

Palaeobiogeography of Devonian and Carboniferous crinoid faunas of Gondwana

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Abstract – Devonian and Carboniferous crinoid faunas of Gondwana are generally not as large or well known as faunas from Laurentia and Baltica. Devonian faunas are known from three regions in Gondwana: Northern Africa (Morocco and Algeria), eastern Australia, and the southwestern edge of Gondwana in a belt extending from the Karoo Basin of South Africa through West Falkland Island into the Chaco Basin of Argentina and Bolivia, into Columbia. Most faunas are of Early Devonian age, mostly Emsian. No faunas are recognized from the Frasnian and only one specimen has been referred to questionable Famennian strata. Australian and Northern Africa faunas show closer affinity to Baltica faunas at the generic level. The Australian and southwestern edge Gondwanan faunas have the most endemic genera. These may be cold water Devonian faunas or they may support a generally warmer global climate for the Devonian as the southwestern edge faunas were living at 60° to 85° S latitude.

Early Carboniferous crinoid faunas are known from Northern Africa, India, eastern Australia, and South America. Most faunas are of late Tournaisian or Viséan age and dominated by camerates. Early Tournaisian and Namurian faunas are few. All known faunas lived within 35° of the palaeoequator and are judged to be warm water faunas. Two endemic genera are recognized in the Australian fauna and one in the Indian fauna.

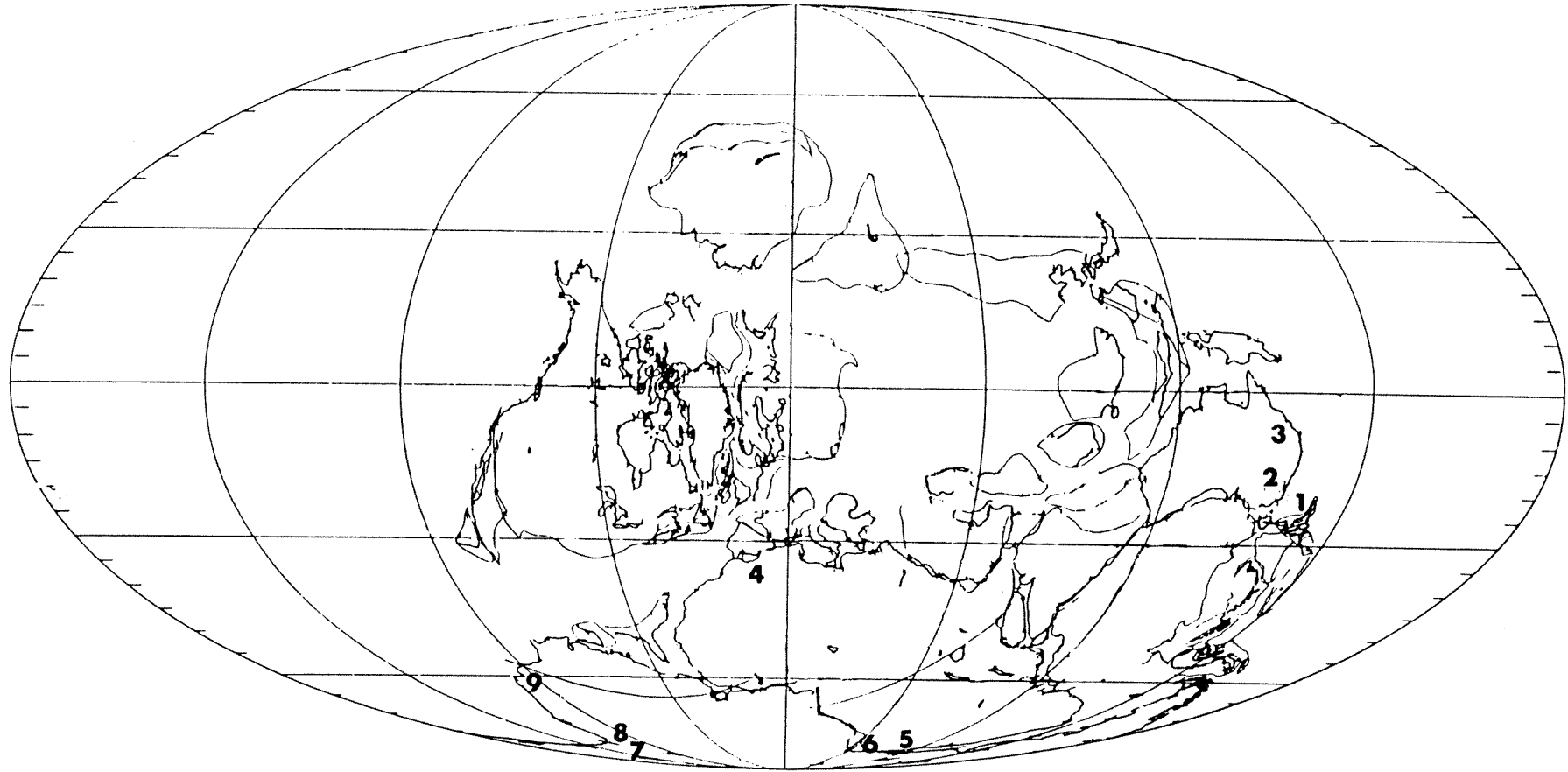
Late Carboniferous Westphalian faunas are known from Brazil, Algeria, Pakistan, and eastern Australia. Stephanian faunas are unknown. Faunas are dominated by poteriocrininids. The Brazilian and Algerian warm water faunas were living within 30° of the palaeoequator while the Australian fauna from Queensland was living between 45° and 50° S latitude. The Australian fauna is considered a cooler water fauna that lived in a slightly warmer interglacial between Gondwana Carboniferous glaciations. One endemic genus is recognized in the Algerian fauna and three endemic genera are recognized in the Queensland fauna.

INTRODUCTION

The first crinoids from Gondwana were reported in the mid 1800s when Sharpe and Salter (1856) and Salter (1856) described a Devonian camerate crown from South Africa and de Koninck (1863) described a Carboniferous poteriocrinitid crown from the Salt Range of what is today Pakistan. The other 91 Devonian taxa (Appendix 1) were described between 1913 and 1990. Most of the taxa were reported from North Africa (Larrauri y Mercadillo 1944; Le Maitre 1954; Termier 1936; Termier, H. and G. 1949, 1974; Termier, G. and H. 1950; Le Menn 1990a, 1990b; Le Menn and Regnault 1993; Prokop and Petr 1987; Turek 1988) and Australia (Philip 1961; Hill *et al.* 1967; Bates 1972; Jell and Holloway 1983; Jell *et al.* 1988). South American taxa were described by Branisa (1965), McIntosh (1981, 1983, 1987, 1988) Waisfeld (1989), and Haude (1995). Two taxa were described, one each, from West Falkland

Island (Kirk 1913; Castellano 1967) and New Zealand (Prokop 1970). Taxa reported from India between 1976 and 1985 are not included in this study, as they are probably from Europe and considered to be from Gupta-fabricated localities (Webster 1991).

A number of additional Carboniferous crinoids (Appendix 2) were reported from Australia (de Koninck 1877–1878, 1898; Etheridge 1892a; Etheridge 1892b; Dun and Benson 1920), Brazil (Katzer 1903, 1933; Strimple 1960; Lane 1964), and Pakistan (Reed 1925) in the late 1800s and early 1900s, but most faunas have been reported within the last 50 years from North Africa (Delpy 1941; Termier, G. and H. 1947, 1950; Pareyn 1961; Strimple and Pareyn, 1982; Bowsher and Strimple 1986) and Australia (Campbell and Bein 1971; Lindley 1979, 1988; Webster and Jell 1999). *Proampelocrinus himalayaensis* Gupta and Webster



Late Early Devonian (Emsian)

Figure 1 Plate reconstruction for the late Early Devonian, Emsian, showing Early Devonian crinoid localities for Gondwana continents. Locality numbers are: 1 - New Zealand; 2 - Australia, New South Wales; 3 - Australia, Queensland; 4 - North Africa, Morocco and Algeria; 5 - South Africa; 6 - West Falkland Island; 7 - Argentina; 8 - Bolivia; 9 - Columbia. Multiple localities represented by localities 2, 3, and 4. Map modified from Scotese and McKerrow 1990.

