

Permian palynostratigraphy: a global overview

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Abstract: Permian palynostratigraphic schemes are used primarily to correlate coal- and hydrocarbon-bearing rocks within basins and between basins, sometimes at high levels of biostratigraphic resolution. Up to now, their main shortcoming has been the lack of correlation with schemes outside the basins, coalfields and hydrocarbon fields that they serve, and chiefly a lack of correlation with the international Permian scale. This is partly because of phytogeographical provinciality from the Guadalupian onwards, making correlation between regional palynostratigraphic schemes difficult. However, local high-resolution palynostratigraphic schemes for regions are now being linked either by assemblage-level quantitative taxonomic comparison or by the use of single well-characterized palynological taxa that occur across Permian phytogeographical provinces. Such taxa include: *Scutasporites* spp., *Vittatina* spp., *Weylandites* spp., *Lueckisporites virkkiae*, *Otynisporites eotriassicus* and *Converrucosisporites confluens*. These palynological correlations are being facilitated and supplemented with radiometric, magnetostratigraphic, independent faunal and strontium isotopic dating.



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Palynostratigraphy is the use of palynomorphs (defined as organic-walled microfossils 5–500 μm in diameter) in correlating and assigning relative ages to rock strata. As such, it is a branch of biostratigraphy and follows the rules of biostratigraphic practice: for example, those set out by Rawson *et al.* (2002).

The Permian, falling between 252.2 and 298.9 Ma, was a period of intense change in which the giant continent of Pangea as a whole moved north, and in which, through the early part of the Period, a transition from icehouse to greenhouse conditions occurred (e.g. Fielding *et al.* 2008), alongside the decline in coal swamps and the establishment of widespread evaporite deposits (Henderson *et al.* 2012). The end of the Period saw a major extinction of fauna such as fusulinacean foraminifers, trilobites, rugose and tabulate corals, blastoids, acanthodians, placoderms, and pelycosaurs; a dramatic reduction in bryozoans, brachiopods, ammonoids, sharks, bony fish, crinoids, eurypterids, ostracodes and echinoderms (Henderson *et al.* 2012); and, although many conifers (e.g. glossopterids, cordaites) became extinct at the end of the Permian, there is no evidence of major extinction in the plants (Gradstein & Kerp 2012). Amongst the most important changes in land plants is the replacement, near the end of the Carboniferous, of arborescent lycophytes by arborescent tree ferns; arborescent lycophytes only persisted into the Guadalupian in China. The arborescent horsetails also declined by the end of the Carboniferous. In the Permian, a great variety of new seed plant groups appeared such as cycads, ginkgos, voltzialean conifers and glossopterids. The latter are

important biostratigraphic markers for the Permian of Gondwana and include several hundred species. It is estimated that by the Lopingian about 60% of the world's flora consisted of seed plants (Gradstein & Kerp 2012).

These large-scale evolutionary changes in plants, filtered by local and regional effects, are responsible for the palynological succession that provides opportunities for subdivision on which palynostratigraphic schemes are built. However, the pronounced phytogeographical differentiation of the Permian has a powerful effect on palynostratigraphy, such that schemes differ considerably across Pangea and correlation between schemes is even now tentative or incomplete. In the Gondwana phytogeographical province, for example, it is difficult to correlate to the standard Permian stages; and the Carboniferous–Permian and Permian–Triassic boundaries are not precisely correlateable into Gondwana basins using palynology (Stephenson 2008a).

Until recently, progress in correlation was hampered by the lack of fundamental stratigraphic standards such as stage Global Stratigraphic Sections and Points (GSSPs); however, since 1997 (Jin *et al.* 1997; Henderson *et al.* 2012) a number of GSSPs have been established within the Pennsylvanian–Permian succession, the most important of which is the basal Permian GSSP at Aidaralash Creek in the southern Urals (Jin *et al.* 1997; Henderson *et al.* 2012), and the basal Triassic GSSP at Meishan section D, Changxing County, Zhejiang Province, South China (Yin *et al.* 2001). Since these developments, there have also been other

advances contributing to the precision and utility of palynological biostratigraphy in this interval, including radiometric and faunal dating of palynological biozones, and limited high-resolution correlation between continents using a well-defined palynological species.

Palynological research in the Permian is extensive, being partly driven by exploration for coal (e.g. in India and Australia), and oil and gas (e.g. in the Middle East, South America, Australia and the Barents Sea), but has tended to be regional or local in focus (see Truswell 1980). A number of authors (Bharadwaj 1969; Kemp 1975; Bharadwaj & Srivastava 1977; Balme 1980; Truswell 1980; Utting & Piasecki 1995; Warrington 1996; Price 1997; Playford & Dino 2005; Azcuy *et al.* 2007; Stephenson 2008*a*) have attempted to summarize the research or to correlate the main biozones across regions, but correlation has been tentative. Among the difficulties acknowledged by these previous reviewers are disparate stratigraphic and taxonomic methods practised in different parts of the world, and different standards of documentation of palynological data.

The approach taken in this paper is to survey the palynostratigraphic schemes in the main phytogeographic provinces and then to attempt synthesis; and so the focus is on palynostratigraphy not taxonomy. Given the plethora of palynological literature on this interval, the review is necessarily selective. Most recent published palynostratigraphic schemes (e.g. since 2000) have emanated from South American and Middle Eastern basins. In the following account, age assignments related to these and other schemes reflect those of the original authors but may not necessarily use modern chronostratigraphic nomenclature, thus a variety of stratigraphic stage and other nomenclature is used in this paper. For the convenience of the reader, a chart showing correlations of the main chronostratigraphic subdivisions used internationally is shown in Figure 1.

Permian palynostratigraphic schemes use pollen and spores almost exclusively. While it is recognized that marine palynomorphs (acritarchs) may be present in Permian rocks, no study has sought to produce a palynostratigraphy based purely on

	Standard	Russia	Tethys	Western Europe	China	North America	
Lopingian Late Permian	Changhsingian 254.2	?	? Dorashamian	Thuringian	Changhsingian	?	
	Wuchiapingian 259.8		Dzhulfian		Wuchiapingian		
Guadalupian Middle Permian	Capitanian 265.1	Tatarian	Midian	Saxonian	Maokouian	Capitanian	
	Wordian 268.8		Murghabian			?	Wordian
	Roadian 272.3						Kazanian
Cisuralian Early Permian	Kungurian 279.3	Ufimian Kungurian	Kubergandian Bolorian	Rotliegend Autunian	Luodianian	Leonardian	
	Artinskian 290.1	Artinskian	Yakhtashinian			Wolfcampian	
	Sakmarian 295.5	Sakmarian	Sakmarian				
	Asselian 298.9	Asselian	Asselian				Chuanshanian

Fig. 1. Chronostratigraphy of the Permian, modified after Henderson *et al.* (2012).

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Permian acritarchs, although they may show future potential (e.g. Lei *et al.* 2013).

The range of morphology seen in palynomorphs in the Permian is illustrated simply in Figure 2. To improve readability, names of authors of taxa are excluded from the main text of the paper, but the main taxa and their authorship are listed in Appendix A.

Phytogeography of the Permian

Phytogeographical provinciality makes correlation difficult because it tends to reduce the number of taxa in common between assemblages in different provinces. In general, it seems reasonable to expect geographical parity between palaeobotanical provinces and palynological provinces since plants and palynomorphs are biologically linked (Hart 1970). However, palynomorphs are subject to much wider distribution than plant remains; similar or identical palynomorphs may be produced by unrelated plants (Meyen 1969); and taphonomic factors may affect the preservation of palynomorphs and

plant macrofossils differently (Utting & Piasecki 1995). Balme (1970), Sullivan (1965), Turnau (1978) and Van der Zwan (1981) surveyed the hazards of the reconstruction of palaeophytogeographical provinces by palynology. The value of pollen and spore taxa as indices of low-rank plant taxa is limited because the plant affinities of most Palaeozoic spore and pollen genera and species are unknown, and because botanical and palynological taxonomy are independent of one another. Despite this, the broad palynological characteristics of a region at a certain time are thought to be representative of the high-rank palaeobotanical characteristics of that region (Utting & Piasecki 1995).

