

# The Early Permian fossil record of Gondwana and its relationship to deglaciation: a review

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**Abstract:** Deglaciation sequences of Early Permian age in Gondwana have until now been distinguished mainly on lithological criteria by reference to climate-sensitive lithologies and associated geochemistry; whereas identification on biotic criteria such as vegetational or faunal change has not been employed. Present palaeontological data, which are widely-scattered geographically and of different stratigraphic scales and resolutions, show diversity increase from glacial conditions to post-glacial conditions. Amongst the marine fauna, a cold-water fauna consisting of bivalves such as *Eurydesma* and *Dellopecten*, and brachiopods such as *Lyonia* and *Trigonotreta*, were established in the earliest post-glacial marine transgressions. Above this is a more diverse, increasingly warmer, temperate fauna, including brachiopods, bryozoans, bivalves, cephalopods, gastropods, conularids, fusulinids, small foraminifers, asterozoans, blastoids and crinoids. The polynomorph succession shows change from monosaccate pollen assemblages, associated with fern spores, to more diverse assemblages with common non-taeniate bisaccate pollen. In Oman, where this has been studied in greatest detail, the upland saw changes from a glacial monosaccate pollen-producing flora to a warmer climate bisaccate pollen-producing flora; while in the terrestrial lowlands, a parallel change occurred from a glacial fern flora to a warmer climate colpate pollen-producing and lycopsid lowland flora. The sedimentary organic matter of the associated clastic rocks shows a decreasing  $\delta^{13}\text{C}$  trend believed to reflect palaeoatmospheric change due to post-glacial global warming.

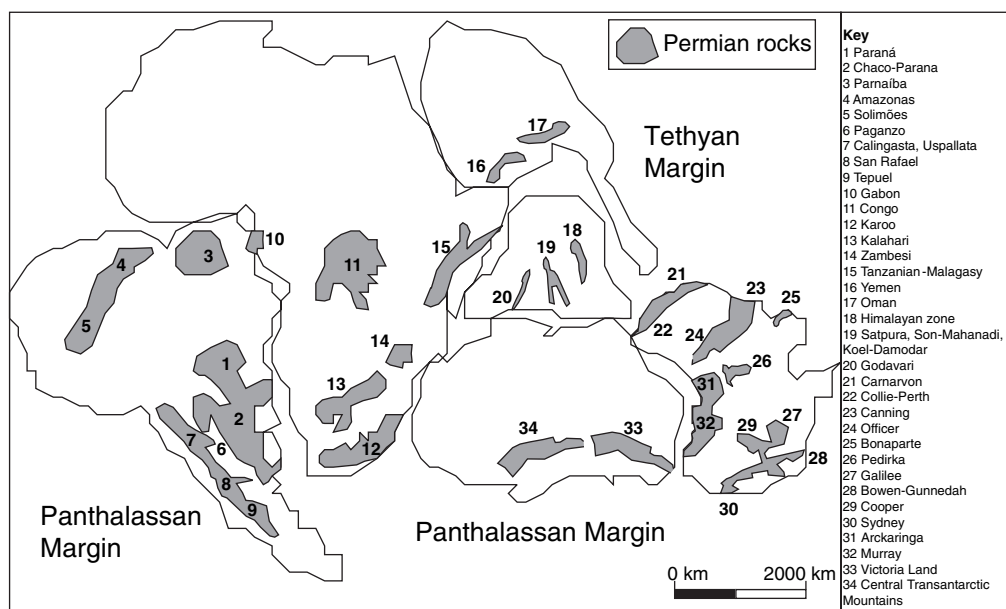
Early Permian farfield isotope studies, compiled by other workers, from brachiopods from the southern Urals, show a  $\delta^{18}\text{O}$  decline of 2.5‰ in the Early Permian (Asselian to Artinskian) and stable  $\delta^{13}\text{C}$  values of around +4.3‰ in the same period. This farfield evidence is in part consistent with palaeontological data since the most likely cause for the decline in  $\delta^{18}\text{O}$  is the return of isotopically light waters to the oceans from melting of glaciers at high latitudes.

At present, we are living in an interglacial stage of the Late Cenozoic ice age that began around the earliest Oligocene (Crowell 1995) and has not yet ended. However, the Carboniferous–Permian ice age is the most widespread and geologically well-represented ice age of the Phanerozoic and has the benefit that it ended more than 270 million years ago, and therefore can be studied in its entirety. By studying the waning glaciation of the Early Permian, we may be able to learn more of the interplay of factors influencing glaciation, and hence of the effects that might be expected in the near future in our own era.

The Late Palaeozoic glaciation of Gondwana comprised three distinct non-overlapping episodes. Though there is some controversy about their precise timing (see e.g. Veevers & Powell 1987; Isbell *et al.* 2003; Jones & Fielding 2004), it appears that two short glaciations occurred in the Frasnian (latest Devonian) and Mid-Carboniferous respectively, and that the glaciogene rocks associated

with them were deposited mainly by alpine glaciers. The third and latest glaciation of Pennsylvanian to Early Permian age is thought to have been more widespread as there is evidence for continental ice-sheets covering a total area of 17.9 to  $22.6 \times 10^6 \text{ km}^2$  (Veevers *et al.* 1994; Veevers & Tewari 1995; López-Gamundí 1997; Wopfner & Casshyap 1997; Isbell *et al.* 2003). The sedimentary rocks deposited in this last major glacial episode occur in cratonic basins (e.g. Kalahari, Rubh al Khali and Paraná basins; Levell *et al.* 1988; Veevers *et al.* 1994) rift basins (e.g. Damodar, Son, Mahanadi basins; Veevers & Tewari 1995); foreland basins (Veevers *et al.* 1994; Stollhofen *et al.* 2000; Jones & Fielding 2004; e.g. Sydney and Karoo basins) and successor basins (central Transantarctic Mountains; Isbell 1999) that are now exposed in South America, the Falkland Islands, Africa, Arabia, Madagascar, Antarctica, India and Australia (Fig. 1).

Two main facies have been recognized (Isbell *et al.* 2003). The first consists of massive diamictite



**Fig. 1.** Chief basins in the Early Permian of Gondwana.

resting on striated surfaces, sheared diamictite and sandstone and shale. These rocks were deposited subglacially as lodgement and deformation till, and in glaciofluvial and glaciolacustrine palaeoenvironments. The second facies association consists of massive diamictite overlying gradational and sharp contacts, stratified diamictite, dropstone-bearing shales and shales without dropstones. These rocks represent diverse styles of glaciomarine deposition including deposition at or near an ice front, rain-out debris from ice shelves or ice tongues, deposition from rafts of ice, and open marine sedimentation.

Within Lower Permian strata, an abrupt change from glacial to post-glacial deposits records the rapid withdrawal of ice from depositional basins throughout Gondwana (Isbell *et al.* 2003). In most basins, a distinct contact between glacial facies below and fluvial, lacustrine and marine clastic facies above occurs. The marine facies may be associated with the *Eurydesma* fauna (Dickins 1984) or with other cold- to temperate-water faunas such as that of the Manendragarh Limestone in India (Chandra 1994; Frakes *et al.* 1975; Shah & Sastry 1975; Venkatachala & Tiwari 1987), the Call-ytharra Formation in Western Australia (Dickins 1992) and the Saiwan Formation/Haushi limestone in Oman (Angiolini *et al.* 2003). Waning of Early Permian glaciation in the Gondwana continent was also manifested in farfield events of Euramerica and Tethys in terms of lithology and plant evolution

(Ziegler *et al.* 2002), macropalaeontology (Angiolini *et al.* 2005), cyclic sedimentation related to eustatic change (Isbell *et al.* 2003), oxygen and hydrogen isotope ratios in pedogenic phyllosilicates (Tabor & Montañez 2002, 2005) and seawater isotope composition (Veizer *et al.* 1999; Korte *et al.* 2005).

The biostratigraphy of Gondwanan Early Permian post-glacial sections is relatively well known in isolation, but the detailed evolution of biota after the glaciation, in the context purely of palaeoclimate rather than in terms of biostratigraphy, is not well studied. The advantages of developing an Early Permian biotic deglaciation model would be in understanding in detail the response of life to increasing temperatures and other climate change. Potentially, measures of extinction rate versus time and versus rate of palaeoenvironmental change (perhaps quantified in terms of per mil  $\delta^{13}\text{C}$  change) could be developed if an Early Permian biotic deglaciation model could be scaled against time. Such measures would be very useful in the study of modern biotic change during global warming. In addition, understanding some of the palaeoclimatic controls on deglaciation may be important in geological environments that are well known for accumulation of coal, gas and oil (see Potter *et al.* 1995), and in understanding the distribution of so-called post-glacial 'hot shales' which can be important source rocks of hydrocarbons.