(1974) is one of the few "Gupta" taxa (Webster 1991) known to be from an India Himalayan locality, as corrected by Ahluwalia (1989).

The purpose of this paper is to summarize the known Devonian and Carboniferous crinoid faunas of Gondwana, compare them to one another, relate them to correlative Laurentian, Baltic, and Chinese faunas, and denote their palaeogeographic distribution. This is considered a preliminary study because three Devonian faunas, two from Australia and one from South Africa, are currently under investigation by P. A. Jell (pers. comm.). These faunas will significantly increase the number of endemic taxa from Gondwana. The recent reports of Chinese Devonian (Chen and Yao 1993; Hou *et al.* 1994; Lane *et al.* 1997) and Carboniferous (Chen and Yao 1993; Lane *et al.* 1996) crinoids provide descriptions of the first major faunas of these ages to be reported from China. They provide a preliminary data base for comparisons, whereas the few specimens previously known from China were too small to use for meaningful comparisons.

DEVONIAN FAUNAS

The 92 reported Devonian crinoids from Gondwana as listed in Appendix 1 do not include taxa based on columnals and may be summarized as follows: 36 taxa identified to the species level, with one species reported from two localities; 7 taxa identified to genus level and referred (aff. or cf.) to a named species; 25 taxa identified only to genus level; 49 genera recognized; 11 unidentified taxa referred to a family or higher classification category; and 12 unclassified, unidentified taxa based on fragmentary specimens and isolated ossicles. Many of the taxa identified only to genus are based on a single specimen and many are based on incomplete material. I currently consider the identifications of several of these tentative at best and I question a few of the other identifications, but would have to see the specimens to verify the identifications.

Most of the Gondwana Devonian taxa are of Early Devonian age, Lochkovian to Emsian. Frasnian faunas are unknown from Gondwana. A single fragmentary specimen has been reported from

Table 1 Generic lists of Devonian crinoid faunas of Gondwana. Genera preceded by an asterisk (*) are endemic.

NEW ZEALAND			
Camerates:			
<i>Megistocrinus</i>			
AUSTRALIA			
Camerates:			
<i>Acanthocrinus</i>	Disparids	Cyatho/Dendrocrininids	
<i>Dolatocrinus</i>	<i>Tiaracrinus</i>	<i>Codiocrinus</i>	
<i>Eucalyptocrinites</i>		<i>Cupressocrinites</i>	
<i>Hexacrinites</i>		<i>Dendrocrinus</i>	
<i>Melocrinites</i>		<i>Kooptoonocrinus</i>	
<i>Monstrocrinus</i>		* <i>Pandanocrinus</i>	
<i>Rhipidocrinus</i>		<i>Parapisocrinus</i>	
* <i>Shimantocrinus</i>		<i>Pernerocrinus</i>	
* <i>Struzocrinus</i>			
<i>Thylacocrinus</i>			
NORTH AFRICA			
Camerates:			
<i>Acanthocrinus</i>	Disparids	Poteriocrininids	Uncertain
<i>Cyttarocrinus</i>	<i>Haplocrinites</i>	<i>Lophocrinus</i>	<i>Edriocrinus</i>
<i>Diamenocrinus</i>	<i>Tiaracrinus</i>		
<i>Griphocrinus</i>			
<i>Hexacrinites</i>			
* <i>Marhoumacrinus</i>			
<i>Monstrocrinus</i>			
<i>Oehlerticrinus</i>			
<i>Rhodocrinites</i>			
<i>Scyphocrinites</i>			
<i>Thylacocrinus</i>			
SOUTHWESTERN GONDWANA			
Camerates:			
* <i>Apurocrinus</i>	Disparids	Cyathocrininids	Poteriocrininids
* <i>Bogotacrinus</i>	* <i>Radicalcarocrinus</i>	<i>Cyathocrinites</i>	<i>Maragnicrinus</i>
* <i>Boliviocrinus</i>		<i>Pyrenocrinus</i>	
* <i>Ophiocrinus</i>			
<i>Pterinocrinus</i>			

questionable Famennian strata of Morocco (Termier, H. and G. 1974).

The Devonian crinoids of Gondwana (Figure 1) are reported from three regions: Australia/New Zealand, Northern Africa, and a belt running across the southwestern margin from the Karoo Basin in South Africa, through West Falkland Island, into the Chaco Basin in Argentina and Bolivia (Tankard *et al.* 1995), into Columbia. Each of these regions is discussed individually.

Most Devonian crinoids of Australia are known from Victoria and New South Wales, with a few from Queensland. They range in age from the Silurian-Devonian transition beds of the Dargile and Humevale Formations (Jell and Holloway 1983) to the late Eifelian and early Givetian Papilio Formation (Jell *et al.* 1988). The largest fauna, 9 taxa, is from the Pragian Garra Formation (Jell *et al.* 1988).

A comparison of the Australian/New Zealand faunas to those reported from non-Gondwana regions (Table 1) was made using an unpublished index compilation (1759-1995) of the Palaeozoic crinoids based largely upon the works of Bassler and Moodey (1943) and Webster (1973, 1977, 1986, 1988, 1993). Of the 18 identified genera from Australia and one from New Zealand, four (*Parapisocrinus*, *Melocrinites*, *Hexacrinites*, and *Cupressocrinites*) are considered cosmopolitan equatorial taxa in the Devonian. Four genera (*Kooptoonocrinus*, *Pandocrinus*, *Shimantocrinus*, and *Struszocrinus*) are Australian endemics. Four genera (*Codiocrinus*, *Rhipidocrinus*, *Tiarocrinus*, and *Monstrocrinus*) are also recognized in Baltica. Three genera (*Megistocrinus*, *Thylacocrinus*, and *Acanthocrinus*) are recognized in both Baltica and Laurentia. *Dolatocrinus* is known from Laurentia. *Dendrocrinus* is a range extension at the Silurian-Devonian transition as Middle Silurian species are recognized in Laurentia and Ordovician and Early Silurian species are recognized in Baltica. Species of *Eucalyptocrinites* are known from the Silurian of Baltica and Laurentia, but only from Baltica and Russia in the Devonian. *Pernerocrinus* is also known from Baltica and Japan. Thus, the Australian faunas have a slightly closer alliance with the Baltic faunas than those of Laurentia.

North African faunas were also compared to non-Gondwana faunas at the generic level, excluding *nomen vetitum* genera. Of the 15 genera recognized in Northern Africa, four (*Haplocrinites*, *Hexacrinites*, *Rhodocrinites*, and *Scyphocrinites*) are considered cosmopolitan equatorial taxa. Five (*Acanthocrinus*, *Cyttarocrinus*, *Griphocrinus*, *Thylacocrinus*, and *Edriocrinus*) are recognized in Baltica and Laurentia. Five (*Lophocrinus*, *Tiarocrinus*, *Oehlerticrinus*, *Monstrocrinus*, and *Diamenocrinus*) are recognized in Baltica, where *Lophocrinus* is known from the Viséan. *Marhoumacrinus* is known in the Devonian of Laurentia. The North African faunas have

stronger taxonomic affinities with Baltic faunas than they do with Laurentian faunas. Even more surprising is that none of the North African genera is in common with Spanish genera.