In broad terms, there was a gradual diversification of phytogeographical provinces from relatively uniform palaeophytogeography in the Devonian to maximum provinciality in the Lopingian (Cleal & Thomas 1991) when four main provinces existed: Gondwana, Euramerica, Angara and Cathaysia (Fig. 3) (Utting & Piasecki 1995). Palaeobotanically, the Gondwana phytogeographical province is distinct from other provinces in the Permian because of the abundance of the glossopterids

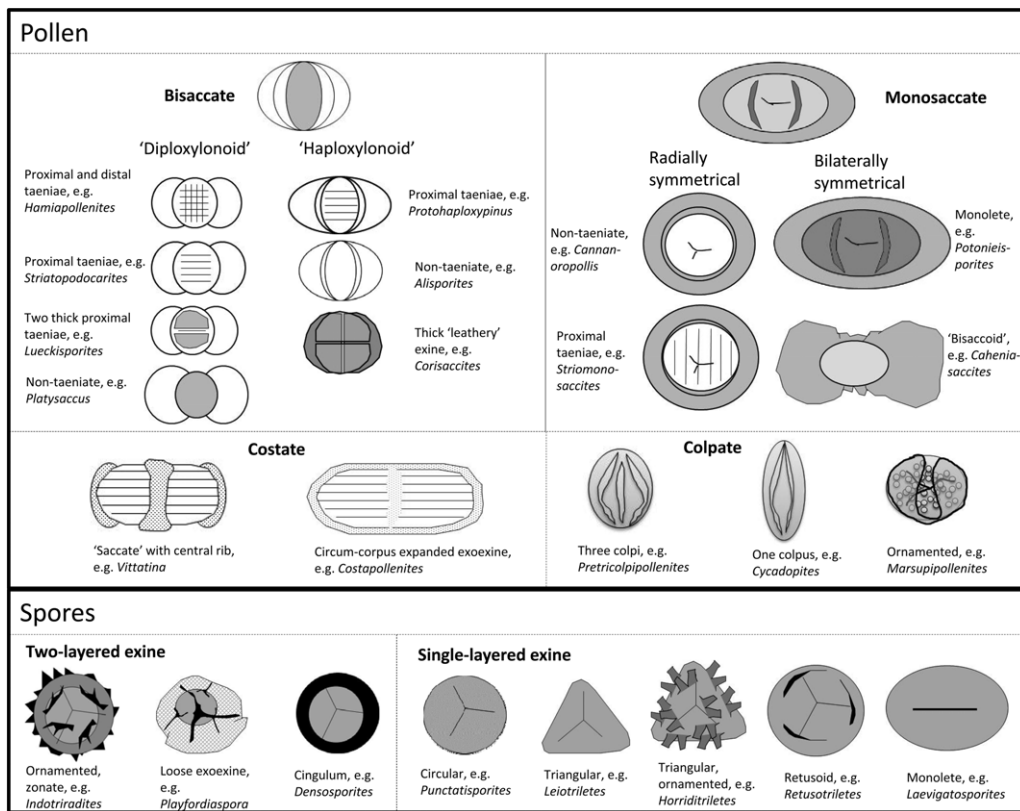


Fig. 2. Range of morphology in Permian palynomorphs.

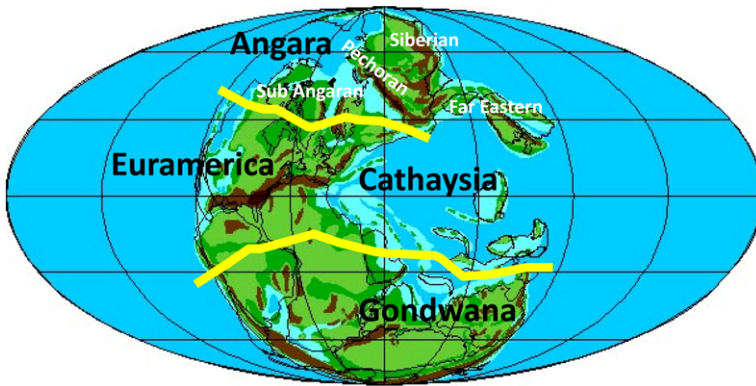


Fig. 3. Phytogeographical provinces of the Permian on a Wordian reconstruction (from the Scotese Palaeomap Project); palaeophytogeography after Utting & Piasecki (1995).

whose leaf impressions (*Glossopteris* and *Gangamopteris*) and more rare associated fruiting bodies (e.g. *Plumsteadia* and *Scutum*) are characteristic. Some conifers, sphenophytes and ferns were also present (Cleal & Thomas 1991). In the northern parts of Gondwana, marattialean ferns and lycophytes were present (Cleal & Thomas 1991). Palynologically, the Gondwana province is, perhaps, the most distinct because of its diversity of taeniate and monosaccate pollen, and the occurrence of restricted genera not yet recorded outside the province: for example, *Guttulapollenites*, *Microbaculispora*, *Dulhuntyispora* and *Corisaccites* (Truswell 1980). However, mixing of floras between Gondwana, Euramerica and Cathaysia is suggested by palaeobotanical studies (Archangelsky & Wagner 1983), and such mixing has been observed by palynologists (e.g. Kar & Jain 1975; Kaiser 1976; Eshet 1990; Nader *et al.* 1993a, b).

Palaeobotanically, the Euramerican province is distinguished by its abundant conifers, marattialean ferns and pteridosperms (Cleal & Thomas 1991). In the Lopingian, aridification caused the vegetation to become sparser and of lower diversity (Schweitzer 1986). Palynologically, a similar impoverishment of species occurs in the Lopingian (Pattison *et al.* 1973; Smith *et al.* 1974). British and west European assemblages are characterized by an abundance of conifer pollen of *Lueckisporites virkkiae*, and by the less abundant genera *Protohaploxylinus*, *Striatoabietes*, *Striatopodocarpites*, *Taeniaesporites*, *Vittatina*, *Falcisporites* and *Klausipollenites* (Smith *et al.* 1974).

According to Utting & Piasecki (1995), Angara was dominated by a cool-temperate flora containing diverse herbaceous sphenophytes and Cordaitales, with the most northerly part (Siberia) having a cold-temperate climate that spread to most of Angara by the Lopingian. According to Hart (1970), the

palynology of Angara is characterized by the abundance of trilete spores rather than by bisaccate and taeniate bisaccate pollen, which are common in the other Permian phytogeographical provinces. Monosaccate pollen of *Cordaitina* is common in the lower parts of the Permian in Angara, whereas the monocolpate pollen *Cycadopites* is common in the upper parts.

Palaeobotanically, the Cathaysia province is distinguished by its gigantopterids, noeggerathialean-like progymnosperms and plants with cycad-like foliage; however, lycophytes, sphenophytes and pteridosperms were also present (Cleal & Thomas 1991). Both palaeobotanists and palynologists report a similarity between Cusurialian floras of Cathaysia and Pennsylvanian floras of Euramerica (Kaiser 1976; Cleal & Thomas 1991; Utting & Piasecki 1995). Kaiser (1976) interpreted the relict flora as being due to the continuing palaeotropical conditions of Cathaysia, which provided a refuge for the tropical vegetation of the Pennsylvanian swamps of Euramerica.

Apart from the Cusurialian abundance of Pennsylvanian Euramerican palynological taxa in Cathaysia, there are also endemic palynological taxa that characterize Cathaysia: for example, *Nixispora* and *Patellisporites* (Utting & Piasecki 1995). The Carboniferous 'relict flora' of Cathaysia appears to persist into the Lopingian in eastern Yunnan, China (Ouyang 1982), where diverse assemblages of genera such as *Torispora*, *Crassispora*, *Triquitrites* and *Laevigatosporites* occur.

Palynostratigraphy

Euramerica

The phytogeographical province of Euramerica is now represented by the areas west of the Ural

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Mountains, Europe, parts of North Africa and North America, and contains the historical type area for the Permian and the present type area for the Early Permian (Cisuralian) in the southern Urals, including the base Permian GSSP at Aidaralash Creek, southern Urals.