The purpose of this chapter is to summarize and synthesize palaeontological and isotopic data relating to post-glacial Early Permian climate change and to discuss the progress and challenges associated with developing an Early Permian biotic deglaciation model.

### Timing of Early Permian deglaciation

Biostratigraphic correlation of facies of most Early Permian deglaciation within the northern Gondwanan basins and in the Karoo, Falkland Island and Antarctic basins indicates that deglaciation took place in the late Asselian or early Sakmarian (Wopfner & Kreuser 1986; Veevers & Powell 1987; Tiwari 1994; Vijaya 1994; Crowell 1995; Wopfner 1999; Eyles *et al.* 2002; Stephenson & Osterloff 2002; Isbell *et al.* 2003; Stephenson *et al.* 2005) in or around the *Granulatisporites confluentis* palynomorph biozone of Foster & Waterhouse (1988). In basins at lower latitudes during the Permian (see Isbell *et al.* 2003), for example the Solimões, Amazonas and Parnaíba basins in present-day northern South America, and along the Panthalassan margin of South America (e.g. the Tepuel, Calingasta, Uspallata and Paganzo basins), glaciation was restricted to the Mississippian and Pennsylvanian (González Bonorino 1992; López-Gamundí *et al.* 1992; Isbell *et al.* 2003). In eastern Australia and Tasmania, there is evidence of post-Sakmarian glaciation in the form of limestones, and the eastern Australian post-Sakmarian succession as a whole has been regarded as being indicative of a cool climate (Dickins 1978, 1996; Martini & Glooschenko 1985; Martini & Banks 1989). Limestones have been reported to occur at three levels in the Bowen Basin (Dickins 1996), and in the Sydney Basin (Dickins 1996; Eyles *et al.* 1998) and Tasmania (Banks & Clark 1987). Dickins (1996) discussed limestones occurrences and noted their coincidence with glendonites, concluding that there is evidence for post-Sakmarian glaciation in the area. Crowell (1995) considered the limestones in the Sydney Basin were large enough to suggest nearby glaciation, whereas those in the Bowen Basin were of rafted iceberg origin and therefore not necessarily suggestive of nearby glaciation. Recent work (Jones & Fielding 2004) also casts doubt on post-Sakmarian glaciation in the Bowen and Galilee basins, and in the New England fold belt of Queensland. Noting the persistence of glaciation, at least in the extreme SE of Australia and in Tasmania, and distribution of deglaciation sediments in other areas of Gondwana, Crowell (1995) concluded that glaciation persisted longer on the polar side of the Gondwana margin than along the Tethyan margin, and Frank *et al.*

(2005) suggested persistent glacial conditions may have been maintained by upwelling of cold water during sea-level highstands.

Aside from SE Australia and the northerly basins of South America, the weight of sedimentological and geochemical evidence therefore indicates that most Gondwanan deglaciation took place in the late Asselian or early Sakmarian (Crowell 1995; Wopfner 1999; Isbell *et al.* 2003). However, the evidence for deglaciation is mainly sedimentological, and biotic change has not, as a rule, been considered. Thus the relationship between sedimentologically defined deglaciation and biotic change during post-glacial warming needs to be examined.

### Sedimentologically defined deglaciation

Most Carboniferous–Permian deglaciation sequences are identified on sedimentological and associated geochemical data (e.g. Theron & Blignault 1975; Charrier 1986; Visser & Young 1990; Bonorino 1992; López-Gamundí *et al.* 1992; Crowell 1995; Visser 1995, 1996, 1997; Dickins 1996; Diekmann & Wopfner 1996; González Isbell & Cúneo 1996; Santos *et al.* 1996; Wopfner & Diekmann 1996; Eyles *et al.* 1997; Gonzalez 1997; Faure & Cole 1999; Apak & Backhouse 1999; Wopfner 1999; Stollhofen *et al.* 2000; Eyles & de Broekert 2001; Scheffler *et al.* 2003). Some studies (e.g. Kneller *et al.* 2004) revealed local detail of glacial melting, changing sediment supply and incidences of local-scale catastrophic sedimentation events. However, a distinction should be made between deglaciation in the sense of glacial melting related to climate warming and attendant biotic response, and sedimentological concepts of deglaciation, which primarily describe the sedimentological (usually fairly local) effects of the demise of glaciers. Visser (1997) defined a deglaciation sequence as ‘... an upward thinning sediment body (or package) deposited seaward of the ice-grounding line during a major recessional phase of a marine ice margin...’ Other authors (e.g. Wopfner 1999) have used much broader definitions not confined to sedimentological criteria or to the marine realm, but encompassing mineralogical and geochemical aspects as well as considering aspects of climate. It seems unlikely that all deglaciation sequences identified purely on sedimentological grounds, for example employing Visser’s definition, would have a biotic response. Studies of deglaciation by Visser (1996, 1997) showed that in close similarity to Holocene marine ice-sheets, the ice-sheets of the Karoo and Kalahari basins of southern Africa were unstable during sea-level fluctuations. During sea-level rise, the

ice-sheet margin loses its points of contact with the ground and therefore the ice-sheet retreats to a stable upglacial position. Thus, Visser (1997) showed that in the Karoo, the primary reason for glacial melting in some parts of the succession is not warming but sea-level change. This has also been established for modern deglaciation, for example in the Irish Sea (Eyles & McCabe 1989). Visser's observations of sea-level change and deglaciation were primarily concerned with explaining sedimentary cycles of varying glacial influence, but these cycles, because they were controlled by sea level, are not the same as climatic 'glacials' and 'interglacials' nor are they likely to relate to coherent parallel changes in biota. Thus, care is needed when identifying deglaciation sequences that might be studied for biotic change.

Eyles *et al.* (2002) demonstrated a similar independence of sequences interpreted to be of deglacial origin from simple climate warming. They commented that models like those developed by Visser that link deglaciation to sea-level change, and which assume therefore that events or key lithologies have sequence-stratigraphic global correlation significance, may be flawed because of local tectonic controls. Eyles *et al.* (2002) applied a new Early Permian palynological biozonation across six western Australian basins (Bonaparte, Canning, Carnarvon, Collie, Gunbarrel and Perth basins), and concluded that shales previously considered to be of a common deglacial eustatic origin were of different ages. They concluded that some 'post-glacial shales' were present due to local tectonic subsidence rather than deglacial eustatic sea-level rise.

Thus, the key point in identifying successions for study of biotic response to deglaciation is to be able to distinguish between sequences interpreted to be deglacial in origin, caused primarily by local tectonics, sea-level rise or climate change. Clearly, these are linked casually but for an understanding of biotic change in relation to deglaciation only those sequences identified as being related to climate change are worthy of detailed further study.

### **Previous studies of biotic change associated with Asselian–Sakmarian Gondwana deglaciation**

Gondwana glacial deposits are well known for the almost complete lack of macrofauna between the Namurian–Westphalian and late Asselian (Kemp *et al.* 1977; Truswell 1980; Jones & Truswell 1992); however, palynomorphs in the form of spores and pollen, and other non-terrestrial propagules, are quite common in the same deposits. The post-glacial (post-mid-Asselian) macrofauna and

macroflora is also more diverse, reflecting climatic amelioration, and includes brachiopods, bivalves, gastropods, conularids, bryozoans, echinoderms, barnacles, foraminifera, ostracods, fishes, asterozoans, nautiloids, ammonoids, insects and plants (see e.g. Dickins 1957; Hudson & Sudbury 1959; Cousminer 1965; Closs 1970; Frakes *et al.* 1975; Shah & Sastry 1975; Venkatachala & Tiwari 1987; Foster & Waterhouse 1988; Archbold 1990; Chandra 1994; Vijaya 1994; Archbold & Dickins 1996; Pant 1996; Angiolini *et al.* 1997, 2003, 2004, 2006; Gonzalez 1997; Waterhouse 1997; Briggs 1998; Leonova 1998; Archbold 1999, 2000; Foster & Archbold 2001; Larghi 2005). Similarly, palynomorphs indicate a general increase in diversity in post-glacial Early Permian sediments (Bharadwaj 1969; Truswell, 1980; Stephenson *et al.* 2003). However, most studies of both palynology, fauna and flora have been concerned with taxonomy or biostratigraphy, rather than been aimed at detailed study of climate change.

