with the globally high sealevel.

h) Maximum regional diversity (31 species/subspecies) in the *Virginoceras erraticum* Zone (UD I-J_2, upper part of Zone 12, upper part of Early *rhenana* Zone), followed by a massive extinction (27 species) during a significant regressive phase (top of MN Zone 12). It corresponds in time with the global extinction just prior to the Lower Kellwasser level.

i) Very low diversity and very rare faunas in the lower part of MN Zone 13 (UD I-K, = lower part of Late *rhenana* Zone). The regional lack of faunas from this interval is intriguing but may partly reflect undersampling.

j) Diversification in the latest Frasnian *Crickites lindneri* Zone (UD I-L_{1a}, upper part of MN Zone 13, = upper part of Late *rhenana* Zone) which is characterized by several regional transgressive pulses.

k) Upper Kellwasser Event: A regional decline of ammonoid faunas started at the base of the *linguiformis* Zone (= topmost part of MN Zone 13, UD I-L_{1b}), characterized by a short-termed regression with a spread of neritic faunas (e.g., diverse gastropods). The main extinction lies above a subsequent transgressive level (*Manticoceras guppyi* Bed) within the *linguiformis* Zone (see Becker *et al.* 1991, Becker and House 1997) which correlates with the Upper Kellwasser level but which is not hypoxic. The last *Manticoceras* range up to the last centimeter of the Frasnian. The regional extinction pattern is more gradual than in Europe and North Africa and this may be related to the complete lack of hypoxic Kellwasser facies. The final sudden extinction of manticoceratids must have been caused by factors such as temperature and
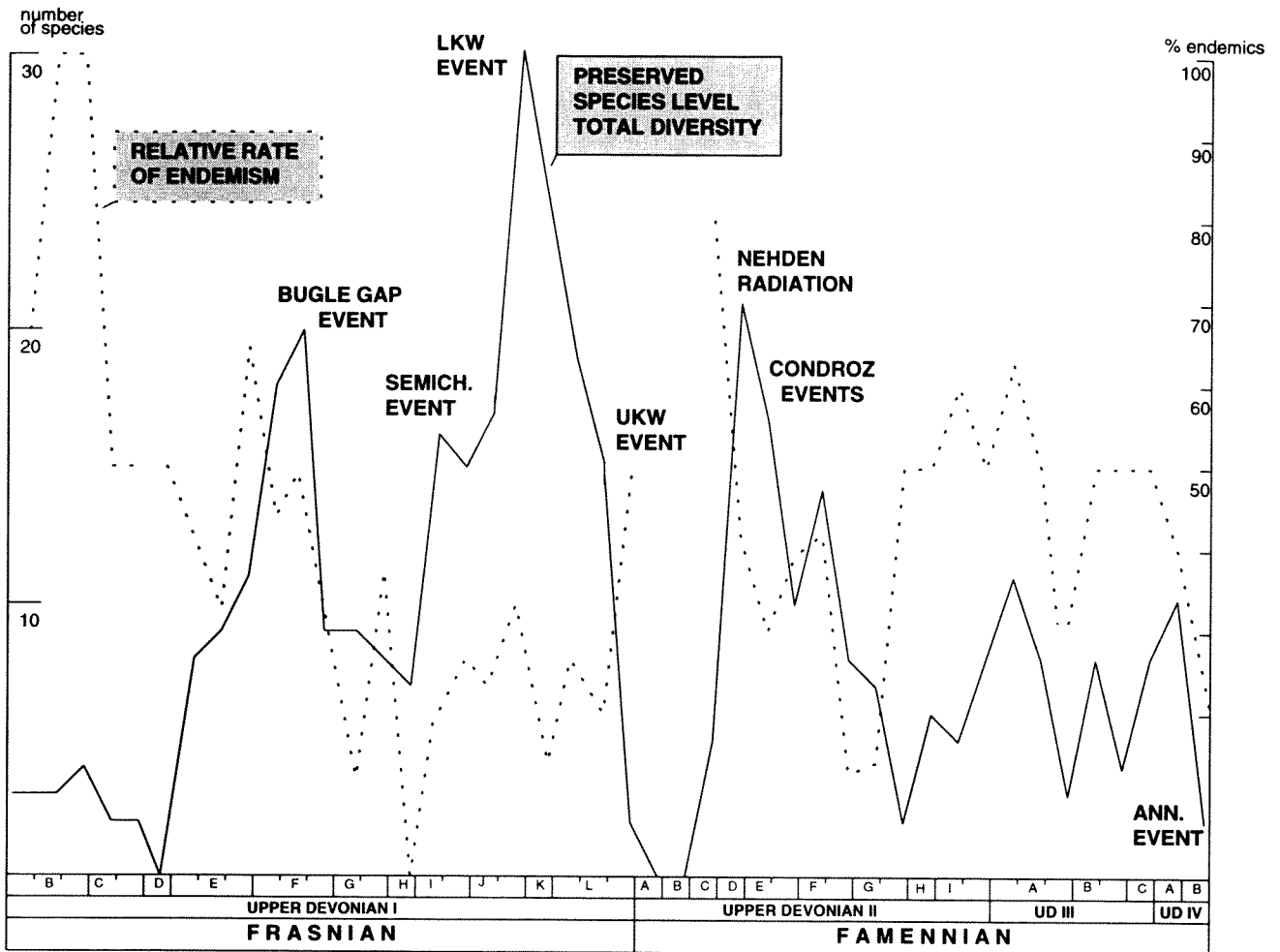
number of species