Knowledge of the palynostratigraphy of the Permian of the southern Urals is hampered by the lack of work since the 1980s. Most work before that date was published in Russian, but was conveniently summarized by Hart (1970) and Warrington (1996). However, the work was regionally based and not gathered into a Urals-wide palynostratigraphic scheme, perhaps because other palaeontological groups (e.g. ammonoids and fusulinacean foraminifers) already provided ample resolution for stratigraphic subdivision.

Only a short, preliminary palynostratigraphic study has been carried out at Aidaralash Creek (Dunn 2001). Dunn (2001) described a section of approximately 50 m of strata from 24.2 m below, to 26 m above, the Carboniferous–Permian boundary. The assemblages contain abundant *Vittatina* (particularly *Vittatina costabilis*) and taeniate bisaccate pollen. The non-taeniate bisaccate pollen *Limitisporites monstrosus* is common throughout and spores are rare. No marked palynological change occurs at the Carboniferous–Permian boundary at the base of Bed 19.5 where the conodont *Streptognathodus isolatus* first appears (Davydov *et al.* 1998).

Faddeeva (1980) in a larger survey of southern Urals palynology considered that Gzhelian (latest Carboniferous) and Asselian assemblages are distinguished by changes in proportions of spores and pollen, in that the Gzhelian assemblages have common spores and few *Vittatina* specimens and pollen, while Asselian assemblages have common saccate pollen (e.g. *Cordaitina* and *Potoniaesporites*) and *Vittatina*. A similar distinction is apparent to the SW in the Donetz Basin according to Inosova *et al.* (1975).

Later assemblages from the Sakmarian of the Urals are dominated by saccate pollen, while Artinskian assemblages contain common spores including *Tuberculatosporites* and *Granulatisporites*, as well as pollen (*Cordaitina* and *Cycadopites*) (Hart 1970). According to Hart (1970), the Kungurian of the Urals is characterized by taeniate bisaccate pollen, and the Kazanian by more diverse assemblages of monosaccate and taeniate bisaccate pollen and an increase in non-taeniate bisaccate pollen. Faddeeva (1980) also noted a change at the base of the Kazanian, including an increase in taeniate and non-taeniate taxa, as well as the appearance of *Lueckisporites*, *Taeniaesporites* and *Vesicaspora*.

Utting *et al.* (1997), in an important paper that constitutes one of the few modern surveys of

Russian Permian palynostratigraphy, compared assemblages from the Ufimian and Kazanian type areas in the southern Urals around Perm and west towards Kazan, with the sub-Angaran palynological biozones of the Sverdrup Basin of the Canadian Arctic. The Ufimian, an original Russian stage recently abandoned by the All Russian Stratigraphic Commission (see Henderson *et al.* 2012), may form part of the upper Kungurian, and the Kazanian is considered equivalent to the Roadian (Fig. 1). Well-preserved palynological assemblages occur in the Ufimian and Kazanian, but Utting *et al.* (1997) recovered no palynomorphs from the Tatarian of the area.

Utting *et al.* (1997) found that many taxa range through the Ufimian and Kazanian: for example, *Florinites luberae*, *Cordaitina uralensis*, *Alisporites plicatus*, *Limitisporites monstrosus*, *Hamiapollenites tractiferinus* and *Weylandites striatus*. Several taxa appear first in the lower Kazanian (e.g. *Lueckisporites virkkiae*), while *Crucisaccites ornatus*, *Weylandites cincinnatus* and *Hamiapollenites bullaeformis* disappear in the lower Kazanian. Taxa of note that are common in the Ufimian and Kazanian sequences include *Protohaploxypinus perfectus*, *Weylandites striatus*, *Alisporites plicatus*, *Limitisporites monstrosus* and *Hamiapollenites tractiferinus* (see Utting *et al.* 1997, fig. 7). At the suprageneric level, it appears that Ufimian assemblages are more spore-rich than those of the Kazanian; the latter is characterized by abundant taeniate bisaccate pollen, and common non-taeniate and polyplicate pollen (see Utting *et al.* 1997, fig. 8).

Although Utting *et al.* (1997) did not recover palynomorphs from the Tatarian in the southern Urals, they referred to other studies (see Utting *et al.* 1997, p. 5) that characterize the Tatarian as being dominated by species of *Protohaploxypinus*, *Vittatina* and *Florinites luberae*. Gomankov (1992) refers to the presence in the lower Tatarian of *Scutasporites unicus*, which is similar to *Scutasporites nanuki* from the Wordian of the Sverdrup Basin, Canada (see later discussion); and Utting *et al.* (1997) noted some similarities between the Russian and Canadian assemblages, although they also noted quantitative differences (see Utting *et al.* 1997, fig. 8), which they attributed to palaeoclimatic differences.

Gomankov *et al.* (1998) described few palynological differences between the Tatarian and Kazanian, but identified four broad assemblage zones for the Tatarian. In ascending order, Zone I is characterized by *Weylandites* and *Lueckisporites virkkiae*, and species of *Protohaploxypinus*, *Taeniaesporites* and *Vittatina*, as well as forms related to *Vittatina* (e.g. *Ventralvittatina* and *Duplivittatina*). Zone II lacks *Ventralvittatina* and *Duplivittatina*, and contains the first appearance of spore

specimens similar to the distinctive *Limatulusporites fossulatus*, as well as *Cladaitina* and *Cordaitina*. Zone III contains fewer specimens of *Cladaitina* and *Cordaitina*, but also contains rare *Scutasporites unicus*. Zone IV sees the first appearance of *Cedripites priscus*, as well as sculptured monoletes spores of the genus *Punctatosporites*.

Much of the European sediments of the Cisuralian to the west of the southern Urals were deposited in restricted basins and are therefore difficult to correlate with beds of similar age in Russia (Utting & Piasecki 1995). Doubinger (1974) and Clayton *et al.* (1977) defined biozones based in the Carboniferous–Permian rocks of France and Germany. Balme (1980) related the base of the Disaccites Striatiti (DS) Zone of Clayton *et al.* (1977) to the base of Unit III of Western Australia (see later discussion) due to the common expansion of the taeniate bisaccate pollen at these horizons. Doubinger *et al.* (1987) and Jerzykiewicz (1987) described a similar abundance of taeniate bisaccate pollen in the Autunian (latest Pennsylvanian–Cisuralian: Fig. 1) of the Lodève Basin, France, and the Intrasudetic Basin of SW Poland, respectively.

Hochuli (1985) documented four biozones based in the Carboniferous–Permian rocks of NE Switzerland. Hochuli (1985) recognized the *Angulisporites splendidus*–*Latensina trileta* (ST) and the *Potonieisporites novicus*/bharadwaji–*Cheiledonites major* (NBM) biozones of Clayton *et al.* (1977),

which range from late Stephanian A to Stephanian D; and two higher biozones (a lower *Vittatina costabilis* (VCI) Zone and an upper *Vittatina costabilis* (VCII) Zone) that Hochuli (1985) considered together to be equivalent to the *Vittatina costabilis* (VC) Zone of Clayton *et al.* (1977) (Fig. 4).

Visscher (1980) and Edwards *et al.* (1997) indicated that a long hiatus (the ‘post-Variscan interval’) exists between the Autunian and the Thuringian (Lopingian) of Europe (Fig. 1), although Schaarschmidt (1980) reported a Kungurian–Kazanian assemblage from Germany. Apart from this assemblage, palynological assemblages from the Guadalupian of Europe appear to be rare: however, palynological assemblages from the Lopingian rocks of Western Europe have been intensively studied (Visscher 1973), but have been shown to be, palynologically, rather homogeneous throughout the sequence (Grebe & Schweitzer 1962; Schaarschmidt 1963; Clarke 1965; Smith *et al.* 1974); the only notable change being a gradual overall impoverishment of the palynoflora occurring in the upper parts of the sequence (Pattison *et al.* 1973). Although several important taxonomic studies emanate from the European Lopingian (e.g. Klaus 1963; Schaarschmidt 1963), possibilities for palynostratigraphic subdivision lie with the variations within the *Lueckisporites virkkiae* palynodemes (lineages) of Visscher (1971) and with changes in the relative abundances of suprageneric groups in, for example,

	Doubinger 1974	Clayton <i>et al.</i> 1977	Hochuli 1985
Upper Autunian	A3	DS	
Lower Autunian	A2	VC	VCII — VCI
Stephanian C/D	A1	NBM	
Stephanian B		ST	
Stephanian A			
Westphalian D		OT	

Fig. 4. Correlations of western European Carboniferous–Permian palynostratigraphic schemes, after Hochuli (1985).