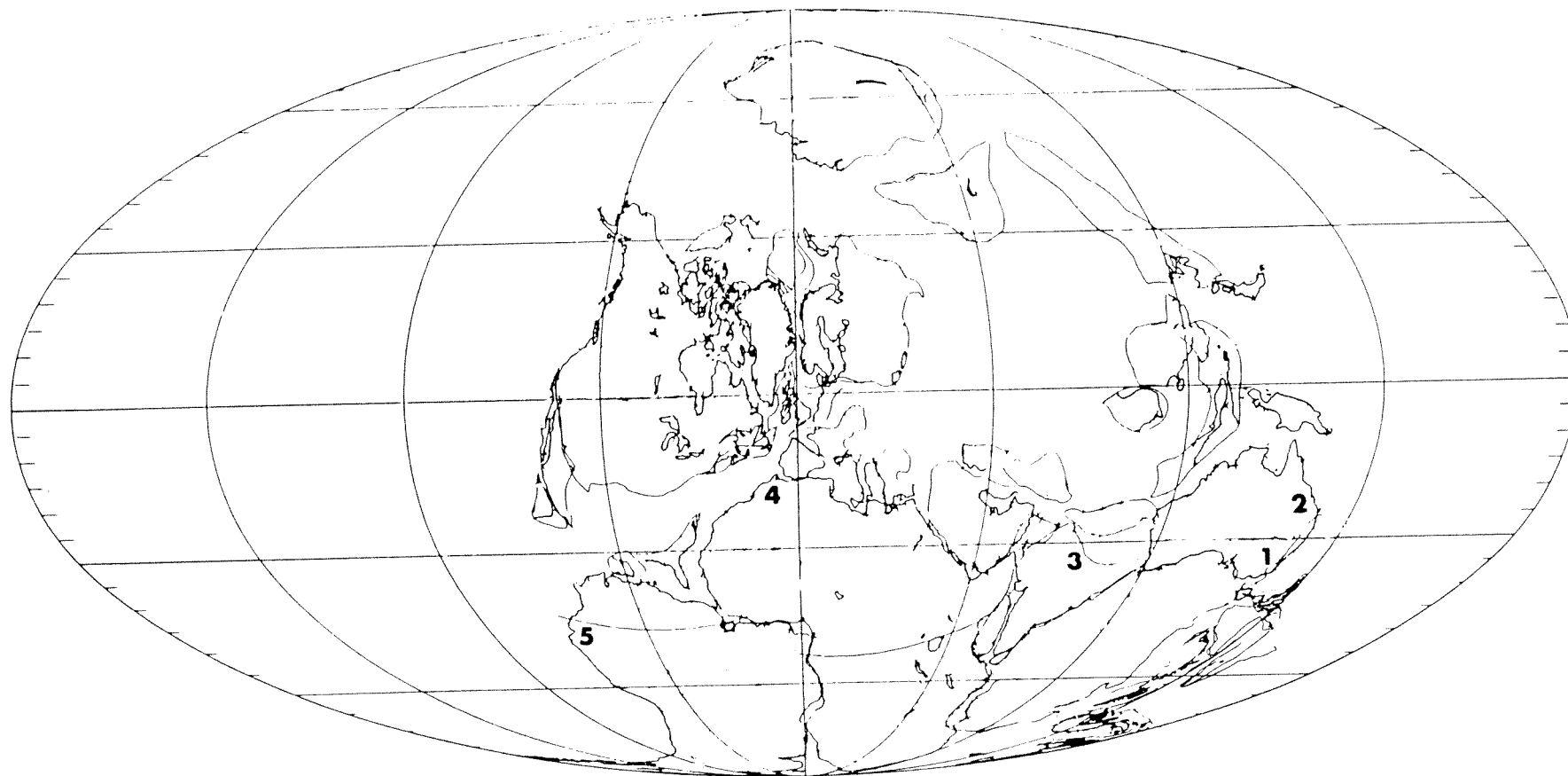
Five (*Apurocrinus*, *Boliviocrinus*, *Bogotocrinus*, *Ophiocrinus*, and *Radicalcarocrinus*) of the nine genera in the southwestern Gondwana faunas are endemics. *Cyathocrinites* is a cosmopolitan taxon. *Maragnicrinus* and *Pyrenocrinus* are known from Laurentia. *Pterinocrinus* is known from Baltica and Laurentia. This fauna has slightly closer affinity to North American faunas than Baltic but is considered poorly known. It does not correlate with other Gondwana faunas as none of the nine taxa are recognized in any of the other faunas. The occurrence of these faunas in the high southern latitudes, greater than 60°S, is well away from the other Gondwana faunas which are all within 40° of the palaeoequator as are all other known Devonian faunas. The endemism in the taxa may reflect a cooler water environment of the higher latitudes, but the crinoid occurrences may support the world wide warm climate of the Early Devonian suggested by Frakes *et al.* (1992).

Few genera are common between Gondwanan localities. Those recognized from Australia and North Africa are: *Hexacrinites*, *Acanthocrinus*, *Monstrocrinus*, *Thylacocrinus*, and *Tiarocrinus*. These common occurrences are all within the equatorial belt localities.

The diversity of all Gondwana Devonian faunas is dominated by camerate crinoids, especially rhodocrinitids which make up approximately one third (four of 11 genera) of the camerates in both the Australian and North African faunas. However, rhodocrinitids have not been reported in the Southwestern Gondwana faunas. Cyathocrininids and dendrocrininids form a significant (7 of 19 genera, 37%) part of the Australian faunas. They are unknown in the North African faunas. Disparids are minor parts of all faunas. Poteriocrininids are reported only from the North African and Southwestern Gondwana faunas. Flexibles have not been reported in the Devonian of Gondwana. In general the Gondwana Devonian crinoid faunas are considered poorly known because fauna diversities are smaller than those in major Baltic and Laurentian faunas and approximately 38% (35 of 92) of the taxa reported are based on incomplete material and not identified.

CARBONIFEROUS FAUNAS

The 122 reported Carboniferous crinoids from Gondwana, excluding columnal taxa, are given in Appendix 2. These faunas may be summarized as follows: 42 taxa identified to the species level, with four species reported from two localities; 4 taxa identified to genus level and referred (aff. or cf.) to



Early Carboniferous (Visean)

Figure 2 Plate reconstruction for the Early Carboniferous, Visean, showing Tournaisian and Visean crinoid localities for Gondwana continents. Locality numbers are: 1 - Australia, New South Wales; 2 - Australia, Queensland; 3 - India; 4 - North Africa, Morocco and Algeria; 5 - Columbia. Multiple localities represented by localities 1, 2, and 4. Map modified from Scotese and McKerrow 1990.

a named species; 56 taxa identified only to genus level; 46 genera recognized; 14 unidentified taxa referred to a family or higher classification category; and 11 unclassified, unidentified taxa based on fragmentary specimens and isolated ossicles. Many of the taxa identified only to genus are based on a single specimen and many are based on incomplete material.

Although most of the Carboniferous faunas are of Tournaisian and Visean age there are significant numbers of Westphalian and Namurian taxa recognized. Namurian taxa identified by G. Ubaghs and J. Wright (in Pareyn 1961) from northern Africa have not been illustrated or described; they are accepted tentatively, pending future study. No Stephanian faunas have been reported from Gondwana. For comparison with non-Gondwana faunas, the Carboniferous faunas are divided into Early and Late Carboniferous. For simplicity Tournaisian and Visean localities are shown on Figure 2, a plate reconstruction for the Visean. It should be noted that all localities, except the one in South America, are within 35° of the palaeoequator. Australian and South American faunas developed

in basins adjacent to the Panthalassa Ocean, North African localities in basins off the closing Phoebeic Ocean, and the Indian locality in a basin along the Tethys Ocean.