Because of their abundance throughout, palynomorphs are the dominant method of biostratigraphic correlation in Gondwanan Lower Permian studies. There are too many studies to be listed here, but a number of publications summarize data for the different regions of Gondwana and form the basis for initial attempts at pan-Gondwanan correlation. These include for South America: Russo *et al.* (1980) and Vergel (1993) for the Chacoparana Basin in Argentina; Césari and Gutiérrez 2000 and Azcuy and Jelin (1980) for the Paganzo Basin, Argentina; Marques-Toigo (1991) and Souza (2003) for the Paraná Basin of Brasil. Archangelsky *et al.* (1980) and Azcuy (1979) also summarized data for the whole of South America. Attempts at pan-African or pan-southern African palynological correlation schemes include those of Falcon *et al.* (1984), Anderson (1977), Falcon (1975), MacRae (1988), Hart (1967) and Millsted (1999). In Arabia, palynological schemes were summarized and presented as a unified preliminary scheme by Stephenson *et al.* (2003). In India, summaries of schemes include those of Tiwari (1994), Venkatachala *et al.* (1995) and Vijaya *et al.* (2001). Early Permian Australian palynostratigraphy was summarized by Kemp *et al.* (1977), Price (1983, 1997) and Foster (1983) but detailed basinal studies have also been published (e.g. Galilee Basin, Jones & Truswell (1992); Collie Basin, Backhouse (1991); Canning Basin, Powis (1979, 1984); Foster & Waterhouse (1988)). In Antarctica, some palynostratigraphy is available for the Asselian–Sakmarian (e.g. Kyle 1977; Farabee *et al.* 1991; Lindström 1995). A few authors have attempted to summarize and correlate across the Gondwana region as a whole using palynology (e.g. Bharadwaj 1969; Kemp 1975; Truswell 1980).

Considering the undoubted wealth of palaeontological, and particularly palynological, data from glacial and deglacial Lower Permian rocks, it is surprising that most studies of biotic change in relation to deglaciation have been rather general in character and have not attempted detailed bed-by-bed or metre-by-metre reconstruction of biotic change. Most have been concerned with generalities reconstructing climate change over long stratigraphic intervals with rather low sampling densities and using data from a wide geographical area (e.g. Dickins 1985, 1992, 1996).

### South America

There have been a number of general studies examining faunal and floral changes through the Upper Palaeozoic in South America. González (1997, p. 235; and references therein) working on the basins of Argentina concluded that '... the origins and extinctions of the major Carboniferous and Early Permian faunal groups are closely associated with sedimentological evidence of climatic alterations due to temperature ranges...'. González (1997) recognized two major faunal groups in the Early Permian of Argentina, the Uspallatian and the Bonetian. The first, characterized by *Cancrinella* cf. *farleyensis* (Etheridge & Dun), was considered by González (1997) to be of Asselian age and to represent glacial conditions, while the second (considered of Sakmarian age) was associated with cold-water transgression and characterized by *Eurydesma*, *Merismopteria*, *Megadesmus* and *Deltopecten*. González (1997) considered that the demise of the Bonetian fauna corresponded with the last Permian glaciation in Argentine basins.

However, the faunal changes described by González (1997) are based on erroneous age attribution (Simanaukas & Cisterna 2001) since his Uspallatian glacial fauna has been shown to be younger (Sakmarian) by Cisterna & Simanaukas (2000). Also, the *Tivertonina jachalensis*–*Streptorhynchus inaequioratus* Biozone of the Tupe Formation of the Paganzo Basin, considered to be Late Carboniferous by González (1997), is given a middle–late Asselian age by Archbold *et al.* (2004).

Cisterna and Simanaukas (2000), Simanaukas Cisterna (2001), Cisterna *et al.* (2002a, b) and Archbold *et al.* (2004) have recently established a revised biostratigraphy and correlation of Upper Carboniferous–Lower Permian brachiopods of the Pre-Cordilleran basins of Argentina (Rio Blanco, Calingasta–Uspallata, Paganzo, Tepuel–Genoa basins). Simanaukas and Cisterna (2001) described an uppermost Carboniferous–Lower Permian macrofaunal assemblage from the El Paso

Formation of the Calingasta–Uspallata Basin. This fauna, previously considered to be Early Carboniferous in age, is recorded in shales between diamictites and shows a gradual increase in biodiversity.

The most complete faunal succession has been described from the Rio Blanco Basin (lower and middle members of the Rio del Penon Formation) as consisting of three brachiopod associations spanning the Asselian–early Sakmarian (Cisterna & Simanaukas 2000). The lower association (Assemblage I) comes from black shales above sandstones, conglomerates and paraconglomerates (diamictites?). The authors do not interpret the faunal succession in terms of biotic change after the Gondwanan glaciation, but they indicate its affinity to the Asselian–Tastubian faunas of Peninsular India and of the Lyons Group and Callytharra Formation of Western Australia. *Trigonotreta* sp. from their Assemblage I is similar to the primitive species of the *Trigonotreta* group such as *Trigonotreta hesdoensis* (Sahni & Dutt) from the Asselian–early Tastubian of Peninsular India. This fauna is regarded as early Asselian by Archbold *et al.* (2004). Interestingly, Associations II and III do not show a significant increase in biodiversity with respect to the lower assemblage, even if some of their characterizing species are similar to species of the Sakmarian of Western Australia (species of *Costatumulus*, *Neochonetes* and *Tivertonina*). According to Archbold *et al.* (2004), assemblages II and III span the middle Asselian–early Sakmarian time interval.

A general study of South American floral change in relation to climate change is that of Goldberg (2004), who studied macro- and microfloral diversity throughout the Permian in the Paraná Basin in southern Brasil and compared this with results from nine Australian Gondwanan basins. Her methodology was to count the number of taxa (genera/species) and graph these against lithostratigraphic and chronostratigraphic units as well as climate-sensitive lithologies. Data points corresponded nominally to the centre of formations so essentially this is a broad-based study too coarse to allow detailed study of post-glacial climate change. The study, however, showed a great increase in microfloral diversity from the Asselian–early Sakmarian Itararé Group (dominantly glacial) to the post-glacial coal-bearing late Sakmarian–early Kungurian Rio Bonito Formation, probably related to climatic amelioration. An accompanying decrease in floral diversity was attributed by Goldberg (2004) to taphonomic and local factors. Australian basins, examined using the same methodology, showed rather inconsistent results with no obvious amelioration even from the Asselian to the Sakmarian.

## Africa

Although this area has been well-studied from the point of view of sedimentological and geochemical aspects of deglaciation (e.g. Visser & Young 1990; Visser 1995, 1996, 1997; Diekmann & Wopfner 1996; Faure & Cole 1999; Wopfner 1999; Stollhofen *et al.* 2000; Scheffler *et al.* 2003), there have been few attempts to relate biotic change to deglaciation, apart from brief references to overall changes in palynomorph assemblages in relation to climate throughout the Permian by Oesterlen & Millstedt (1994) and Nyambe & Utting (1997), and a study of the five Eccca Group coal seams of the Witbank Basin, Transvaal, South Africa (Falcon *et al.* 1984). Though Falcon *et al.* (1984) did not give a chronostratigraphic age for the Eccca Group, recent radioisotopic dates for the Dwyka and Eccca Groups in the Cape Province and Namibia (Bangert *et al.* 1999) suggest that the Eccca Group is Asselian–Sakmarian in age, and is therefore of equivalent age to deglacial sequences studied in, for example, Oman. Falcon *et al.* (1984) suggested that the oldest Witbank seams (Nos 1 and 2), were formed soon after the most ‘... intensive glaciation, characteristic of the Dwyka period’. In similarity with Arabian palynological assemblages of this time, Seam No. 1 is characterized by, amongst others, *Microbaculispora tentula* Tiwari, and abundant radially and bilaterally symmetrical monosaccate pollen. Seam No. 2 is similar but contains greater numbers of non-taeniate bisaccate pollen, and changes between Seams No. 1 and 2 may therefore be similar to those occurring below the *Alisporites indarraensis* Biozone of Oman, and the *Striatopodocarpites fusus* Biozone of the Collie Basin, Western Australia (Backhouse 1991; see later discussion). Falcon *et al.* (1984) suggested that the floral development of the Witbank area was influenced by the proximity of the sea, and by eustatic fall and rise. They suggested that coal-forming periods were associated with regressive periods where large flat coastal lowland areas were available for plant colonization, though this is inconsistent with more recent concepts of sequence stratigraphy that relate coal formation to sea-level rise and high water table levels. Relating regression with glacioeustatic sea-level fall in this way, they therefore considered coal-forming periods to correspond to short-lived glacial advances during Eccca times, though they considered the main trend through the Eccca to be one of overall climatic amelioration and increase in floral diversity.