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the Zechstein Sea Basin (Pattison *et al.* 1973). Visscher (1971) erected six biozones within the Thuringian that are based on a palynodeme of *Lueckisporites virkkiae*.

Recent studies of European Thuringian sedimentary rocks have concentrated on the palaeo-environment (e.g. Bercovici *et al.* 2009) or on the palynological character of the Permian–Triassic boundary in the Alps (Looy *et al.* 2001; Twitchett *et al.* 2001; Spina *et al.* 2015). In North America, only a small number of publications, which concentrate on taxonomy, emanate from the Guadalupian and Lopingian, including those of Wilson (1962), Jizba (1962), Tschudy & Kosanke (1966) and Clapham (1970).

In North Africa, a palynostratigraphic scheme for a Carboniferous–Permian transition sequence was defined by Brugman *et al.* (1988) from cuttings samples from borehole A1-19 in NE Libya. On the basis of the ranges of taxa, Brugman *et al.* (1988) proposed two assemblage biozones: a lower Assemblage Zone A and an upper Assemblage Zone B. The top of the lowest biozone was defined by Brugman *et al.* (1988) as the stratigraphic level of the disappearance of *Lycospora pusilla*, a spore type particularly characteristic of the Euramerican coal belts of the Pennsylvanian. Brugman & Visscher (1988) and Brugman *et al.* (1988) believed this level to approximate to the Permian–Carboniferous boundary. The main difference across the boundary between Assemblage Zone A and an upper Assemblage Zone B is the loss in the latter of taxa of Euramerican affinity, including *Endosporites ornatus*, *Crassispora kosankei* and *Spelaeotriletes* spp.

Brugman & Visscher (1988) also identified Sakmarian–?Ufimian assemblages in A1-19. Assemblages containing *Lueckisporites virkkiae* was recorded from Tunisia by Kilani-Mazraoui *et al.* (1990).

Angara

Angara was divided into four by Utting & Piasecki (1995), including the Sub-Angara, Far Eastern, Pechoran and Siberia subprovinces (Fig. 3). Sub-Angara occupied a more southerly position in Permian palaeogeographical reconstructions, while Siberia was to the NE, at high Permian latitudes.

The palynostratigraphy of Sub-Angara is the best studied of these subprovinces as a result of work carried out in the 1980s and 1990s in the Canadian Arctic Sverdrup Basin by the Canadian Geological Survey, and work related to oil exploration in the Barents Sea and Svalbard.

Utting (1989) established five preliminary palynological biozones in the Sverdrup Basin from shallow basin margin facies; later, Utting (1994) refined the ages and detailed characteristics of two of the biozones: the Wordian *Ahrensisporites*

thorsteinssonii *Scutasporites nanuki* and the Roadian *Alisporites plicatus*–*Jugasporites compactus* concurrent range zones (Fig. 5). The ages of the biozones are based mainly on ammonoids, conodonts, brachiopods and foraminifers from the associated fossiliferous beds of shallow and deep basinal facies.

Utting (1994) considered that the two Sverdrup Basin biozones were Sub-Angaran in character and correlateable with assemblages in western Canada, Alaska, Greenland, Svalbard, the Barents Sea, the Pechora Basin and the northern Russian Platform. However, the Wordian *Ahrensisporites thorsteinssonii*–*Scutasporites nanuki* Concurrent Range Zone differs from assemblages further south in the Urals in the type area of the Kazanian Stage (see the previous discussion). The Sverdrup Basin assemblages are dominated by trilete spores, non-taeniate and taeniate bisaccate pollen, and polyplicate taxa. Utting's detailed studies do not show large differences in the overall suprageneric character of assemblages across the Roadian and Wordian (see Utting 1994, fig. 7), but a number of taxa are confined to particular biozones including *Crinallites sabinensis*, *Cladaitina kolodae* and *Sverdrupollenites agluatus* to the *Alisporites plicatus*–*Jugasporites compactus* Concurrent Range Zone, and *Striatoabieites borealis* and the eponymous species to the *Ahrensisporites thorsteinssonii*–*Scutasporites nanuki* Current Range Zone. The latter biozone differs markedly from the succeeding Griesbachian *Tympanicysta stoschiana*–*Striatoabieites richteri* Assemblage Zone, which was accounted for by Utting (1994) as being due to a sedimentary hiatus and climatic differences.

Mangerud (1994) established two biozones for the Cisuralian–Guadalupian in the offshore Norway Finnmark Platform: the *Dyupetalum* sp.–*Hamiapollenites bullaeformis* Assemblage Zone of ?Kungurian–Ufimian age, and the Kazanian–?Tatarian *Scutasporites* cf. *unicus*–*Lunatisporites* spp. Assemblage Zone, as well as recognizing an older biozone previously established in Spitsbergen by Mangerud & Konieczny (1993) – the Cisuralian *Hamiapollenites tractiferinus* Assemblage. The *Hamiapollenites tractiferinus* Assemblage is dominated by species of *Vittatina* including *V. costabilis* and *V. saccata*, but also contains taeniate bisaccate pollen including *Protohaploxypinus* and *Striatopodocarpites*; and distally taeniate bisaccate pollen such as *Hamiapollenites tractiferinus* and *H. bullaeformis*. The *Dyupetalum* sp.–*Hamiapollenites bullaeformis* and *Scutasporites* cf. *unicus*–*Lunatisporites* spp. assemblage zones are similar except for the occurrence in the upper biozone of *Scutasporites* cf. *unicus* and the occurrence of *Hamiapollenites bullaeformis* in the lower biozone. According to Mangerud (1994) and Nilsson *et al.* (1996), the

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Standard		Russia	Arctic Canada, Utting 1889	Arctic Canada, Utting 1994	East Greenland, Piasecki 1984	Spitsbergen, Mangerud & Konieczny 1993	Barents Shelf, Mangerud 1994
Lopingian	Changhsingian	?					
	Wuchiapingian						
Guadalupian	Capitanian	Tatarian			?		
	Wordian						
	Roadian	Kazanian	<i>Taeniaesporites</i> sp.	<i>Ahrensisporites thorsteinssonii</i> – <i>Scutasporites nanuki</i>	<i>Protohaploxypinus</i>	<i>Kraeuselisporites</i>	
Cisuralian			<i>Alisporites insignis</i> – <i>Triadispora</i> sp.	<i>Alisporites plicatus</i> – <i>Jugasporites compactus</i>	?		<i>Scutasporites</i> cf. <i>unicus</i> – <i>Lunatisporites</i> spp.
	Kungurian	Kungurian			<i>Vittatina</i>		<i>Dyupetalum</i> sp. - <i>Hamiapollenites bullaeformis</i>
	Artinskian	Artinskian	<i>Limitisporites monstruosus</i> – <i>V. costabilis</i>			<i>Hamiapollenites tractiferinus</i>	<i>Hamiapollenites tractiferinus</i>
	Sakmarian	Sakmarian	<i>W. striatus</i> – <i>P. perfectus</i>		<i>Potanieisporites</i>		
	Asselian	Asselian	<i>Potanieisporites</i> spp. - <i>Vittatina</i> sp.				

Fig. 5. Sub-Angara palynostratigraphic schemes, adapted from Utting (1989, 1994) and Mangerud (1994).

Finmark Platform and other Barents Sea sequences can be correlated across the northern Atlantic, to Spitsbergen, Greenland and the Canadian Arctic (Fig. 5) (Mangerud & Konieczny 1993; Utting 1994).