The Australian faunas (Table 2) have: two endemic genera (*Glyphyocrinus*, *Manillacrinus*), six cosmopolitan genera (*Amphoracrinus*, *Actinocrinites*, *Platycrinites*, *Dichocrinus*, *Synbathocrinus*, *Cyathocrinites*), five genera (*Periechocrinus*, *Sampsonocrinus*, *Litocrinus*, *Abrotocrinus*, *Holcocrinus*) also recognized in Baltica and Laurentia, three genera (*Aacocrinus*, *Cribanocrinus*, *Histocrinus*) also known in Laurentia, and two genera (*Dialutocrinus*, *Eumorphocrinus*) also found in Baltica. The reports of "*Poteroicrinites*" and "*Poteroicrinus*" are considered poteroicrininids, but incorrect identifications, and may represent additional endemics. The faunas are strongly dominated by camerates, 11 of 18 genera.

North African Visean faunas are also dominated by camerates, five of 10 genera. These faunas have five cosmopolitan taxa (*Actinocrinites*, *Amphoracrinus*, *Platycrinites*, *Synbathocrinus*, *Poteroicrinites*) and five genera (*Rhodocrinites*,

Table 2 Generic lists of Early Carboniferous crinoids from Gondwana. Genera preceded by an asterisk (*) are endemic. Genera followed by a pound sign (#) are from the faunal lists of Pareyn (1961).

AUSTRALIA, TOURNAISIAN			
Camerates:	Disparids	Cyathocrininids	Poteroicrininids
<i>Aacocrinus</i>	<i>Synbathocrinus</i>	<i>Cyathocrinites</i>	<i>Histocrinus</i>
<i>Actinocrinites</i>			<i>Holcocrinus</i>
<i>Cribanocrinus</i>			<i>Poteroicrinites</i>
<i>Dialutocrinus</i>			" <i>Poteroicrinus</i> "
<i>Dichocrinus</i>			
<i>Eumorphocrinus</i>			
* <i>Glyphyocrinus</i>			
* <i>Manillacrinus</i>			
<i>Periechocrinus?</i>			
<i>Platycrinites</i>			
AUSTRALIA, VISEAN			
Camerates:	Disparids		
<i>Aacocrinus</i>	<i>Litocrinus</i>		
<i>Dialutocrinus</i>			
<i>Platycrinites</i>			
<i>Sampsonocrinus</i>			
NORTH AFRICA, VISEAN			
Camerates:	Disparids	Poteroicrininids	Flexibles
<i>Actinocrinites</i>	<i>Synbathocrinus</i>	<i>Abrotocrinus</i>	<i>Taxocrinus</i>
<i>Actinocrinites#</i>		<i>Poteroicrinus</i>	<i>Eutaxocrinus#</i>
<i>Amphoracrinus</i>		<i>Rhabdocrinus#</i>	
<i>Platycrinites</i>			
<i>Rhodocrinites</i>			
INDIA, LATE TOURNAISIAN OR EARLY VISEAN			
Poteroicrininids			
* <i>Proampelocrinus</i>			
SOUTH AMERICA, PROBABLY EARLY CARBONIFEROUS			
Poteroicrininids			
<i>Lophocrinus?</i>			

Abrotocrinus, *Rhabdocrinus*, *Taxocrinus*, *Eutaxocrinus*) also known from Baltica and Laurentia. Some of the specimens currently identified as *Actinocrinites* may belong to other actinocrinitid genera. Three of the North African cosmopolitan genera (*Actinocrinites*, *Platycrinites*, *Synbathocrinus*) are also recognized in the Australian faunas, adding to the cosmopolitan aspect of these genera and showing some generic level correlation of the two faunas. Neither the Australian nor North African faunas show a significantly stronger affinity with Baltic or Laurentian faunas and no affinity with Spanish faunas at the genus level.

The Tournaisian or Visean *Proampelocrinus* from India is an endemic related to *Ampelocrinus*, a Visean form in England and Namurian and Westphalian taxa of Laurentia. *Lophocrinus?* is from South America (Columbia) and of uncertain, but probably Early Carboniferous age. *Lophocrinus* is a Visean genus known from Germany and Spain. The Indian and South American taxa may not be correlated with the Australian or North African faunas on the basis of the crinoids because no genera are currently recognized as common.

Namurian and Westphalian localities are plotted on Figure 3, a plate reconstruction for the Westphalian. North African and South American

localities are within 35° of the palaeoequator, whereas Australia and Pakistan localities are between 45° and 50° S latitude. The Australian and Pakistan localities are interpreted as representing warm highstand sealevel phases between Gondwana lowstand glacial stages. North African and South American localities are considered to have been within the warmer equatorial belt.

Namurian faunas (Table 3) of North Africa are dominated by poteriocrinitids (6 genera) and camerates (5 genera) followed by flexibles (3 genera) and a disparid. No endemic genera are currently recognized in these faunas. These faunas have five cosmopolitan genera (*Actinocrinites*, *Amphorocrinus*, *Platycrinites*, *Rhodocrinites*, *Synbathocrinus*), five genera (*Pleurocrinus*, *Aphelecrinus*, *Fifeocrinus*, *Phanocrinus*, *Eutaxocrinus*) also known from Baltica and Laurentia, three genera (*Hydreionocrinus*, *Ureocrinus*, *Zeacrinites*) also found in Baltica, two genera (*Cibolocrinus*, *Mysticocrinus?*), also known from the Laurentia. However, *Mysticocrinus?* is considered a misidentification of an uncertain flexible crinoid and *Cibolocrinus* is most diverse and abundant in the Permian of Timor. The faunas show a slightly closer relationship with Baltic faunas than with Laurentian faunas. They also represent the

Table 3 Generic lists of Namurian and Westphalian crinoids from Gondwana. Genera preceded by an asterisk (*) are endemic. Genera followed by a pound sign (#) are from the faunal lists of Pareyn (1981).

NORTH AFRICA, NAMURIAN

Camerates	Disparids	Poteriocrininids	Flexibles
<i>Actinocrinites</i> #	<i>Synbathocrinus</i> #	<i>Aphelecrinus</i> #	<i>Cibolocrinus</i>
<i>Amphorocrinus</i> #		<i>Fifeocrinus</i> #	<i>Mysticocrinus?</i>
<i>Platycrinites</i> #		<i>Hydreionocrinus</i> #	<i>Eutaxocrinus</i> #
<i>Pleurocrinus</i> #		<i>Phanocrinus</i> #	
<i>Rhodocrinites</i> #		<i>Zeacrinites</i> #	
		<i>Ureocrinus</i> #	

AUSTRALIA, WESTPHALIAN

Camerates:	Cyathocrininids	Poteriocrininids
* <i>Denarioacrocrinus</i>	* <i>Kopriocrinus</i>	<i>Prininocrinus</i>
	* <i>Neerkolocrinus</i>	