30

RELATIVE RATE OF ENDEMISM

20

BUGLE GAP EVENT

SEMICH. EVENT

LKW EVENT

PRESERVED SPECIES LEVEL TOTAL DIVERSITY

NEHDEN RADIATION

CONDROZ EVENTS

UKW EVENT

10

ANN. EVENT

% endemics

100

90

80

70

60

50

B | C | D | E | F | G | H | I | J | K | L | A | B | C | D | E | F | G | H | I | A | B | C | A | B

UPPER DEVONIAN I | UPPER DEVONIAN II | UD III | UD IV

FRASNIAN | FAMENNIAN

Figure 7 Canning Basin relationships between preserved total species-level diversity and the relative (percentage) rate of endemism (interrupted lines). Low-diverse/highly endemic faunas alternate with species-rich/more cosmopolitan faunas. However, there is also a smaller-scale positive correlation between changes in diversity and endemism.

salinity that are not very obvious in the sedimentary record.

l) Earliest Famennian beds (UD II-A/B, *Pa. triangularis* to Middle *crepida* Zones), spanning ca. 2 ma, have no ammonoids at all. Regionally, there were no ammonoid survivors at all.

m) The rapid Nehden Adaptive Radiation (UD II-C/D, Upper *crepida* Zone to lowermost *rhomboidea* Zone) produced the second regional diversity peak, which correlates well with a global and regional sealevel high.

n) The Lower Condroz Event at the end of UD II-D (*Oxytornoceras* n.sp. Zone) led to a significant extinction which, however, was balanced by new forms entering in UD I-E (*Praemeroceras petterae* Zone, middle part of *rhomboidea* Zone).

o) Diversity remained moderately high during the higher parts of UD II and in the lower part of UD III (upper part of *rhomboidea* Zone to Uppermost *marginifera* Zone), but there were several faunal overturns, for example between UD I-F and I-G (within basal

marginifera Zone) and in the lower part of UD III-A. The low diversity of UD-G_2 and UD III-A_3 reflects inadequate sampling. The global and regional transgression at the base of UD II-G (classical do IIß, *Maeneceras subvaricatum* Zone) is marked by the immigration of the oldest sporadoceratids but not by a diversification.

p) The immigration of pseudoclymenids took place during a minor diversification phase (UD III-B) and their sudden extinction (within the Lower *trachytera* Zone) represents a highly interesting small-scale global extinction event that is not reflected by a change in lithofacies.

q) The immigration of the oldest clymenids (base of UD III-C, ca. base of Upper *trachytera* Zone) and prolobitids produced another minor diversity increase but faunas remained of very low diversity in comparison with those from the Urals, Poland, and Germany. At the end of the regional *Protactoclymenia euryomphala* Zone there was a small-scale extinction, correlating

with a basin-wide regression and discontinuity in the ammonoid record.

r) *Annulata*-Event: The global hypoxic and transgressive *Annulata* Event (Upper *trachytera* Zone) allowed only a minor diversification in the haematitic Piker Hills Formation but enabled the spread of ammonoids to New South Wales (see Jenkins 1968). Regionally, the post-event major regression caused a drastic decline of ammonoid faunas from which the group did not recover in the Middle Paleozoic.

s) The final extinction of the last and very rare Canning Basin clymenids (*Protoxyclymenia, Falciclymenia*) took place in the upper part of UD IV, probably still within the *postera* Zone but precise conodont data are not available from the shallow-water carbonates.