There are relatively few studies of Early Permian fauna from southern Africa. Non-marine arthropod ichnotaxa attributed to crustaceans are reported from the shallow lacustrine Eccca Group

that overlies the Upper Dwyka shales (Braddy & Briggs 2002), and Dickins (1961) reported *Eurydesma* from the Dwyka beds.

## Arabia

It has long been known that deposits of the Permo-Carboniferous glaciation extended to Oman in the Arabian Peninsula in the form of the Al Khilata Formation. This formation is present in the subsurface in much of the southern part of Oman south of the Oman Mountains and extends northwestward beneath the Rub ‘al Khali into Saudi Arabia (Braakman *et al.* 1982; Levell *et al.* 1988; Al-Belushi *et al.* 1996). The distribution of climate-sensitive lithologies within the overlying lower Gharif member of the Gharif Formation *sensu* Hughes Clarke (1988) indicates that post-glacial climate change must have occurred in Oman (Wopfner & Diekmann 1996; Wopfner 1999). Much of the Al Khilata Formation is composed of diamictites. These are succeeded by the Rahab member, which is considered to be a post-glacial lacustrine unit (Hughes Clarke 1988; Levell *et al.* 1988; Wopfner 1999). The lowest lower Gharif member sediments are sandstones and mudstones of probable fluvial origin, but above these is a restricted marine interval marked by the acritarch *Ulanisphaeridium omanensis* Stephenson & Osterloff, which is termed the ‘maximum flooding shale’ (Guit *et al.* 1995) and represents a possible post-glacial eustatic flooding event (Sharland *et al.* 2001; Stephenson & Osterloff 2002).

Above the ‘maximum flooding shale’, in the subsurface of South Oman, are beds correlative with the outcropping Saiwan Formation of north central Oman (Guit *et al.* 1995; Sharland *et al.* 2001). Angiolini *et al.* (2003) described faunal evidence for warming within the Saiwan Formation, by observing the development of a pioneer cold-water brachiopod community (*Pachycyrtella* palaeo-community) at its base (late early Sakmarian), followed by a more mature secondary ecological community of a wider marine biota of late Sakmarian age. The *Pachycyrtella* pioneer palaeo-community records the evolution from glacial to cool temperate climate conditions between the early and late Sakmarian, and colonized the unoccupied environment provided by the sharp transgression at maximum deglaciation (Angiolini *et al.* 2003). This pioneer palaeo-community is characterized by (1) random distribution pattern over a limited area, (2) clustering in groups, (3) numerical dominance (>85%), (4) suspension feeding, (5) rapid rates of reproduction and growth (*r*-strategy), (6) early maturity and (7) high mortality rates in the juveniles. The disappearance of the basal palaeo-community is related to a drastic change in the

physical environment, recording the interplay of final Gondwanan deglaciation and initial Neotethys opening (Angiolini *et al.* 2003). The secondary ecological succession developed rapidly, indicating significant climatic amelioration and more stable environmental conditions (Angiolini *et al.* 2003). Biodiversity indices significantly increase from the pioneer palaeocommunity (Margalef index 0.2–1.9; Shannon–Wiener index 0.1–1.5; equitability generally <0.5) to the overlying more mature palaeocommunity (Margalef index 1–2.8; Shannon–Wiener index 0.5–2.4; equitability 0.8–1). Climate change continued into middle Gharif member times since that unit contains common calcrete horizons and redbeds (Guit *et al.* 1995).

The palynological succession within the Rahab and lower Gharif members in well sections Thuleilat (TL)-16 and -42 in south Oman allows detailed metre-by-metre reconstruction of floral changes within the deglaciation period (Stephenson & Osterloff 2002; Stephenson *et al.* 2005). The reconstruction relies on palynomorphs in the sedimentary rocks accurately representing the hinterland vascular plant communities. In broad terms, the numbers and variety of palynomorphs are probably an adequate guide to the numbers and variety of plants on the hinterland, but factors such as differing yields of spores and pollen by different plants, and processes such as sorting, may cause taphonomic biases.

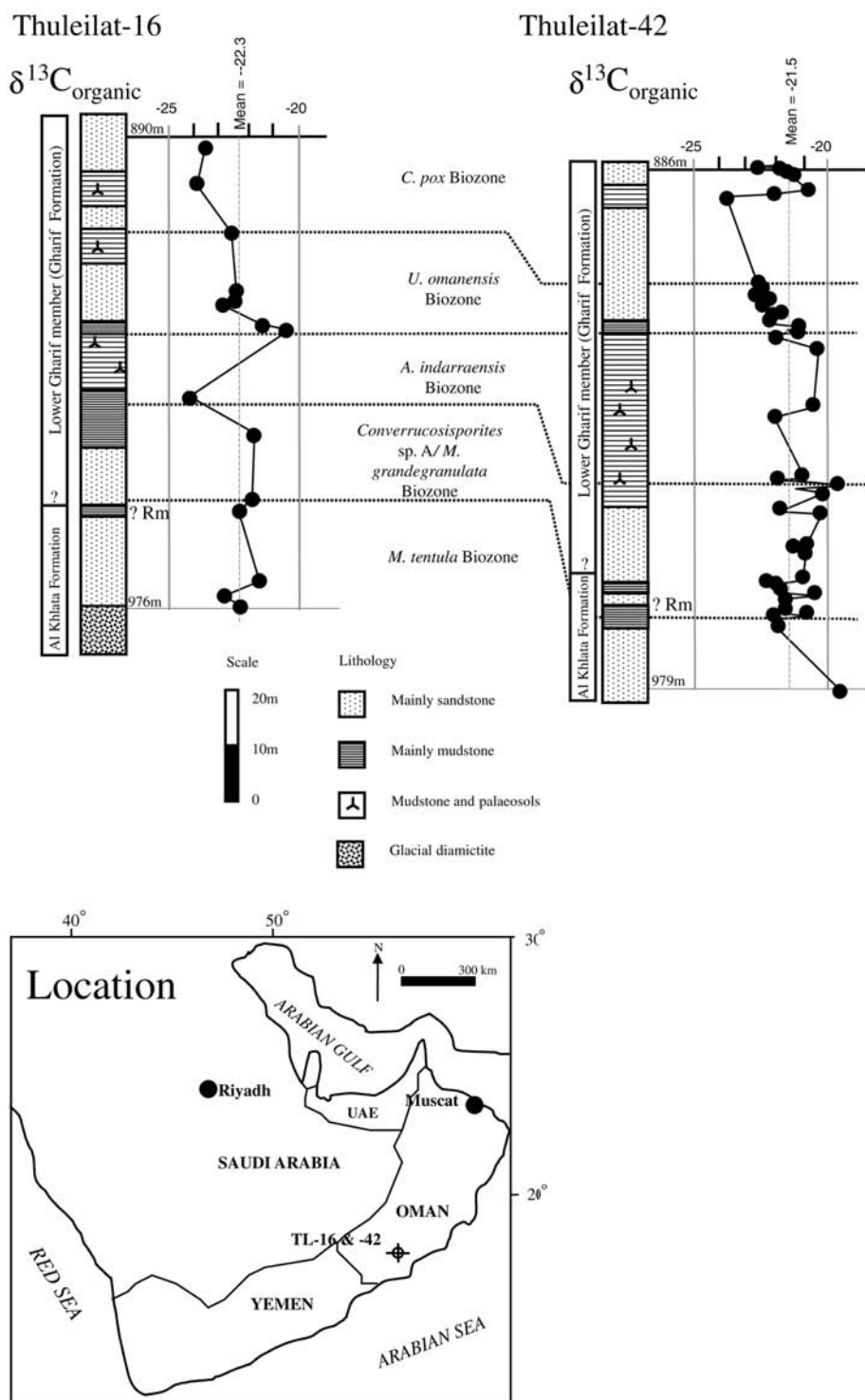
In the lowest part of the section (below 940 m in TL-16 and 944 m in TL-42; Figs 2 and 3), a cold climate fern wetland community was present on lowland outwash alluvial plains while on the surrounding uplands or better-drained ground, a primitive conifer community developed (Stephenson & Osterloff 2002; Stephenson *et al.* 2005). There is also evidence that a specialized autochthonous freshwater algal palaeoecology occupied small ponds in the fern lowland wetland environment. Later in the post-glacial period (above 940 m in TL-16 and 944 m in TL-42), these communities were replaced. In the lowland alluvial plains, a cycad-like and lycopsid vegetation developed, while in the uplands or better-drained areas a taeniate- and non-taeniate bisaccate pollen-producing glossopterid or other gymnospermous flora was established. Later (above 925 m in TL-16 and 915 m in TL-42), restricted marine conditions occurred in parts of the sedimentary basin; within the bodies of brackish or salt water, an ephemeral microflora and fauna (indicated by rare acritarchs and microforaminiferal linings) developed. This restricted marine transgression probably advanced from the northeast (Konert *et al.* 2001) and may represent the first major deglacial eustatic sea-level rise of the Permian in the Arabian region (Stephenson & Osterloff 2002; Stephenson *et al.* 2005).