NORTH AFRICA, WESTPHALIAN

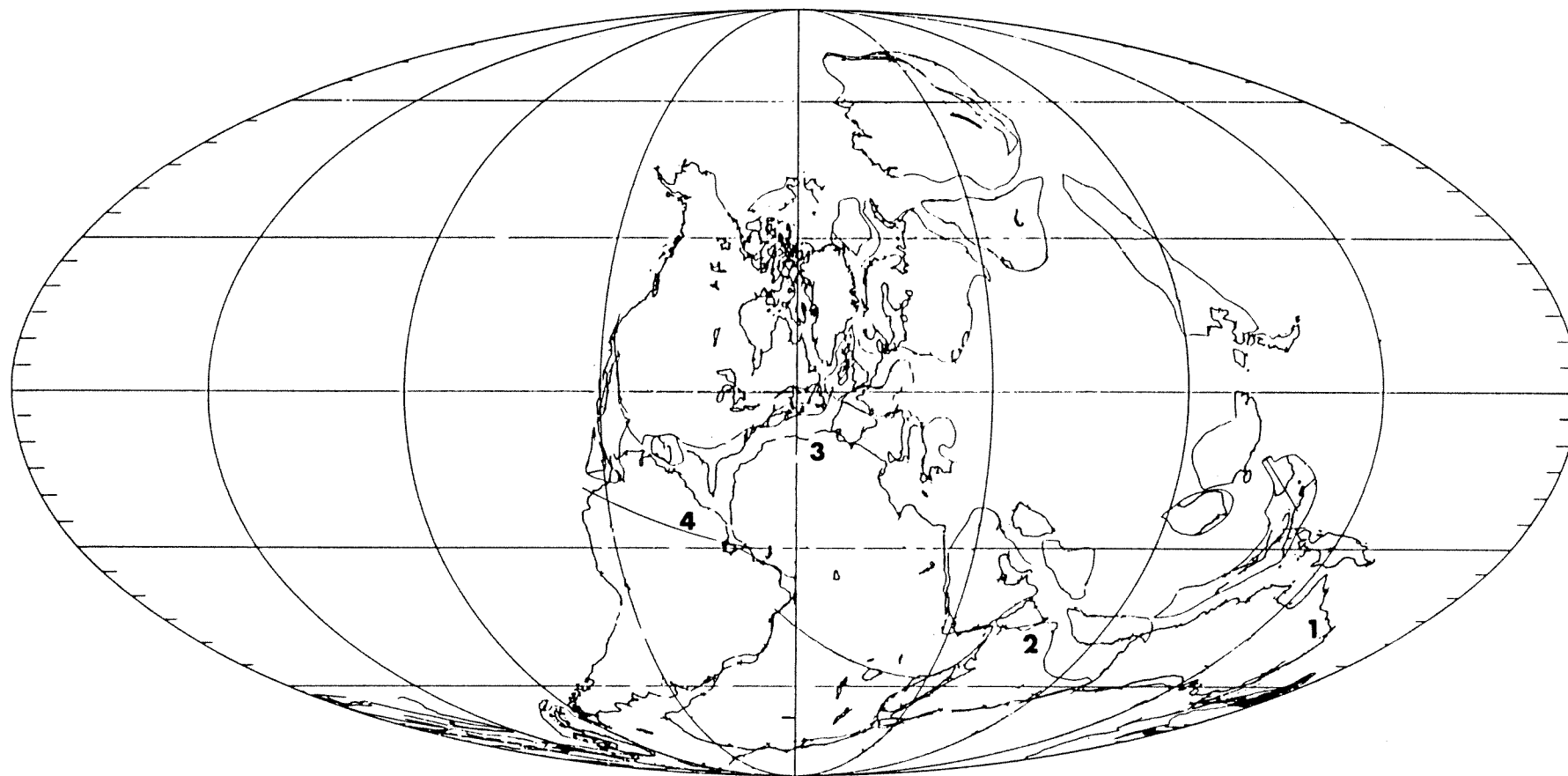
Camerates:	Poteriocrininids	Flexibles
* <i>Becharocrinus</i>	<i>Abrotocrinus</i>	<i>Taxocrinus</i>
<i>Dichocrinus</i>	<i>Apographiocrinus</i>	
<i>Platycrinites</i>	<i>Blothrocrinus?</i>	
<i>Pleurocrinus</i>	<i>Erisocrinus</i>	
	<i>Parulocrinus</i>	
	<i>Stuartwellerocrinus?</i>	

SOUTH AMERICA, WESTPHALIAN

Poteriocrininids
<i>Erisocrinus</i>
<i>Parulocrinus</i>

PAKISTAN, LATE CARBONIFEROUS

Poteriocrininids
<i>Graphiocrinus</i>
<i>Woodocrinus</i>



Late Carboniferous (Westphalian)

Figure 3 Plate reconstruction for the Late Carboniferous, Westphalian, showing Namurian and Westphalian crinoid localities for Gondwana continents. Locality numbers are: 1 - Australia, Queensland; 2 - Pakistan; 3 - North Africa, Morocco and Algeria; 4 - Brazil. Multiple localities represented by localities 2 and 3. Map modified from Scotese and McKerrow 1990.

changeover from camerate dominance of older Early Carboniferous faunas to the poteriocrininid dominance of younger Early Carboniferous and Late Carboniferous faunas. The presence of three flexibles in these faunas is the greatest known in any Devonian or Carboniferous fauna of Gondwana. Except for the cosmopolitan genera (*Actinocrinites*, *Platycrinites*, *Amphoracrinus*, *Synbathocrinus*) none of the North African taxa is recognized in the Chinese Carboniferous faunas reported by Chen and Yao (1993) and Lane *et al.* (1996) or the Japanese faunas reported by Minato (1951) and Hashimoto (1984). Only *Actinocrinites* and *Platycrinites* are known in the Japanese faunas.

Westphalian faunas are more widely known in Gondwana (Table 3). The Australia fauna contains three endemics (*Denarioacrocrinus*, *Kopriacrinus*, *Neerkolocrinus*) and *Prininocrinus*, a genus previously known only from the Late Devonian of northwestern Canada. The cyathocrininid genera *Kopriacrinus* and *Neerkolocrinus* are late Palaeozoic representatives of the Euspirocrinidae, a family most diverse in the Silurian. They are considered holdovers in Australia. None of the Australian Westphalian genera is known in other Gondwana faunas.

North African faunas are the most diverse Westphalian faunas known from Gondwana. They are dominated by poteriocrininids, 6 genera, and camerates, 4 genera. These faunas contain one endemic genus (*Becharocrinus*), two cosmopolitan genera (*Dichocrinus*, *Platycrinites*), five genera (*Abrotocrinus*, *Apographiocrinus*, *Blothrocrinus?*, *Erisocrinus*, *Taxocrinus*) also known from Baltica and Laurentia, and two genera (*Parulocrinus*, *Stuartwellerocrinus?*) also found in Laurentia. Although the identifications of *Blothrocrinus* and *Stuartwellerocrinus* are considered incorrect, the specimens are poteriocrininids and may represent new genera. Overall the fauna has a slightly closer Laurentian aspect than Baltic and contains two genera, *Erisocrinus* and *Parulocrinus*, in common with Brazil.

The two poteriocrininid taxa from undesignated Late Carboniferous strata of Pakistan are possibly Namurian as *Woodocrinus* is known from Tournaisian into Namurian strata of England. *Graphiocrinus* is a longer ranging, Early Carboniferous to Late Permian, cosmopolitan form recently reported from China (Lane *et al.* 1996).

CONCLUSIONS

Gondwana Devonian and Carboniferous crinoid faunas generally show less diversity than Laurentian and Baltic faunas of the same age. At this time it is uncertain how much of the difference is an artifact of lack of collection of the Gondwanan faunas or other factors such as environmental differences, etc.

Gondwana faunas contain the equatorial cosmopolitan taxa previously recognized in, and taxa related to the families that tend to dominate, most coeval Laurentian and Baltic faunas. Most Gondwana endemic genera are assignable to families previously recognized in Laurentia and Baltica. Perhaps most surprising is that the Gondwana genera are not common to those of the Spanish block as reported by Breimer (1962).

Recognition of taxa living in high latitudinal regions of the Devonian are the earliest known in the Palaeozoic. These taxa lived in a tectonic trough extending across southwestern Gondwana from the Karoo Basin in South Africa to the Falkland Islands through the Chaco Basin in Argentina and Bolivia into Columbia. They are poorly known and represent an endemic family in addition to forms known from Laurentia and Baltica.