Palaeobiogeography and regional diversity

Low diversity faunas have a relative high percentage (50% or more) of endemic forms and seem to contain specialists that were adapted to local/regional environmental conditions which were not favourable for many other species. This applies to early Frasnian (UD I-B/C) and some Famennian (UD II/III) faunas. Relatively low rates of endemism (< 20% of taxa) were found during some but not all transgressive episodes. Examples are the basal Rhinestreet eustatic pulse (*Naplesites housei* Zone, UD I-G$_1$), the "*semichatovae* Transgression" (UD I-J$_1$), the latest Frasnian diversification (*Crickites lindneri* Zone, UD I-L$_{1a}$) and the two eustatic rises during the *marginifera* Zone (UD II-F$_2$ and II-G$_1$). It is suggested that differences in ammonoid diversity and endemism during individual transgressive phases reflect varying overprints of the basin subsidence history and by associated regional ecological developments.

The relationships between total (preserved) diversity and the relative rate of endemism (% of endemic species in each zone) are depicted in Figure 7. The alternation of low-diverse/highly-endemic and diverse/weakly-endemic assemblages can be seen with more endemic phases in the early Frasnian and in the late lower to middle Famennian. In addition, however, the second order peaks and lows show parallel trends suggesting that during each diversification there was also an incoming of endemic taxa, probably from elsewhere. This is supported by the fact that not only cosmopolitan but also endemic forms show record gaps (regional "Lazarus phases"). A good proportion of endemic species is also of cryptic origin; direct ancestors are not known from the region. Many of the Canning Basin forms must have lived outside the studied sections, at least episodically.

Conclusions

The analysis of Canning Basin Upper Devonian ammonoid faunas allows a range of conclusions that are of importance for the general understanding of palaeobiogeographic relationships in Middle Palaeozoic pelagic environments and for a better placing of northwest Australia in the complex framework of Upper Devonian crustal plates:

1) Canning Basin ammonoid faunas consist to a varying degree of (semi-)cosmopolitan (pantropical), endemic and "spot taxa". The latter emphasize the incompleteness of the known fossil record and are important markers for biogeographic links.

2) Endemism was low at the generic but very significant at the species level. This seems to reflect the wide spatial distance between populations of the eastern and western parts of the tropical Prototethys. Pantropical genepools existed contemporaneously only in some but not in all ammonoid groups. Canning Basin faunas belong to a small-sized subprovince of the Prototethys Province.

3) Closest similarities existed with Germany, and to a lesser degree with other European-North African-Appalachian regions. The Transarctic Route was only episodically significant for the dispersal of some taxa such as *Timanites* and *Praemeroceras*.

4) The individual structural evolution of basins (crustal blocks) determining the spread of outer shelf ammonoid biofacies and not the establishment or dismiss of biogeographic barriers was the major controlling factor of Upper Devonian ammonoid distribution patterns. Asian plates adjacent to northwestern Australia mostly lacked suitable facies. An equal or greater importance of biofacies rather than biogeographic factors was also suggested for conodonts by Klapper (1995).

5) The lack of a general biogeographic barrier between northwest Australia and the western Prototethys and Urals regions contradicts the plate tectonic reconstructions of Scotese and McKerrow (1990) and Metcalfe (1996) but is mostly in agreement with that of Heckel and Witzke (1979).

6) There is no clear correlation between the rate of endemism and morphology or higher level taxonomy (families). The different spreading success of various groups has to be interpreted in the light of the changing global sealevel. It could be argued that a Canning Basin faunal province was established and destructed in a fine sequence of episodes with fluctuating isolation.

7) The Upper Kellwasser event near the Frasnian-

Famennian boundary interrupted the Canning Basin ammonoid record totally for ca. 2 ma, but caused no fundamental biogeographical change.

8) All known global extinctions of the Frasnian to middle Famennian, even small-scale events such as the koenenitid and pseudoclymenid extinctions, can be recognized in the Canning Basin. Magnitudes and phases, however, were strongly influenced by regional factors. The Bugle Gap Event at the end of UD I-E$_2$ (upper part of *punctata* Zone) was a significant regional extinction.

9) Analyzed zone by zone, there was an alternation of low diverse/endemic and highly diverse/cosmopolitan faunas. "Lazarus Phases" of endemic forms and a small-scale positive correlation between diversity trends and the relative rate of endemism suggest that many forms may episodically have lived outside the studied sections. True endemism was probably somewhat lower than is evident from current data.

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