There is very little modern palynological work on the basins to the north of Sub-Angara. Hart (1970) and Utting & Piasecki (1995) summarized palynological work from the Taimyr, Kuznets and Tungus areas in Siberia, concluding that the main difference between the lower and upper parts of the Permian is that monosaccate pollen are replaced by monosulcate pollen such as *Cycadopites*. To the east of Angara, in the Far Eastern subprovince, Utting & Piasecki (1995) summarized the generalized palynology in the Xinjiang, Tianshan, Kunlun and Junggar areas. More recent work by Zhu *et al.* (2005) compared the Junggar Basin with the Tarim Basin, which belonged to the Euramerican

Province at least prior to the Cisuralian. According to Zhu *et al.* (2005), the Junggar Basin Permian contains mainly terrestrial sediments and the Lower (1), Middle (2) and Upper (3) Permian palynofloras are characterized, respectively, by: (1) the overwhelming dominance of taeniate bisaccate pollen; (2) the high content of *Cordaitina* and taeniate bisaccate pollen; and (3) by the appearance of many newly evolved forms with a 'Mesophytic aspect'. These latter include pollen and spores of 'advanced conifers and ferns' including distinctive taxa such as *Lueckisporites virkkiae*, *Scutasporites xinjiangensis*, *Klausipollenites schaubergeri*, *Falcisporites zapfei*, *Eucommidites*, *Dictyophyllidites* and abundant small bisaccate pollen (e.g. *Vitreisporites*). Zhu *et al.* (2005, fig. 2) showed stratigraphic ranges of important taxa in the Permian sequences of the Junggar and Tarim basins.

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Metcalf *et al.* (2009) focused on the Permian–Triassic non-marine sequence at Dalongkou and Lucaogou in the Junggar Basin, and defined three assemblages, two of Lopingian age and an upper assemblage of probable Early Triassic age. The oldest is the *Tuberculatosporites homotuberculatis*–*Potonieisporites* sp. Q assemblage. Apart from the eponymous species, this assemblage contains monosaccate pollen, including *Cordaitina uralensis*, and rare specimens of *Scutasporites* cf. *unicus*. The youngest Permian assemblage, the *Klausipollenites schaubbergeri*–*Reduviasporonites chalastus*–*Syndesmorion stellatum* assemblage, is again dominated by the eponymous taxa, but also contains common non-taeniate bisaccate pollen, abundant algal remains (see Foster & Afonin 2006) and common *Scutasporites* cf. *unicus*. Other taxa include *Lueckisporites virkkiae*, *Lunatisporites transversundatus*, *Lunatisporites pellucidus*, *Platysaccus queenslandi*, *Alisporites splendens* and *Striatoabieites richteri*. Among spores making their appearance in this assemblage are *Leptolepidites jonkeri*, *Limatulasporites fossulatus* and *Naumovaspora striata*. The probable alga *Reduviasporonites chalastus* is also common.

The upper assemblage is the *Lundbladisporea foveota*–*Pechorosporites disertus*–*Otynisporites eotriassicus* assemblage. Of note here is the presence of the distinctive megaspore *Otynisporites eotriassicus*. This taxon is considered a useful marker for the base of the Triassic because it occurs in both marine and non-marine sections in Greenland, Italy, Russia and Poland (Foster & Afonin 2005).

Cathaysia

The Cathaysia province is associated with the South China and Indochina blocks of the eastern Palaeotethys Ocean, including the present-day regions of Yunnan, Shanxi, Meishan and Hunan.

In eastern Yunnan, Ouyang (1982) described a Lopingian *Torispora gigantea*–*Patellisporites meishanensis* assemblage dominated by spores similar to many that characterize the Pennsylvanian of Euramerica (a so-called Carboniferous ‘relict flora’), with a rather small representation of gymnosperm pollen. The succeeding *Yunnanospora radiata*–*Gardenasporites* assemblage from the Lopingian Changhsing Formation contains more common taeniate bisaccate pollen and other gymnosperm pollen.

Liu *et al.* (2008) described palynological assemblages from the Cathaysian province of Shanxi, North China, establishing four assemblage zones, in ascending order, the *Torispora securis*–*Torispora laevigata* (SL), the *Torispora verrucosa*–*Pachetisporites kaipingensis* (VK), the *Thymospora thiesseii*–*Striatosporites heyleri* (TH)

and the *Platysaccus minus*–*Gulisporites cochlearius* (MC) assemblage zones. Liu *et al.* (2008) considered that the SL Assemblage Zone correlates approximately with the western European SL Zone of Clayton *et al.* (1977: Westphalian C–D). The VK Assemblage Zone is believed to span the Carboniferous–Permian boundary. According to Liu *et al.* (2008), the upper TH and MC assemblage zones are of Cisuralian age. Liu *et al.* (2011) described Pennsylvanian–Lopingian megaspores from the same sections, establishing four megaspore assemblage zones extending from the Pennsylvanian to the Lopingian. This palynostratigraphic scheme is correlated with the assemblage zones of Liu *et al.* (2008). The lowest biozone is Carboniferous, but the succeeding *Bentzisporites margaritatus*–*Spencerisporites radiatus* (MS) assemblage zone is Kasimovian–Roadian in age based on fusulinids and conodonts. The *Biharisporites grosstriletus* (G) assemblage zone is of Wordian–Capitanian age, while the highest of the assemblage zones of Liu *et al.* (2011), the *Biharisporites* cf. *foskettensis* (F) assemblage zone, is believed to be of Wuchiapingian age. Liu *et al.* (2011) commented that several Carboniferous megaspores characteristic of Euramerica persist into the Guadalupian in Shanxi, North China, indicating that a warm and humid climate prevailed in this area during the Pennsylvanian–Roadian, whereas the climate of Euramerica had already become arid by the end of the Carboniferous. This warm and humid climate in northern China made it a refuge for some typically Euramerican Carboniferous plants.

The only study of the Permian–Triassic boundary sequence in the Cathaysian province and of the GSSP of the basal Triassic is that of Ouyang & Utting (1990). The Changhsing Formation yields a low-diversity assemblage dominated by acritarchs, but contains rare *Klausipollenites* sp., scolecodonts and *Reduviasporonites chalastus*. The lower part of the succeeding Griesbachian Chinglung Formation contains *Lueckisporites virkkiae*, *Klausipollenites schaubbergeri*, *Alisporites* cf. *nuthallensis*, *Protohaploxylinus* spp., *Weylandites* sp., *Cedripites* spp. and *Reduviasporonites chalastus*, as well as ‘taxa of Triassic aspect’ (e.g. *Aratrisporites* cf. *yunnanensis*). Species of *Aratrisporites* have previously been used to correlate the base of the Triassic (e.g. see Metcalfe *et al.* 2009), although strong evidence for their reliability is lacking because species of *Aratrisporites* are known from the Carboniferous of the Middle East and North Africa (e.g. *Aratrisporites saharaensis*; Loboziak *et al.* 1986). Nevertheless, *Aratrisporites* cf. *yunnanensis* first appears 2.7 m above the base of the Triassic at Meishan according to Ouyang & Utting (1990), and thus this taxon might be taken as a local marker for the base of the Triassic.

Gondwana

Of the four phytogeographical provinces, Gondwana underwent the greatest changes through the Permian chiefly because the landmass of Gondwana was comprehensively ice-bound at the beginning of the period and then swiftly underwent deglaciation in the Cisuralian.

The Late Palaeozoic glaciation of Gondwana probably comprised three distinct episodes (Isbell *et al.* 2003); the third and last glaciation was geographically widespread and had continental ice sheets spanning the Carboniferous–Permian boundary through the Moscovian to the Artinskian (Fielding *et al.* 2008). The extent of palaeobotanical isolation and the poverty of flora and fauna during this glacial period mean that palynological assemblages are particularly difficult to relate to the international stages and to the Carboniferous–Permian boundary, with the result that even now Carboniferous and Permian palynological assemblages are difficult to distinguish in Gondwana (Stephenson 2008a).

The sedimentary rocks deposited at this time occur in cratonic basins that are now spread widely apart across Australia, India, Antarctica, southern and central Africa, and South America. The Permian rocks of these cratonic basins contain commercial deposits of coal (e.g. in India, Australia, southern Africa and South America), and oil and gas (in Australia, South America and the Middle East), and thus are amongst the most intensely studied Permian sequences in the world. The need in exploration to access stratigraphic sequences through borehole material (cuttings, core and sidewall core) has meant that palynology is also, by far, the most important biostratigraphic tool used in locally correlating sequences in the Gondwana Permian, mainly for resource exploitation rather than for academic study. Thus, palynostratigraphic schemes tend to be locally focused, although attempts have been made recently to correlate more widely across Gondwana, and from Gondwana to the international Permian scale. Because of this local focus, this part of the review concentrates on parts of Gondwana, and then attempts a synthesis at the end of the section.