A carbon isotope record from organic matter within the same sections of the Al Khlat and lower Gharif formations of TL-16 and -42 shows a  $\delta^{13}\text{C}_{\text{organic}}$  trend from  $-21$  to  $-24\text{‰}$  (Stephenson *et al.* 2005; Figs 2 and 3). The trend may be due to changes in palaeoatmospheric  $\text{CO}_2$  since they cannot be accounted for by changes in organic matter type or preservation. Changing  $^{13}\text{C}/^{12}\text{C}$  ratios in atmospheric  $\text{CO}_2$  are known to occur in response to changes in the proportions of carbonate and organic carbon ‘burial’ (Erwin 1993), and between glacial and interglacial environments due to changes in biomass and productivity (Arens *et al.* 2000). The decreasing trend seen in TL-16 and TL-42 may therefore represent change in the carbon cycle although it is impossible to identify a specific mechanism.

### Australia

The Early Permian of Australia is perhaps the most intensively studied of the former parts of Gondwana, but comparatively few studies address the biotic response to Asselian–Sakmarian deglaciation. After his pioneering work in the 1970s and 1980s, Dickins (1993) summarized the faunal succession of Western Australia in relation to climatic warming in broad terms. Glacial features are present in the Nangetty Formation of the Perth Basin, the Lyons Group of the Carnarvon Basin, and the Grant Group and Paterson Formation of the Canning Basin. Intercalated with, and overlying these, are rocks containing a cold-water marine fauna consisting of the bivalves *Eurydesma* and *Deltopecten*, the gastropod *Keeneia*, and the brachiopods *Lyonia lyoni* (Prendergast), *Rhynchopora australasica* Archbold, *Kiangsiella* sp., *Grumantia* cf. *costellata* Clarke, *Cyrtella australis* Thomas, *Ambikella notoplicata* Archbold and Thomas and *Trigonotreta lyonsensis* Archbold and Thomas. Dickins (1985) recognized five glacial/interglacial phases in the Lyons Group, with the intercalated marine fauna remaining relatively uniform throughout its deposition and indicative of cold water. Above this, in the Fossil Cliff Member of the Holmwood Shale (Perth Basin), the Callythara Formation (Carnarvon Basin) and the Nura Nura Member of the Poole Sandstone (Canning Basin), there is a more diverse, slightly warmer-water fauna, including brachiopods, bryozoans, blastoids and crinoids. Amongst the bivalves, Dickins (1993) considered the bivalve *Edmondia* to indicate warm conditions.

Archbold (1998) revised the faunal succession of Western Australia and showed an increase in biodiversity from the Asselian *Lyonia lyoni* Biozone (7 species), through the Tastubian (early Sakmarian) *Trigonotreta occidentalis* Biozone (10 species) to the Sterlitamakian (late Sakmarian) *Coronalosia*



**Fig. 2.** Correlation of Thuleilat (TL) well sections of Oman based on palynology, and flattened on the base of the *U. omanensis* Biozone. Note that the boundaries between the Rahab member, the Al Khilata Formation and the Gharif Formation are not defined precisely in the Thuleilat wells. ? Rm, possible position of Rahab member. Reproduced with permission from Stephenson *et al.* (2005). Inset map shows location.

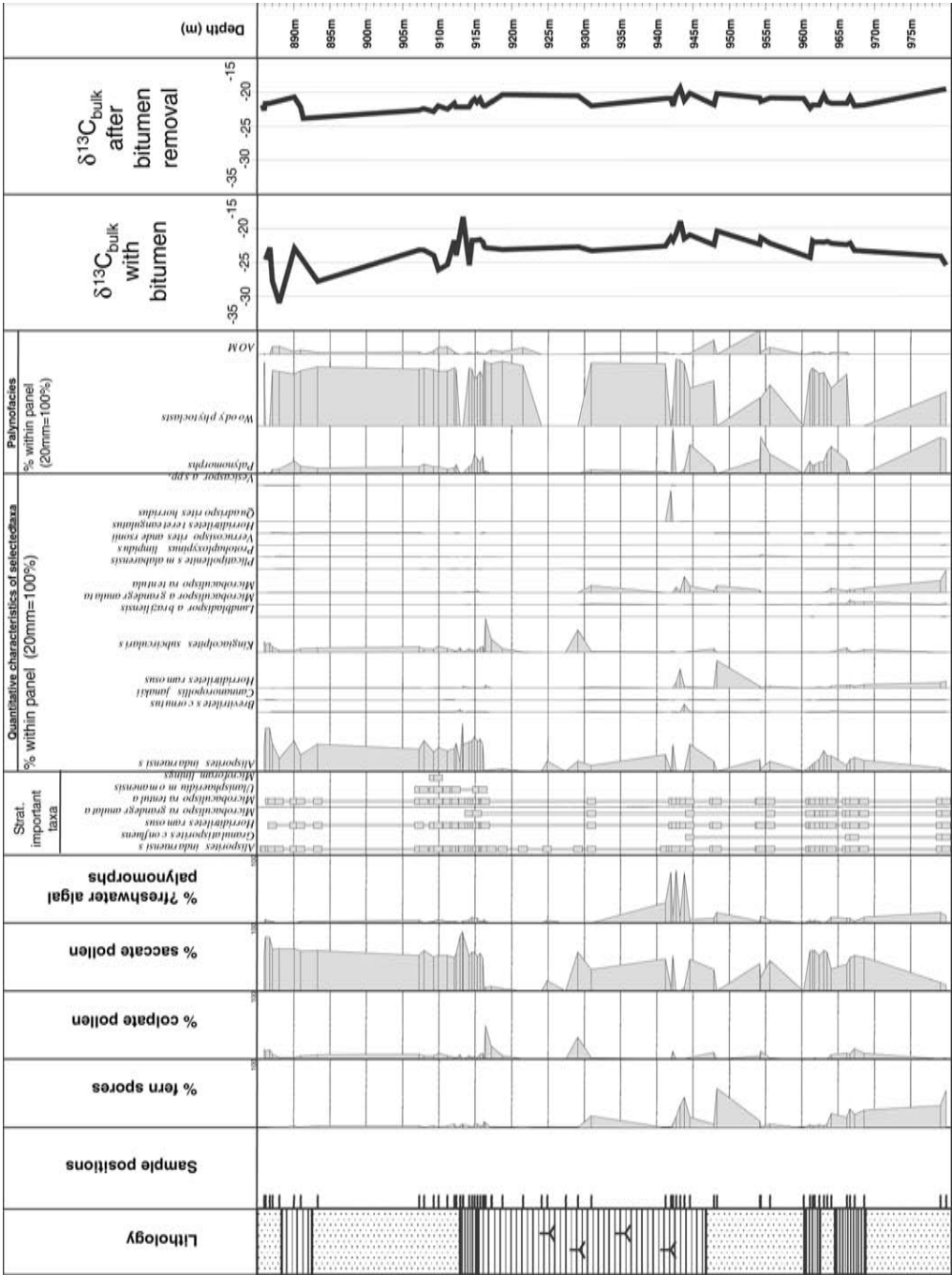


Fig. 3. Gross quantitative palynological character, ranges of selected palynomorphs, palynofacies, and δ<sup>13</sup>C<sub>org</sub> values for the Thuleilat-42 well section. AOM, amorphous organic matter. Reproduced with permission from Stephenson *et al.* (2005).