Carboniferous taxa of Australia, Africa, and South America are interpreted as having lived in interglacial highstand environments. These faunas may represent taxa that moved into or evolved in somewhat cooler environments than the equatorial environments recognized herein for the families or genera to which they are assigned.

No attempt was made to compare the Gondwanan faunas, as recognized, with the few specimens reported from tectonic blocks in southeastern Asia thought to be derived from Gondwana prior to the Permian breakup. Most specimens from these tectonic blocks are columnals (Mansuy 1912, 1920; Reed 1908; Pitakpaivan *et al.* 1969) or disarticulated cup plates (Reed 1908; Pitakpaivan *et al.* 1969). Additional collection within these blocks is needed for evaluation of these faunas and future comparisons.

Additional Devonian and Carboniferous faunas from Gondwana, currently under study, will increase the number of taxa known from some of the areas discussed herein and increase the known distribution within the Devonian of Gondwana. These faunas will significantly increase the number of Gondwanan endemics, and probably modify the general relative abundances of taxa at the class, order, and suborder given herein.

ACKNOWLEDGEMENTS

The reviews of N. Gary Lane and Chris Maples are gratefully acknowledged. This is a contribution to IGCP Project 421: *North Gondwana mid-Palaeozoic bioevent/biogeography patterns in relation to crustal dynamics*.

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Manuscript received March 1999; accepted October 1999.

APPENDICES

Appendix 1 Devonian crinoids of Gondwana. Taxa listed by age, geographic region, and stratigraphic formation if given. Asterisk (*) preceding genus indicates type species of endemic genus. Original identifications of taxa indented below later identifications. Specimens based on loose ossicles or multiple taxa are explained in parentheses after the listing.

Australia:

Late Silurian - Early Devonian, transition beds of Dargile Formation - Humevale Formation

Dimerocrinitidae gen. et sp. nov. Jell and Holloway 1983

**Kooptoonocrinus nutti* Jell and Holloway 1983

Codiocrinus rarus Jell and Holloway 1983

Dendrocrinus saundersi Jell and Holloway 1983

Emsian, "Mount Holly Beds"

Pandanocrinus sp. cf. *P. wellingtonensis* Jell et al. 1988

Pragian, Garra Limestone

Eucalyptocrinites rosaceus Goldfuss 1831. Jell et al. 1988

Melocrinites solus Jell et al. 1988

Inadunate indet. Jell et al. 1988

Pandanocrinus wellingtonensis Jell et al. 1988

Pandanocrinus geuriensis Jell et al. 1988

Polypeltid indet. Jell et al. 1988

**Shimantocrinus distinctodorsus* Jell et al. 1988

Spyridiocrinid gen. et sp. nov. Jell et al. 1988

**Struszocrinus dulciculus* Jell et al. 1988

Late Pragian, "Loyola Limestone"

Eucalyptocrinites fonzi Jell et al. 1988

Early Pragian, Shield Creek Formation, Martins Well Limestone Member

**Pandanocrinus martinswellensis* Jell et al. 1988

Parapisocrinus sp. Jell et al. 1988

Crinoid gen. et sp. nov. Hill et al. 1967 (camerate calyx)

Gasterocomid indet. Jell et al. 1988

Early Pragian olistoliths

Eucalyptocrinites inchoatus Philip 1961

Hexacrinites? sp. Philip 1961

Thylacocrinus? *ignotus* Philip 1961

Pragian, Lilydale Limestone

Pernerocrinus discus Bates 1972

Pernerocrinus sp. Bates 1972

Late Emsian - Eifelian, undifferentiated Broken River Group

Carpocrinid indet. Jell et al. 1988

Crinoid Indet. 1 Jell et al. 1988

Eifelian - Givetian, Papilio Formation

Cupressocrinites abbreviatus Goldfuss 1839. Jell et al. 1988

Rhipidocrinus crenatus (Goldfuss 1831). Jell et al. 1988

Rhodocrinus crenatus (Goldfuss 1831). Pictet 1857 (sic)

Rhipidocrinus? sp. Jell et al. 1988

Dolatocrinus peregrinus Jell et al. 1988

Melocrinites tempestus Jell et al. 1988

Givetian, Burdekin Limestone

Cupressocrinites abbreviatus Goldfuss 1839. Jell et al. 1988

Crinoid Indet. 2 Jell et al. 1988

New Zealand:

Undesignated Early Devonian, Reefton Group

Megistocrinus reeftonensis Prokop 1970

Argentina:

Early Devonian, probably Emsian

Cyathocrinites elongatus (Knod 1908). Castellano 1967

Pterinocrinus? *australis* Haude 1995

**Radicalcarocrinus huenickeni* Haude 1995

Cyathocrinitid Waisfeld 1989

Maragnicrinus? sp. Waisfeld 1989; Webster 1997

Bridgerocrinus sp. Waisfeld 1989

Calceocrinid Waisfeld 1989, p. 277, Fig. 5, no. B

Bolivia:

- Early Devonian, Emsian?, Icla Series or uncertain horizon
 Crinoidea indet. 1 Branisa 1965 (three advanced inadunate crowns)
 Crinoidea indet. 2 Branisa 1965 (calyx, order indeterminate)
 Crinoidea indet. 6 Branisa 1965 (anal tube? plates)
 Crinoidea indet. 7 Branisa 1965 (two inadunate crowns)
 Crinoidea indet. 8 Branisa 1965 (camerate?)
 Emsian?, Belen Formation
 **Apurocrinus sucrei* McIntosh 1981
 Eifelian, Sicasica Formation
 **Boliviocrinus isaacsoni* McIntosh 1988

Columbia:

- Emsian - Eifelian, Floresta Formation
 **Bogotocrinus scheibei* Schmidt 1937. McIntosh 1987

West Falkland Island:

- Emsian?, Fox Bay Formation?
Pyrenocrinus? doubleti (Kirk 1913). McIntosh 1983
Botryocrinus doubleti Kirk 1913. Castellano 1967; McIntosh 1983

South Africa:

- Early Devonian, probably Emsian, Bokkeveld Series (Sharpe and Salter 1856)
 **Ophiocrinus stangeri* Sharpe and Salter 1856

North Africa:

- Late Silurian, late Pridoli or Early Devonian, early Lochkovian, Algeria
 **Marhoumacrinus legrandi* Prokop and Petr 1987
 Lochkovian, Algeria
Scyphocrinites sp. Turek 1988
 Pragian, Morocco
Acutobrachiola sp. 1 Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachials)
Acutobrachiola sp. 2 Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachials)
 cf. *Acutobrachiola* sp. Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachials)
Basotheca sp. Termier, H. and Termier, G. 1974. (*nom. vet.*) (basal plate? or basal circlet?)
Hexumbrella sp. Termier, H. and Termier, G. 1974. (*nom. vet.*) (tegminals?)
Latibrachiola sp. 1 Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachials)
Microradioles sp. Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachials)
Radiobrachiola sp. 1 Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachials)
 Coblenzian, Algeria
Acanthocrinus aff. *jaekeli* Schmidt 1942. Le Maitre 1958a
 Coblenzian or Couvinian, Morocco
 Codiocrinidae? Le Maitre 1958a. (theca)
 Coblenzian or Emsian, Chefar El Ahmar Formation, Algeria
Tiarocrinus rarus (Barrande) 1887. Le Menn 1990a
 Siegenian, Algeria
Oehlertocrinus sp. Le Menn 1975
 Siegenian, Morocco
 Fragments de Crinioïdes indéterminés Termier, G. and Termier, H. 1950
 Emsian, Morocco
 Fragment of a brachiale Termier, H. and Termier, G. 1974 (brachial)
Radiobrachiola sp. 2 Termier, H. and Termier, G. 1974 (*nom. vet.*) (brachials)
Cyttarocrinus laghdadensis Le Menn and Regnault 1993
 Emsian, La Grange Limestone, Algeria
Tiarocrinus moravicus Ubaghs and Boucek 1962. Le Menn 1990a
Monstrocrinus sp. Le Menn 1990b
 Undesignated Early Devonian, Morocco
Diamenocrinus sp. Termier, G. and Termier, H. 1950
Haplocrinites? sp. Termier, H. and Termier, G. 1974 (tegmenal)
 Indéterminé Termier, G. and Termier, H. 1950 (brachials)
Scyphocrinites elegans Zenker 1833
Scyphocrinus elegans (Zenker 1833). Termier 1936 (sic). Termier, H. and Termier, G. 1949; 1950 (sic)
Scyphocrinites spp.
Scyphocrinus spp.
 Termier, G. and Termier, H. 1947 (sic)
 Termier, G. and Termier, H. 1950 (sic)