South America. Palynostratigraphy has progressed most recently in four regions: the Tarija and Chaco-paraná basins in northern Argentina, the Paganzo and other basins in central western Argentina, the Claromecó Basin in eastern Argentina, and the Paraná and Amazonas basins in Brazil. For reviews of earlier literature pertaining to South America see Azcuy (1980) and Archangelsky *et al.* (1980). Referring generally to South American basins, Azcuy (1980) and Archangelsky *et al.* (1980) considered Pennsylvanian palynological assemblages

(e.g. Palynozone I of Azcuy 1980) (Fig. 6) to be dominated by monosaccate pollen (e.g. *Potoniopsisporites*) and zonate spores (e.g. *Ancistrospora* and *Lundbladisporea*), with taeniate bisaccate pollen being rare. Permian assemblages (e.g. Palynozone III of Azcuy 1980) contain more taeniate bisaccate pollen, *Vittatina* and *Cristatisporites*. Superimposed on these general trends are a large number of other more subtle changes that indicate variation between South American basins and which have allowed a number of separate basin-specific palynostratigraphic schemes to evolve (e.g. see Vergel 1993; Archangelsky & Vergel 1996; Césari & Gutiérrez 2000; Playford & Dino 2000, 2002; di Pasquo 2003; Di Pasquo *et al.* 2003; Souza & Marques-Toigo 2003; Souza *et al.* 2003; Pérez Loinaze & Césari 2004; Souza 2006; Balarino 2014) (Fig. 6).

In general, the biostratigraphy of the basins is difficult to relate to the international stages of the Carboniferous and Permian (Archangelsky *et al.* 1980) because of the scarcity of marine faunas: however, indirect comparisons with sequences containing palynomorphs and cosmopolitan faunas and floras (e.g. Marques-Toigo 1974; Cisterna *et al.* 2011) allow some tentative dates to be assigned. Since 2007, the most marked progress has been made in integrating radiometric dates with palynological biozones, allowing limited – not always reconcilable – calibration of the latter with the international scale. Amongst the most important of these studies are those of Césari (2007), Guerra-Sommer *et al.* (2008), Césari *et al.* (2011), Mori *et al.* (2012) and di Pasquo *et al.* (2015).

In the first of the studies, Césari (2007) noted radiometric dates in the San Rafael Basin in central western Argentina and in the Paraná Basin in southern Brazil that suggested numerical ages for biozones established by Césari & Gutiérrez (2000) and Souza & Marques-Toigo (2003) in those basins, respectively. Thus, the *Lueckisporites*–*Weylandites* Assemblage Biozone of Césari & Gutiérrez (2000) in the San Rafael Basin contains a horizon dated at 266.3 ± 0.8 Ma (Wordian), while the *Lueckisporites virkkiae* Interval Biozone of Souza & Marques-Toigo (2003) in the Paraná Basin contains a dated horizon of 278.4 ± 2.2 Ma (Kungurian).

Guerra-Sommer *et al.* (2008) reported an age of 285.4 ± 8.6 Ma (Artinskian) within the Paraná Basin Faxinal coal seam, which is assigned to the *Hamiapollenites karooensis* Sub-biozone of the *Vittatina costabilis* Interval Biozone of Souza & Marques-Toigo (2003). Mori *et al.* (2012) noted a date of 281 ± 3.4 Ma (Artinskian) for another horizon within the *Lueckisporites virkkiae* Interval Biozone of the Paraná Basin in the Candiota coal mine.

Césari *et al.* (2011, fig. 6) produced a helpful synthesis of the palynostratigraphy and radiometric dating of the Carboniferous and Cisuralian sequence

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System or part	South America Azcuay (1980)	Chaco-Paraná, Argentina Playford & Dino (2002) Vergel (1993)		NW Argentina Césari & Gutiérrez (2000)	N Argentina, Bolivia Tarija Basin, Di Pasquo (2003)	E Argentina, Claromecó Basin, Balarino (2014)	Brazil, Paraná Basin Souza & Marques- Toigo (2003)	Brazil, Amazonas Basin Playford & Dino (2000)
Upper Permian		?		?	?	<i>T. toreutos</i> – <i>R. chalastus</i> Assemblage Zone		<i>T. toreutos</i> – <i>R. chalastus</i> Assemblage Zone
Middle Permian		Striatites Zone					<i>L. virkkiae</i>	
Lower Permian	Palynozone IV	Cristatisporites Zone	Upper	LW	<i>L. virkkiae</i>	<i>C. confluens</i> – <i>V. vittifera</i> Assemblage Zone	<i>V. costabilis</i>	<i>V. costabilis</i>
			Middle		?			
?	Palynozone III		Lower	FS	<i>V. costabilis</i>			
Upper Carb.	Palynozone II	Potoniésporites- Lundbladisporea Zone	Upper	DM	TB		<i>C. monoletus</i>	<i>R. cephalata</i>
					MR			<i>S. heyleri</i>
	Palynozone I		Lower		BC	<i>A. cristatus</i>	<i>I. unicus</i>	
							<i>S. incrass.</i>	
							<i>S. triangulus</i>	

Fig. 6. Correlation of South American palynostratigraphic schemes after Stephenson (2008a), Balarino (2014) and di Pasquo *et al.* (2015). Biozone codes: Césari & Gutiérrez (2000) DM, *Raistrickia densa*–*Convolutispora muriornata*; FS, *Fusacolpites fusus*–*Vittatina subsaccata*; LW, *Lueckisporites*–*Weylandites*; di Pasquo (2003) BC, *Dictyotriletes bireticulatus*–*Cristatisporites chacoaranensis*; MR, *Granulatisporites micronodosus*–*Reticulatisporites reticulatus*; TB, *Marsupollenites triradiatus*–*Lundbladisporea braziliensis*.

across Argentina and Brazil correlating the San Rafael and Paraná basin biozones and using radiometric dates to relate South American palynological biozones to those of Namibia and Australia.

di Pasquo *et al.* (2015) gave radiometric dates from five volcanic ash beds within the Cisuralian Copacabana Formation in central Bolivia (Tarija Basin). The five dates (cited as preliminary and published only in the non-peer reviewed Permian ICS Newsletter *Permophiles*, **53**, Supplement 1) are 298, 295.4–295.1 and 293 Ma (for two ash layers approximately 25 m apart stratigraphically), and 292.1–291.3 Ma. According to di Pasquo *et al.* (2015), these dates suggest an Asselian age for the '*Vittatina costabilis* assemblage' and an Asselian–Sakmarian age for the '*Lueckisporites virkkiae* assemblage' of di Pasquo *et al.* (2015, fig. 4). This latter date is clearly inconsistent with other dates for the *Lueckisporites virkkiae* Interval Biozone of Souza & Marques-Toigo (2003) in the Paraná Basin (e.g. see Césari *et al.* 2011).

The accuracy of radiometric dates is important for discussion of the stratigraphic occurrence of *Lueckisporites virkkiae*, and inaccuracies inherent in radiometric dating may be the cause of apparent discrepancy in its first appearance, otherwise it is

possible that *Lueckisporites virkkiae* has a diachronous first occurrence strongly reducing its value as a possible Euramerica–Gondwana 'bridging taxon'.

Another possibility is that *Lueckisporites virkkiae* is being misidentified or that the conception of the taxon being used by taxonomists is too wide. The original concept of *Lueckisporites virkkiae* Potonié & Klaus (1954) was of a diploxyloloid bisaccate pollen grain with a wide separation of sacci (e.g. see Potonié & Klaus 1954, text-fig. 5, pl. 10, fig. 3; Klaus 1963, p. 300). Clarke (1965) allowed more haploxyloloid specimens within *Lueckisporites virkkiae* in his emendation of the species, referring to these as 'variant B'. di Pasquo *et al.* (2015) did not illustrate the specimens that they attribute to *Lueckisporites virkkiae*, but the specimen illustrated by Mori *et al.* (2012, fig. 3j) is strongly haploxyloloid and lacks evidence of a prominent cappa or exoexinal taeniae. It appears closer to *Corisaccites alutas*. Haploxyloloid specimens of *Lueckisporites virkkiae* (using the conception of Clarke 1965) are difficult to separate from *C. alutas*, although Venkatachala & Kar (1966) regarded *C. alutas* as 'subsaccate', and subsequent authors have described *C. alutas* as having poorly inflated 'leathery' sacci, the exoexine of which is

structurally indistinguishable from that of the corpus (see Stephenson 2008b).