*irwinensis* (formerly *Strophalosia irwinensis*) Biozone (40 species). There is a slow trend in increase of biodiversity between the first two biozones (Asselian to Tastubian in age), but a sudden shift occurs in the Sterlitamakian *Coronalosia irwinensis* Biozone. This biotic change is consistent with the water-temperature curve established by Archbold & Shi (1995) and based on the presence/absence of Tethyan brachiopod genera, which are considered indicators of warm water. According to this curve, cold-water temperatures (5 °C) in the *Lyonia lyoni* Biozone evolved to warmer temperatures (20 °C) in the *Coronalosia irwinensis* Biozone, which is characterized by high biodiversity and by the invasion of a significant number of Tethyan genera (about 14). Also oxygen isotope data available for Lower Permian Australian spiriferids (Compston 1960; Lowenstam 1961, 1964) indicate the potential for a significant temperature change during Asselian–Tastubian times and late Artinskian times.

In recent reviews of the palaeobiogeography of Australasian brachiopod faunas, Archbold (2000, 2001) demonstrated the striking difference in generic and specific composition of brachiopods on either side of the continent. The eastern side of Australasia was affected by cold-water currents: eastern Australia marine faunas have a strong link with New Zealand and New Caledonia and a lower diversity than coeval Western Australian (western) faunas. They show an increase in biodiversity from south (Tasmania) to north (Bowen Basin, Queensland) which is interpreted as reflecting an increase in temperature from cold to cool temperate. Clarke (1990) illustrated brachiopod and bivalve assemblages from glendonite-bearing siltstones above the glaciogene sequence in Tasmania and interpreted these as cold-water low-diversity faunas.

The eastern Australian brachiopod biozonation of Briggs (1998) shows a slight increase in the number of taxa from the Asselian *Lyonia bourkei* Biozone to the Tastubian *Strophalosia concentrica* and *Strophalosia subcircularis* biozones with a reverse trend in the Sterlitamakian *Bandoproductus walkomi* Biozone. A significant increase in diversity is recorded later, in the lower Artinskian *Echinalosia curtosa* Biozone. This biotic change is consistent with persistence of cold climate and glaciation in eastern Australia during the late Sakmarian (Frank *et al.* 2005).

In palynological terms, few deglaciation sequences have been studied to the same level of detail as the Rahab and Lower Gharif members of Oman, hence close comparisons are not possible. However, sequences in Western Australia studied by Backhouse (1991) allow some comparison. Backhouse (1991) noted decreases in monosaccate

pollen and later increases in small bisaccate pollen within and just above a section assignable to the *Granulatisporites confluens* Biozone of Foster & Waterhouse (1988). Backhouse (pers. comm., 2000) considered the bisaccate pollen to be closely similar to *Alisporites indarraensis* Segroves. No *Ulanisphaeridium omanensis*-bearing horizon was reported by Backhouse (1991) though the low sample frequency of Backhouse's study may not have been sufficient to detect such a narrow horizon.

Lithostratigraphic similarities between the deglaciation sequences in Oman and the Canning Basin, Western Australia have been noted by Wopfner (1999). The scarcity of palynological information from the Canning Basin sequences does not allow close comparison, but it is notable that the acritarch *Ulanisphaeridium berryense* McMinn, a taxon closely similar to *U. omanensis*, was recorded by Foster & Waterhouse (1988) from the upper parts of the sequence assigned to the *G. confluens* Biozone in Calytrix No. 1 well in the Canning Basin.

## India

It has long been known that the dominantly continental Early Permian strata of the lower Talchir Formation and overlying Karharbari Formation (Indian Peninsula) contain both glaciogene diamictites (Ghosh & Mitra 1972; Frakes *et al.* 1975) and thin marine intercalations (Sastry & Shah 1964). Shah and Sastry (1975) considered the marine beds at Manendragarh and Rajhara to be within the lower and middle parts of the Talchir Formation, and those at Umaria and Badhaura to be in the basal part of the Karharbari Formation. They further considered the two sets of marine beds to have been deposited by separate transgressions, the earlier in the Asselian, the later in the Sakmarian. However, Frakes *et al.* (1975) considered there to be no difference in the faunas at Umaria and Manendragarh and assumed them to be of the same age, being characterized chiefly by the shelly fauna *Eurydesma*, *Peruvipsira* and *Trigonotreta*. Dickins & Shah (1979) supported the view of Shah & Sastry (1975) and reported a list of foraminifers, bryozoans, brachiopods, bivalves, gastropods and crinoids from Manendragarh and Umaria suggesting correlation to the Lyons Group marine faunas of Western Australia. The more diversified marine fauna from Badhaura, with more than 17 brachiopod species, is considered younger and correlateable to the Callytharra Formation of Western Australia. According to Archbold *et al.* (1996), the Manendragarh brachiopod fauna is characterized by *Trigonotreta hesdoensis* (Sahni & Dutt), which is one of the most primitive species of the

genus (Angiolini *et al.* 2005). Slightly younger (late Tastubian) is *Trigonotreta narsarhensis* (Reed); a later evolutionary form of *T. hesdoensis* from Umaria which is associated with *Bandoproductus umariensis* (Reed), *Arctitreta* sp., *Tomioopsis barakerensis* (Reed) (= *Ambikella*) and *Cleiothyridina* sp. The Badhaura fauna is more diversified, containing species of the genera *Semilingula*, *Arctitreta*, *Derbyia*, *Strophalosia*, *Aulosteges*, *Cyrtella*, *Neospirifer*, *Crassispirifer*, *Ambikella*, *Hoskingia*, *Fletcherithyrus* and *Gilledia*, and is considered to be at least Sterlitamakian in age by Archbold *et al.* (1996). Apart from the discussion of Dickens (1985), who recognized the Umaria beds as representing the Tastubian post-glacial eustatic rise, no attempt has been made to link the biotic change with the post-glacial climatic change in India.

Venkatachala and Tiwari (1987) suggested that other marine intervals could be identified within the Talchir Formation on the basis primarily of palynomorphs such as acritarchs and leiospheres. Although no detailed attempts have been made to link climate change with macrofaunal and macrofloral change through the Talchir and Karharbari formations, palynomorphs have been studied with this aspect in mind (e.g. Banerjee & D'Rozario 1990; Tiwari 1994; Vijaya 1994; Venkatachala *et al.* 1995; Pant 1996; Vijaya *et al.* 2001). The most detailed of these studies in relation to the Early Permian is that of Vijaya (1994). Within the Talchir Formation, Vijaya (1994) recognized three phases recording an upsection increase in microfloral diversity. The earliest of these (Phase I, considered of Asselian age) is characterized by common radially and bilaterally symmetrical monosaccate pollen and simple trilete spores. Phase II is characterized by sculptured monosaccate pollen, taeniate bisaccate pollen and more common sculptured spores. Finally, Phase III, considered of early Sakmarian age, is characterized by a maximum diversity of forms. Vijaya (1994) considered Phase III to correlate with the *Granulatisporites confluens* Biozone. These palynological changes cannot be directly related to facies changes in a single section, since Vijaya (1994) presents the data in a generalized way, but clearly the sequence is deglacial in form and has some similarity with palynological changes recorded elsewhere in Gondwana. Similar phases attributed to climatic warming were also suggested by Banerjee & D'Rozario (1990).

### Antarctica

Late Palaeozoic rocks of glacial origin outcrop in the central Transantarctic Mountains, Victoria Land and the Ellsworth Mountains of west Antarctica. Isbell and Cúneo (1996) demonstrated rapid

change from glacial to sediments of post-glacial origin within the Weller Coal Measures of southern Victoria Land. In an investigation of the palaeoenvironment of the Weller Coal Measures, Francis *et al.* (1993) considered that winter temperatures were low during deposition, suggesting that adjacent uplands were probably still glaciated. They also suggested that summer temperatures were nevertheless adequate for a peat-forming flora and forest vegetation (evidenced from very large *in situ* *Glossopteris* stumps). The forests may have been deciduous (Taylor *et al.* 1992), reflecting such seasonality, and the leaves of *Glossopteris* are often found in thick mats (Francis *et al.* 1993). The age of the Weller Coal Measures and underlying diamictites, and therefore of the date of this rapid deglaciation, are uncertain however, and can only be placed between Eastern Australian Palynological Stage 2 (see Evans 1969; Barrett & Kyle 1975) and Stage 4 (Kyle 1977). Thus, the deglaciation cannot be directly correlated with others in for example Oman and the Collie Basin, Western Australia.