- Eifelian, Algeria
 **Griphocrinus nodulosus* (Hall 1862). Le Maitre 1958a
 Lecanocrinid Le Maitre 1954
 **Tiarocrinus quadrifrons* Schultze 1866. Le Maitre 1954, 1958a, 1958b
- Eifelian, Morocco
Hexacrinites? sp.
Hexacrinus? sp. Termier, G. and Termier, H. 1950
- Couvinian, Algeria
Thylacocrinus aff. *vannioti* Oehlert 1878. Le Maitre 1958a
Edriocrinus cf. *pocilliformis* Hall 1859. Le Maitre 1954
 Lecanocrinidae? Le Maitre 1958a
- Couvinian, Morocco
Retibrachiola sp. 1 Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachial)
- Couvinian - Givetian, Morocco
Arcobrachiola sp. 1 Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachial)
- Givetian, Morocco
Haplocrinites clio (Hall 1862). Termier, G. and Termier, H. 1950
- Givetian, Algeria
Haplocrinites aff. *clio* (Hall 1862). Le Maitre 1958b
- Famennian?, Morocco
Brachiola sp. Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachial)
- Late Devonian or Early Carboniferous, Morocco
Brachiola sp. Termier, H. and Termier, G. 1974. (*nom. vet.*) (brachial)
- Undesignated Devonian, Morocco
 Cyathocrinoidea indéterminé Termier, G. and Termier, H. 1950. (thecae)
- Undesignated Devonian, Spanish Sahara
Lophocrinus aff. *minutus* (Roemer 1850)
Poteriocrinus aff. *minutus* Roemer 1850. Larrauri y Mercadillo 1944 (sic)
Rhodocrinites aff. *quinquangularis* Miller 1821. Larrauri y Mercadillo 1944

Appendix 2 Carboniferous crinoids of Gondwana. Taxa listed by age, geographic region, and stratigraphic formation if given. Asterisk (*) preceding genus indicates type species of endemic genus. Original identifications of taxa indented below later identifications. Specimens based on loose ossicles or multiple taxa are explained in parentheses after the listing. Taxa that I consider misidentified are indicated by a following notation. Taxa from faunal lists of Pareyn (1961) have not been illustrated or described and tentatively accepted pending study.

Australia, Queensland

- Early or middle Tournaisian, Neil's Creek Clastics
Actinocrinites sp. 2 Webster and Jell 1999
- Late Tournaisian, Rockhampton Group, Malchi Formation
Actinocrinites sp. 1 Webster and Jell 1999
Actinocrinites? sp. 3 Webster and Jell 1999
Aacocrinus sp. 1 Webster and Jell 1999
Manillacrinus brownei (Dun & Benson 1920) Webster and Jell 1999
Platycrinites sp. 2 Webster and Jell 1999
Platycrinites sp. 3 Webster and Jell 1999
Platycrinites sp. 4 Webster and Jell 1999
 Camerate indet. Webster and Jell 1999
Poteriocrinites smithii (Etheridge 1892b) Webster and Jell 1999
 Poteriocrinid cup indet. Webster and Jell 1999 (sic)
 Poteriocrinid arms indet. #1 Webster and Jell 1999 (sic)
 Poteriocrinid arms indet. #2 Webster and Jell 1999 (sic)
 Taxocrinid indet. Webster and Jell 1999
 Sagenocrinitoid indet. Webster and Jell 1999
- Tournaisian, Tellebang Limestone
Aacocrinus acylus Webster and Jell 1999

Australia, New South Wales

- Late Tournaisian, Namoi Formation
Cribanocrinus biseriatus Campbell and Bein 1971
 **Glyphyrocrinus expansus* Lindley 1988
Manillacrinus acanthus Webster and Jell 1999
 **Manillacrinus brownei* (Dun and Benson 1920). Campbell and Bein 1971
Cactocrinus? *brownei* Dun and Benson 1920. Campbell and Bein 1971

- Platycrinites testudo* Campbell and Bein 1971
Platycrinites sp. 1 Webster and Jell 1999
Holcocrinus barrabaensis Webster and Jell 1999
Histocrinus sp. nov. Campbell and Bein 1971
 Late Tournaisian, Goonoo Goonoo Mudstone
Manillacrinus sp. Campbell and Bein 1971
Platycrinites testudo Campbell and Bein 1971
Platycrinites? crokeri Campbell and Bein 1971
Platycrinites? sp. 1 Campbell and Bein 1971
Platycrinites? sp. 2 Campbell and Bein 1971
Platycrinites sp. 2 Campbell and Bein 1971
Synbathocrinus ogivalis de Koninck 1878, 1898; Campbell and Bein 1971
Cyathocrinites sp. Campbell and Bein 1971
Cyathocrinites sp. Campbell and Bein 1971
 Platycrininitid indet. Campbell and Bein 1971
Synbathocrinus sp. Campbell and Bein 1971
 Late Tournaisian, Dangarfield Formation
Eumorphocrinus elongatus Lindley 1979
Glaphyrocrinus expansus Lindley 1988
Glaphyrocrinus minutus Lindley 1988
 Unknown horizon, late Tournaisian?, possibly Namoi Formation
 Rhodocrinitid gen. nov. Webster and Jell 1999
Dichocrinus cf. *D. laudoni* Broadhead 1981. Webster and Jell 1999
 Scytalocrinid? indet. Webster and Jell 1999
 Late Tournaisian or early Visean, Mirari Limestone
Periechocrinus? sp. ind. Etheridge 1892b (crushed cup)
Actinocrinites spp. Etheridge 1892b
 Probably late Tournaisian or early Visean, Glen William Sandstone
Dialutocrinus polydactylus (Miller 1821). Wright, J. 1955a (not *D. polydactylus*, GDW)
Actinocrinus polydactylus (Miller 1821). de Koninck 1863. de Koninck 1877–1878
Actinocrinites polydactylus Miller, J. S. 1821. de Koninck 1898. Wright, J. 1955a
Platycrinites laevis? Miller 1821. de Koninck 1877–1878 (basal circllet, not a *Platycrinites*, GDW).
 Horizon unknown, probably late Tournaisian or early Visean
Periechocrinus indicator Etheridge 1892
Poteriocrinus radiatus? de Koninck 1877 (*non* Austin and Austin 1842) (part of a basal circllet)
Poteriocrinus tenuis? de Koninck 1877 (*non* Miller 1821), p. 159, Pl. 6, figs. 7–7a (basal plate)
- Australia, Queensland
 Visean, Baywulla Formation
Litocrinus sp. Webster and Jell 1999
 Visean?, Caswell Creek Group
Aacocrinus sp. 1 Webster and Jell, 1999
Sampsonocrinus cannindahensis Webster and Jell 1999
Dialutocrinus sp. Webster and Jell 1999
Platycrinites nux? (Etheridge 1892b). Webster and Jell 1999
- Australia, New South Wales
 Visean?, Flagstaff Formation?
 Actinocrinitid indet. Webster and Jell 1999
- Australia, Queensland
 Westphalian, Neerkol Formation
 **Denarioacrocinus neerkolensis* Webster and Jell 1999
Denarioacrocinus? ornatus Webster and Jell 1999
 **Neerkolocrinus typus* Webster and Jell 1999
Kopriacrinus mckellari Webster and Jell 1999
Prininocrinus namoiensis Webster and Jell 1999
 Undescribed crinoid. Etheridge 1892a
 Undescribed crinoid. Etheridge 1892a
 Impression of crinoid calyx Etheridge 1892a
- North Africa, Algeria
 Visean, P¹
 cf. *Rhabdocrinus scotocarbonarius* (Wright 1937). Pareyn 1961
 Visean, P²
Platycrinites sp. Pareyn 1961
Eutaxocrinus nov. sp. Pareyn 1961
Actinocrinites sp. Pareyn 1961