To maintain the value of *Lueckisporites virkkiae* as a biostratigraphical marker may mean rejecting the emendation of Clarke (1965) and retaining the original concept of *Lueckisporites virkkiae* Potonié & Klaus, 1954 as a diploxyloloid bisaccate pollen grain with a wide separation of sacci (see Stephenson 2008b). It may also be valuable to start comparative studies between South American Gondwanan and Euramerican localities focusing on the genera *Lueckisporites* and *Corisaccites*.

Such uncertainties over correlation mean that, at present, it is not possible to accurately correlate South American biozones to the international scale (Fig. 6). However, Vergel (1993) and Playford & Dino (2002) correlated the Carboniferous–Permian boundary in the Chacoparaná Basin to the boundary between the *Potonieisporites*–*Lundbladispota* Zone and the *Cristatisporites* Zone.

Africa. Much palynological research in southern African Permian sequences has been aimed at the correlation of coal seams (Falcon *et al.* 1984; Aitken 1994; Millsted 1999): however, more general schemes have been proposed (Hart 1969; Falcon 1975; Anderson 1977; MacRae 1988).

In the most detailed and extensive study covering more than 35 boreholes, four surface localities and more than 1000 samples, Anderson (1977) erected seven biozones for the Permian. The lowest, Zone 1 (Anderson 1977, fig. 8), contains common *Microbaculispora*, monosaccate pollen (grouped mainly under *Vestigisporites*) and non-taeniate bisaccate pollen (grouped mainly under *Pityosporites*). Anderson (1977) considered Zone 1 to be Sakmarian in age. The succeeding Zone 2 (Sakmarian–Artinskian), divided into four subzones, is chiefly distinguished by its higher numbers of zonate spores, although the highest subzone of Zone 2, and Zone 3 (Artinskian), are characterized by very abundant non-taeniate bisaccate pollen. Taeniate bisaccate pollen become common only in the highest subzone of Anderson's Zone 3.

Anderson's Zone 4 (Artinskian–Wordian) contains common taeniate bisaccate pollen with small numbers of proximal taeniae which were referred to *Lueckisporites* by Anderson (1977), but would be referred by modern taxonomists to *Corisaccites*, *Guttulapollenites* and, possibly, *Taeniaesporites*, as well as to *Lueckisporites*. Zone 5 (Capitanian) is marked by common *Vittatina*. Amongst other changes, a marked drop in *Vittatina* marks the base of Zone 6. Zones 6 and 7 (Lopingian) are similar, but are distinguished by the differing proportions of their constituent species (Anderson 1977).

The work of Anderson (1977) was not only based on a large palynological database, but also

on extensive description, and particularly illustration, of important taxa. Backhouse (1991) used these data for a comparison and correlation with palynological biozones established in the Western Australian Collie Basin (Fig. 7). This study remains one of the most rigorous intercontinental palynological correlations yet completed for the Gondwana phyto-geographical province, and, although correlation to the international stages is necessarily tentative, the

System/Stage		Karoo Basin biozones, Anderson (1977)		Collie Basin biozones, Backhouse (1991)
		Strat	Biozone	
Permian	?Ufimian	Upper Ecca	4d	<i>Protohaploxypinus rugatus</i>
				<i>Didicriletes ericianus</i>
	?Kungurian	Middle Ecca	4c	<i>Dulhuntyispora granulata</i>
			3d	<i>Microbaculispora villosa</i>
			3c	<i>Praecolpatites sinuosus</i>
			3b	
			3a	<i>Microbaculispora trisina</i>
	Artinskian	Lower Ecca	2d	<i>Striatopodocarpites fusus</i>
			2c	
			2b	<i>Pseudoreticulatispora pseudoreticulata</i>
	Sakmarian	Dwyka	2a	
			1	<i>Converrucosisporites confluens</i>
	Asselian	Dwyka		Stage 2
?				
Carboniferous				

Fig. 7. Correlation of Karoo and Collie Basin biozones, after Backhouse (1991).

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correlation of lithological units between Western Australia and southern Africa is probably robust.

Other studies have also applied Australian palynostratigraphic schemes in southern Africa (Mills-Teed 1993, 1999; Stephenson & McLean 1999). In east and central Africa, palynostratigraphic schemes were developed by Hart (1965a) and Utting (1978). Extensive taxonomic studies in that region were carried out by Bose & Kar (1966, 1976) and Bose & Maheshwari (1968).

Unlike South America, only a few ash layers provided opportunities for direct dating of palynological biozones in Africa. However, Stephenson (2009) recovered palynological assemblages of the *Converrucosporites confluens* Opper Zone from the Ganigobis Shale Member of Namibia, close to Ash layer IIb, which was radiometrically dated as 302.0 ± 3.0 Ma (Pennsylvanian: Gzhelian or Kasimovian) (see Bangert 2000). Thus, the *Converrucosporites confluens* Opper Zone may range earlier than previously thought and may influence age considerations of non-calibrated palynological biozones, such as those of Backhouse (1991) discussed earlier.

Recent work on the palynology of South African coal seams (Götze & Ruckwied 2014, Ruckwied *et al.* 2014) concentrated on using perceived climatic changes expressed in palynological sequences to correlate across South African basins. Barbolini & Bamford (2014) established two biozones in the Mmamantswe coalfield (Lower Ecca) in Botswana.

Arabia, the Middle East, Pakistan and India. The broad character of Cisuralian assemblages in the southern parts of the Middle East, and Pakistan and India, are similar to those of Africa and South America in that monosaccate pollen and simple trilete spores dominate the lowest glaciogene horizons, and these are succeeded by horizons with more diverse assemblages containing taeniate and non-taeniate bisaccate pollen, cycad pollen, and fern spores. Above this level in the late Cisuralian and Guadalupian, the assemblages of Arabia, the Middle East and Pakistan begin to diverge from those of the more southerly part of Gondwana probably because of more rapid climate warming due to the fact that these areas were already of lower latitude and were rapidly moving north (e.g. Stephenson *et al.* 2008b).

In Arabia, there are palynostratigraphic schemes for Oman (Besems & Schuurman 1987; Love 1994; Stephenson & Osterloff 2002; Penney *et al.* 2008; Stephenson *et al.* 2008a) and Saudi Arabia (Stump & van der Eem 1995); and these, as well as in-house oil company schemes, have been synthesized by Stephenson *et al.* (2003) and Stephenson (2006) to a standard palynozonation for the entire Arabian Peninsula, which also has application in the wider

Middle East (e.g. see Nader *et al.* 1993a; Stolle 2007; Angiolini & Stephenson 2008; Jan *et al.* 2009; Stephenson *et al.* 2013; Stephenson & Powell 2013, 2014). The chief unifying features of the standard palynozonation that occur throughout the Arabian Peninsula are, towards the base, the presence of common monosaccate pollen, as well as taxa such as *Anapiculatisporites concinnus* (characterizing Oman and Saudi Arabia Palynological Zone 1 (OSPZ1): ?Pennsylvanian) (Fig. 8), and above this the appearance of *Microbaculispora* and *Horriditriletes* (characterizing OSPZ2: ?Pennsylvanian–Asselian).