Lindström (1995), however, showed detailed palynological changes occurring within the *Granulatisporites confluens* Biozone in rocks in western Dronning Maud Land. She correlated these changes with the lower Weller Coal Measures and the underlying Darwin Tillite and considered the rocks to have been deposited in a cold climate, not far from active glaciation. The sections Lindström (1995) studied were stratigraphically rather short (both less than 10 m) and so probably represent a 'snapshot' of climate change, but some of the changes are consistent with those noted in Oman, Peninsular India and Western Australia. At Lindström's Locality A, for example, the highest samples are dominated by non-taeniate bisaccate pollen, whilst monosaccate pollen dominate the lower part of the section. *Granulatisporites confluens* occurs throughout, apart from two sample levels toward the centre of the section.

Few Early Permian macrofossils have been described from Antarctica. Kelly *et al.* (2001) reported *Cancrinella* sp. in bioturbated mudstones from locality B at Alexander Island (Antarctic Peninsula) which according to Archbold *et al.* (2004) is comparable to *Costatumulus* sp. B. of the Rio Blanco basin Association II (Argentina) and given a middle-late Asselian age.

### Farfield isotope and atmospheric studies

There are relatively few studies using isotopes which are specific to the Early Permian; but there are low-resolution isotope curves which record seawater composition for most of the Phanerozoic based on compilations of the carbon and oxygen

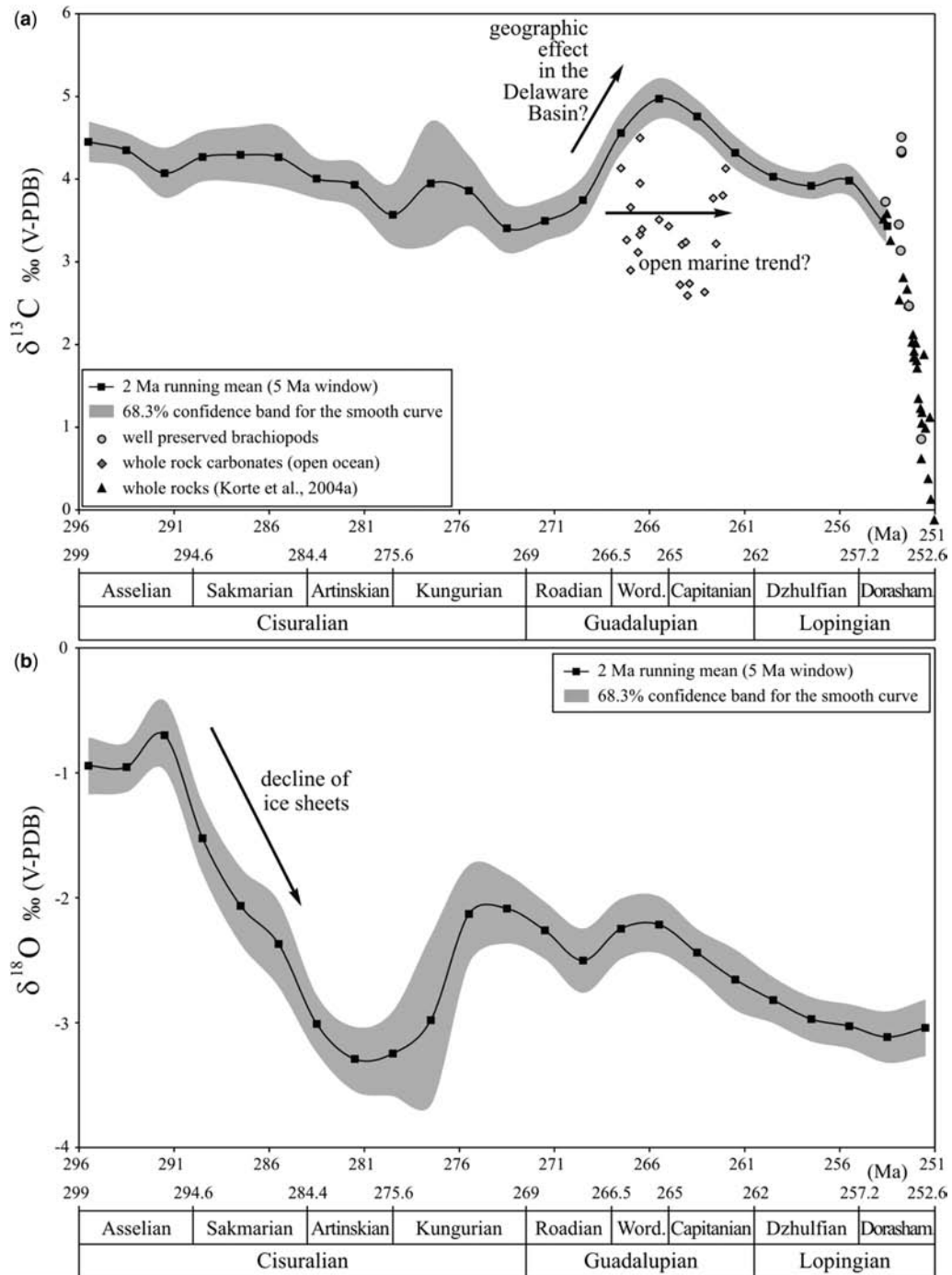
isotope composition of brachiopods (e.g. Veizer *et al.* 1999). Through the Phanerozoic, changes in marine  $\delta^{13}\text{C}$  are interpreted in terms of global changes in burial and re-oxidation of organic matter; although other processes such as release of low  $\delta^{13}\text{C}$  volcanic or mantle  $\text{CO}_2$  into the atmosphere, discharges of oceanic methane and overturn of low  $\delta^{13}\text{C}$  anoxic bottom waters are all described (Korte *et al.* 2005). Variation in  $\delta^{18}\text{O}$  in brachiopod shells is thought to be largely due to the growth and retreat of continental glaciers, although multimillion-year variations in  $\delta^{18}\text{O}$  may also be a function of interactions of the oceans with the lithosphere driven by tectonics (e.g. Veizer *et al.* 1997). The Phanerozoic seawater curves show that in the Early Permian there was a rapid decline in  $\delta^{18}\text{O}$  despite the curve for  $\delta^{13}\text{C}$  being rather flat (Veizer *et al.* 1999). The only dedicated Permian isotope seawater curves are based on a compilation of data from brachiopods from a series of discrete basins. The  $\delta^{18}\text{O}$  data show this decline of 2.5‰ in the Early Permian (Asselian to late Artinskian) (Fig. 4, see also Korte *et al.* 2005), over a timespan of 10 million years. The study of Korte *et al.* (2005) is also one of few that describes rigorous screening of brachiopod carbonate data for diagenetic alteration using a combination of microtextural and trace element content.

However, the Early Permian brachiopod data given in Korte *et al.* (2005) are entirely derived from the southern Urals (sections from Usolka, Sakmara and Dalnij Tyulkas; references in Korte *et al.* 2005). The southern Urals were palaeoequatorial at this time, and therefore climatically distinct from the cold-climate seas in which most post-glacial Gondwanan brachiopods lived. However, Korte *et al.* (2005) assumed that southern Urals brachiopods lived in basins that were open to the Palaeotethys Ocean, and so were capable of reflecting a global signal. Korte *et al.* (2005) considered a 2‰ spread in both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in coeval brachiopods as sufficient to allow for global differences including variations in seawater temperature with latitude (James *et al.* 1997; Brand *et al.* 2003). Korte *et al.* (2005) therefore assumed that the decline in  $\delta^{18}\text{O}$  in the Early Permian Urals brachiopods is a global signature and not a geographical artefact, so that the data can represent far-field evidence to help decipher changing environment around Gondwana. In general, the  $\delta^{13}\text{C}$  data in the Early Permian are stable around +4.3‰. In contrast, the  $\delta^{18}\text{O}$  data from the Asselian and lower Sakmarian brachiopods have values between +0.1 to -2.3‰ (the latter being the highest of all the values throughout the Permian); values drop to -3.5‰ in the late Artinskian. Korte *et al.* (2005) considered that the most likely cause for this decline in  $\delta^{18}\text{O}$  is the

return of isotopically light waters to the oceans from melting of Permian glaciers at high latitudes (Fig. 5). This explanation is not entirely consistent with evidence from brachiopods and palynology (see earlier discussion), because that suggests deglaciation was confined to the Asselian and Sakmarian. Given that the Late Palaeozoic and Pleistocene glaciations were probably of similar magnitude (Crowley & Baum 1992), it has been calculated that we can ascribe an approximate 2.3‰ increase in seawater  $\delta^{18}\text{O}$  to the 'ice volume effect' (Korte *et al.* 2005). The maximum range in data we see over this period is 3.6‰ (+0.1‰ to -3.5‰ shown on fig. 7 of Korte *et al.* 2005). Therefore, the remaining 1.3‰ in  $\delta^{18}\text{O}$  could be caused by an increase in temperature of approximately 5 °C in the Urals. Korte *et al.* (2005) concluded therefore that the decline of the Gondwana ice-sheet was due to global warming because of the requirement for both temperature and ice volume to explain the  $\delta^{18}\text{O}$  variation.