North Africa, Morocco

Visean

- Base indéterminé Termier, G. and Termier, H. 1950 (infrabasal? circlet)
- Actinocrinus* sp. Delpy 1941 (sic)
- Tegminale? de *Platycrinus* sp. Termier, H. and Termier, G. 1950 (tegmen plate).
- Taxocrinus* sp. Termier, G. and Termier, H. 1950
- Platycrinus* sp. Termier and Termier 1950 (sic) (brachials and radials).
- Platycrinus* sp. Delpy 1941 (sic)

Late Visean

- Amphoracrinus rochi* Delpy 1941. Termier, G. and Termier, H. 1950 (not an *Amphoracrinus*, GDW)
- Abrotocrinus ornatus* Termier, G. and Termier, H. 1950
- Bras Termier, G. and Termier, H. 1950 (partial arm)
- Bras pinulifère Termier, G. and Termier, H. 1950 (arm segment)
- Base de Flexibilia Termier, G. and Termier, H. 1950 (infrabasal? circlet)
- Plaque de Flexibilia indéterminée Termier, G. and Termier, H. 1950 (basal)
- Platycrinus* sp. Termier and Termier 1950 (sic)
- Platycrinus* sp. Termier and Termier 1950 (sic)
- Poteriocrinus crassus* (Miller 1821). Termier, G. and Termier, H. 1950 (sic) (set of arms)
- Rhodocrinites skourensis* (Delpy 1941)
- Rhodocrinus skourensis* Delpy 1941; Termier, G. and Termier, H. 1950 (sic)
- Synbathocrinus* sp. Termier, G. and Termier, H. 1950

North Africa, Algeria

Early Namurian E¹

- Amphoracrinus* nov. sp. A. Pareyn 1961
- Amphoracrinus* nov. sp. B. Pareyn 1961
- Actinocrinites* sp. A Pareyn 1961
- Actinocrinites* sp. B Pareyn 1961
- Pleurocrinus* sp. Pareyn 1961
- Rhodocrinus* sp. Pareyn 1961
- Synbathocrinus* nov. sp. Pareyn 1961
- Aphelocrinus* sp. or *Fifeocrinus* sp. Pareyn 1961
- cf. *Fifeocrinus tielensis* (Wright 1936). Pareyn 1961
- Ureocrinus* cf. *idoliolus* (Wright 1936). Pareyn 1961
- Phanocrinus* nov. sp. Pareyn 1961
- Zeacrinites* nov. sp. Pareyn 1961
- Eutaxocrinus* nov. sp. Pareyn 1961

Early Namurian, E²

- Phanocrinus* sp. Pareyn 1961
- Phanocrinus* nov. sp. Pareyn 1961
- Hydreionocrinus* nov. sp. Pareyn 1961

Namurian

- Cibolocrinus africanus* Strimple and Pareyn 1982

North Africa, Morocco

Namurian

- Bras d'un Crinoïde indéterminé Termier, G. and Termier, H. 1950 (brachials)
- Mysticocrinus?* sp. Termier, G. and Termier, H. 1950 (not a *Mysticocrinus*, GDW)

North Africa, Algeria

Early Westphalian

- **Becharocrinus paradoxus* (Termier and Termier 1950). Termier, H. and Termier, G. 1955
- Triacrinus paradoxus* Termier, G. and Termier, H. 1950

North Africa, Morocco

Early Westphalian

- **Becharocrinus paradoxus* (Termier and Termier 1950). Termier, H. and Termier, G. 1955
- Triacrinus paradoxus* Termier, G. and Termier, H. 1950
- Indéterminé Termier, G. and Termier, H. 1950 (partial theca)
- Dichocrinus?* sp. Termier, G. and Termier, H. 1950
- Parulocrinus* spp. Termier, G. and Termier, H. 1950

North Africa, Morocco

Westphalian

- Blothrocrinus balconi* Termier, G. and Termier, H. 1950 (not a *Blothrocrinus*, GDW)
- Dichocrinus* cf. *radiatus* Münster 1839. Termier, G. and Termier, H. 1950
- Base indéterminé Termier, G. and Termier, H. 1950 (infrabasal? circlet)
- Base indéterminé Termier, G. and Termier, H. 1950 (infrabasal? circlet)

cf. *Apical glyptus* Moore 1939. Termier, G. and Termier, H. 1950 (*nom. vet.*) (infrabasal?)
Apographiocrinus spp. Termier, G. and Termier, H. 1950
Abrotocrinus spp. Termier, G. and Termier, H. 1950 (not *Abrotocrinus* GDW)
Abrotocrinus spp. Termier, G. and Termier, H. 1950 (infrabasal or basal circllet, gen. indet. GDW)
 Bras de Crinoïde pinnule Articulata Termier, G. and Termier, H. 1950, (pinnules)
 Calices indéterminé Termier, G. and Termier, H. 1950 (theca)
Erisocrinus spp. Termier, G. and Termier, H. 1950
Parulocrinus wallacei Termier, G. and Termier, H. 1950
Platycrinites sp. Bowsher and Strimple 1986, (after Termier, G. and Termier, H. 1950)
Platycrinus sp. Termier, G. and Termier, H. 1950 (sic)
Pleurocrinus tuberculatus (Miller 1821)
Platycrinites tuberculatus Miller, J. S. 1821. Termier, G. and Termier, H. 1950
 Radiale d'un Dendrocrinoïdea indéterminé. Termier, G. and Termier, H. 1950
Stuartwellerocrinus? sp. Termier, G. and Termier, H. 1950
Taxocrinus spp. Termier, G. and Termier, H. 1950

North Africa, Morocco, undesignated Carboniferous

Platycrinus sp. Termier, H. and Termier, G. 1947 (sic)

Pakistan, Late Carboniferous

Graphiocrinus yarkhunensis Reed 1925

Pakistan, undesignated Carboniferous

Woodocrinus cometa (de Koninck 1863)

Philocrinus cometa de Koninck 1863

India, late Tournaisian or early Viséan

**Proampelocrinus himalayaensis* Gupta and Webster 1974. Ahluwalia (1989)

South America, Columbia, undesignated Early Carboniferous, probably Viséan

Lophocrinus? n. sp. Schmidt, W. E. 1937

South America, Brazil, Late Carboniferous, early Westphalian

Erisocrinus loczyi Katzer 1903; 1933

Parulocrinus tapajos (Strimple 1960). Webster 1981

Dicromyocrinus tapajos Strimple 1960. Lane 1964