Another Early Permian farfield temperature change reconstruction from a study of oxygen and hydrogen isotope ratios in pedogenic phyllosilicates is that of Tabor & Montañez (2005). The Midland Basin of Texas and the southern Anadarko Basin of Oklahoma were equatorial during the Early Permian. The phyllosilicates have  $\delta\text{D}$  and  $\delta^{18}\text{O}$  values that are thought to represent Early Permian meteoric waters at a specific temperature. Using the mineral-water temperature-dependent fractions equations, it was shown that the palaeotemperature of phyllosilicate crystallization ranged from  $22 \pm 3$  °C to  $35 \pm 3$  °C (calcite  $\delta^{18}\text{O}$  data) across the Carboniferous–Permian boundary in the East Midland basin.

One of the few open marine isotope records from the Early Permian has been reported from the Karoo Basin, South Africa (Scheffler *et al.* 2003). The basin contains organic matter thought to be almost entirely of marine origin, and this was measured for  $\delta^{13}\text{C}$ . The  $\delta^{13}\text{C}$  composition of marine organic matter is often thought to reflect the  $\delta^{13}\text{C}$  signature of atmospheric  $\text{CO}_2$  and therefore reflect changes in  $p\text{CO}_2$  (Scheffler *et al.* 2003). The lowest  $\delta^{13}\text{C}$  values therefore represent full glacial conditions, while deglaciation is represented by higher  $\delta^{13}\text{C}$ . The Karoo Basin has  $\delta^{13}\text{C}_{\text{organic}}$  which increases (< -25‰ to -22‰) from 308 to 288 Ma, a trend that Scheffler *et al.* (2003) compared to Veizer *et al.*'s (1999)  $\delta^{13}\text{C}$  data from equatorial shelly carbonates for the same time period. The trend to increasing  $\delta^{13}\text{C}$  values in both the Karoo organic matter and equatorial carbonates is thought to represent the same global  $p\text{CO}_2$  shift. The Eccia Group which has the highest  $\delta^{13}\text{C}_{\text{organic}}$  values is thought to have been, at least in part, deposited during the earliest Asselian.



**Fig. 4.** Running  $\delta^{13}\text{C}$  mean (a) and  $\delta^{18}\text{O}$  mean (b) (2 Ma step, 5 Ma window), based on well-preserved brachiopod shells for the interval 296–253 Ma. The Early Permian brachiopod data are entirely derived from the Southern Urals, which were in a palaeo-equatorial position, although it is assumed that the brachiopods were living in basins which were open to the Tethys Ocean. Reproduced with permission from Korte *et al.* (2005).



## Further study

The Early Permian rocks of Gondwana that can be related to climate-forced deglaciation are well-represented sequences of pre-Cenozoic glaciation, and therefore form an invaluable resource to develop a Gondwana biotic deglaciation model. The advantages of developing such a deglaciation model would be in understanding the response of life to increasing temperatures and other climate change, and might be useful in the study of modern biotic change during global warming. However, to achieve such a model, a number of factors need to be considered:

1. More detailed bed-by-bed interdisciplinary palaeontological studies of measured sections demonstrably related to climate-forced deglaciation must be carried out. Clearly, such studies are limited to sections with well-preserved fossils and more or less continuous stratigraphical fossil occurrence. While this may be possible for palynology, it is unlikely to be possible for macrofossils, which in post-glacial Early Permian sequences are stratigraphically and geographically rather isolated. Palynological assemblages that are defined quantitatively would be important in such studies, but such assemblages at least in glaciogenic sediments, have been shown to be influenced by facies (Stephenson 1998), and reworking (Osterloff *et al.* 2004). Similarly, factors related to differential spore or pollen production by different plants can influence the quantitative characteristics of palynological assemblages (Wilson 1963), as can over-representation of natural diversity due to excessive taxonomic splitting. Thus, study of biotic change needs to compensate for such factors.

2. Sections for study must be coeval so that similarities (due to general climate change) and differences (presumably due to local responses to deglaciation) can be distinguished. However, establishing isochroneity is very difficult, and it is likely that palynological data will be required to correlate sequences – while also defining climate change – so there will be attendant problems of circularity of argument. An advantage of establishing a Gondwana-wide palynostratigraphy, uniting the four or five schemes presently in existence for the former continents of Gondwana, would also be in allowing other palaeontological data, of which there are considerable amounts, to be used. It is also possible that final glacial events may be of slightly different ages in different places. This has already been established on a large scale, since glaciation in southeast Australia can be shown to have persisted into the Artinskian, but also there may be variations in periods of maximum rate of biotic change from region to region, due to differing palaeolatitudes, for example. Finally, many of the

post-glacial sequences for which only palynological information is available are mainly non-marine, for example in India and Arabia. Non-marine glacial basins are known for numerous disconformities and non-sequences, and for large-scale cyclical reworking of older sediments. It may not always be possible, even under the best biostratigraphical circumstances, to be able to correlate such rocks across a large continent.

## Conclusions

1. The Early Permian rocks of Gondwana that can be related to climate-forced deglaciation are perhaps the best-known and best-represented sequences of pre-Cenozoic glaciation, and therefore form an invaluable resource for future research, to develop a Gondwana biotic deglaciation model.

2. Present data, which are widely scattered geographically and of different stratigraphic scales and resolutions, clearly show diversity increase from glacial conditions to post-glacial conditions.

3. Amongst the marine fauna, a cold-water marine fauna consisting of bivalves such as *Eurydesma* and *Deltopecten*, and brachiopods such as *Lyonia*, were established in the earliest post-glacial marine transgressions that did not affect all of Gondwana. Above this is a more diverse, slightly warmer, cold temperate fauna, including brachiopods, bryozoans, blastoids and crinoids like those of the Saiwan Formation of Oman. A summary of marine faunal and palynological changes in Gondwanan Early Permian deglaciation sequences is shown in Figure 5.

4. The palynomorph succession, which covers the deglaciation period more fully, shows some consistency across Gondwana in Asselian–Sakmarian rocks. Very broadly, a change from monosaccate pollen assemblages, associated with fern spores, to more diverse assemblages with common non-taeniate bisaccate pollen, occurs through the deglaciation period (Fig. 5). In Oman, where this has been studied in greatest detail, the upland saw changes from a glacial monosaccate pollen-producing flora to a warmer climate bisaccate pollen-producing flora; in the lowlands, a parallel change occurred from a glacial fern flora to a warmer-climate colpate pollen-producing and lycopsid lowland flora. The sedimentary organic matter of the clastic rocks of the sequence records a corresponding  $\delta^{13}\text{C}$  trend (from approximately  $-21$  to  $-24\text{‰}$ ) believed to reflect palaeoatmospheric change due to post-glacial global warming.

5. Of the few Early Permian farfield isotope studies, the most detailed (Korte *et al.* 2005), compiled from brachiopods from the southern Urals, shows a  $\delta^{18}\text{O}$  decline of  $2.5\text{‰}$  in the Early

Permian (Asselian to Artinskian) and stable  $\delta^{13}\text{C}$  values of around +4.3‰ in the same period. This farfield evidence is in part consistent with Gondwanan palaeontological data since the most likely cause for the decline in  $\delta^{18}\text{O}$  is the return of isotopically light waters to the oceans from melting of glaciers at high latitudes.

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