The base of OSPZ3 is defined chiefly by the abrupt increase in the small non-taeniate bisaccate pollen *Pteruchipollenites indarraensis* from approximately 10 to 50 or 60% of assemblages (Stephenson 2015). Other taxa that occur first consistently in OSPZ3 are the taeniate bisaccate pollen *Striatopodocarpites cancellatus* and *S. fusus*, and the taeniate ‘circumstriate’ pollen taxa, such as *Circumstriatites talchirensis* and *Striasulcites tectus*. *Kingiacolpites subcircularis* is common throughout

Chronostratigraphy		Palynostratigraphy, Stephenson <i>et al.</i> 2003	Palynostratigraphy, Penney <i>et al.</i> 2008
Capitanian	Guadalupian	OSPZ6	
Wordian		OSPZ5	
Roadian			
Kungurian	Cisuralian	OSPZ4	
Artinskian		OSPZ3	c
Sakmarian			b
			a
Asselian/ Sakmarian ?		OSPZ2	2141C
		2141B	
		2141A	
		2165B	
		2165A	
	Carb.?	OSPZ1	2159B
			2159A

Fig. 8. Palynostratigraphic schemes of the Arabian peninsula.

this biozone, occasionally reaching 50% of assemblages. OSPZ3 is believed to be Sakmarian in age (Stephenson 2015).

The chief distinguishing characteristic of OSPZ4 (?Artinskian–Kungurian: Stephenson *et al.* 2003) is the common occurrence of *Barakarites rotatus*, *K. subcircularis* and *P. limpibus*, although *C. alutas*, *P. amplus*, *Plicatipollenites* spp., *Striatopodocarpites* spp., *S. tectus*, *Strotersporites* spp., *Vesicaspora* spp., *Vittatina costabilis* and *Vittatina* spp. are also present. OSPZ5 (?Roadian–Wordian) is characterized by, amongst others, *Distriatites insolitus*, *Playfordiaspora cancellosa* and *Thymospora opaqua*; and OSPZ6 (?Wordian–Capitanian: Stephenson 2008*b*) is characterized by ?*Florinites balmei* and *Protohaploxypinus uttingii*. A high-resolution palynozonation mainly aimed at correlation in hydrocarbon basins of Oman can be correlated with the OSPZ scheme (Penney *et al.* 2008) (Fig. 8)

Palynological data on higher parts of the sequence to the Permian–Triassic transition is not available in the western part of the Middle East because lithologies are not suitable for palynomorph preservation. However, to the east of the region in the Salt Range of Pakistan, this part of the Permian sequence is represented by rocks that contain both palynomorphs and well-preserved fauna. Balme (1970), in a pioneering taxonomic work on the Salt Range, defined many of the taxa of value in palynostratigraphy of Permian–Triassic Tethyan and Gondwanan palynostratigraphy, although Balme (1970) did not define biozones himself. More recently, Hermann *et al.* (2012) defined two latest Permian assemblages in the Salt Range ('Chhidru 1' and 'Chhidru 2') present in the uppermost Chhidru Formation (Changhsingian). Chhidru 1 (the *Protohaploxypinus* spp.–*Weylandites* spp. Association) is dominated by gymnosperm pollen, including common *Klausipollenites* spp. (including *K. schaubergeri*) and *Protohaploxypinus* spp., (including *P. limpibus*), as well as *Weylandites lucifer* and *Alisporites* spp. Spores are very rare. Chhidru 2 (the *Kraeuselisporites wargalensis*–*Protohaploxypinus* spp. Association) is characterized by abundant cavate trilete spores such as *Kraeuselisporites wargalensis* and *Kraeuselisporites* spp. According to Hermann *et al.* (2012), the range of *K. wargalensis* is restricted to Chhidru 2. The top of Chhidru 2 is characterized by the last occurrences of *Klausipollenites schaubergeri* and *Lueckisporites* spp. (including *Lueckisporites virkkiae*).

In India, much of the taxonomic work in the 1960s was directed at correlation between coal seams, and not at correlation with other Gondwana sequences or international stages of the Permian. Major taxonomic studies were confined mainly to one or other of the 'lithostratigraphic stages' of the peninsular Indian Permian (in ascending order:

Talchir, Karharbari, Barakar, Barren Measures and Raniganj) and did not span larger parts of the sequence (Truswell 1980). However, attempts have been made to synthesize data into palynostratigraphic schemes for the entire Indian Permian (e.g. Tiwari & Tripathi 1992) and some limited correlations of Indian palynostratigraphy with international stages have been made (Tiwari 1996; Vijaya 1996).

The biozones of Tiwari & Tripathi (1992) are well defined, but are not dated using the international scale. The earliest of these biozones, the *Potoniaesporites neglectus* Biozone, from the lowest glaciogene sediments of the Talchir Formation is dominated by monosaccate pollen, but lacks taeniatae bisaccate pollen. The base of the succeeding *Plicatipollenites gondwanensis* Biozone is marked by diversification and the appearance of taeniatae bisaccate pollen, and the biozone above (*Parasaccites korbaensis* Biozone) in the upper Talchir Formation by fern spores such as *Microbaculispora tentula*. The base of the succeeding *Crucisaccites monoletus* Biozone of the Karharbari Formation is marked by the first appearances of the eponymous taxon, as well as taxa such as *Marsupipollenites*. The ages of these biozones are considered to range from the Asselian to Sakmarian (Vijaya 1996). The succeeding biozones of Tiwari & Tripathi (1992) are, in order of decreasing age, the *Scheuringipollenites barakarensis*, *Faunipollenites varius*, *Densipollenites indicus*, *Gondisporites raniganjensis* and *Densipollenites magnicarpus* biozones. Tiwari (1996) attempted to date 'palynoevents' through the Indian Permian: for example, the decline of monosaccates (Palynoevent 3) was considered to be late Artinskian, and the first appearance of *Densipollenites* (Palynoevent 4) as Kungurian–Ufimian – although these were not related to the biozones of Tiwari & Tripathi (1992).

Despite the fact that there has been some consolidation of schemes in India, local palynostratigraphic schemes continue to be developed in the cratonic basins. In Andhra Pradesh, Aggarwal & Jha (2013) defined eight Permian palynological biozones for the Godavari Graben, linking these with climate changes, although not to the international Permian scale. Jha *et al.* (2014), also working in the Andhra Pradesh Godavari Graben, identified two assemblages (Palynoassemblage-I and -II) dated as Lopingian. In northern India in Kashmir, Tewari *et al.* (2015) identified Permian–Triassic assemblages broadly correlated to the *Densipollenites magnicarpus* and *Klausipollenites decipiens* biozones of peninsular India (see Tiwari & Tripathi 1992).

Australia. Australia has the best-documented Cisuralian sequences of Gondwana and, owing to

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the presence of rare marine intervals, some calibration of palynological biozones with international stages has been possible using marine macrofaunas (e.g. Leonova 1998; Archbold 1999). Later palynological biozones in the Guadalupian and Lopingian are more difficult to date due to the lack of marine fauna (in coal and red beds), although there are tie points (Foster & Archbold 2001): for example, the record of a single specimen of the ammonoid *Cyclolobus persulcatus*, from the Cherrabum Member of the Hardman Formation, in

the Canning Basin, Western Australia (Foster & Archbold 2001), dated as ‘post-Guadalupian’ by Glenister *et al.* (1990) and ‘Capitanian–Dzhulfian’ by Leonova (1998). Such tie points allow spot dates to be applied to the otherwise well-developed palynostratigraphy.

A feature of palynostratigraphy in the Australian Permian is significant endemism, with the result that separate palynozonations developed in western and eastern Australian basins in the earliest period of palynological investigation (Fig. 9). In the west, eight assemblage biozones (units I–VIII), ranging in age from Pennsylvanian to Lopingian, were recognized; while, in the east, five assemblage biozones (stages 1–5) encompass the same interval (Evans 1969; Kemp *et al.* 1977; Foster 1979; Truswell 1980; Price 1983, 1997). The precise relationship between these schemes, and the ages of the biozones, remains speculative (see Jones & Truswell 1992) (Fig. 9), but there are broad similarities across the continent (see Balme 1980, text-fig. 4).

In the lower parts of the glaciogene sequence (Stage 1), radially and bilaterally symmetrical monosaccate pollen is dominant, and taeniate and

System/ Stage Ages after Backhouse (1991)	Eastern Australia		Western Australia				
	Kemp <i>et al.</i> (1977)	Price (1983, 1997)	Balme (1980)	Backhouse (1991)			
Permian	?Kungurian	?Ufimian	APP5	Unit VII	<i>D. parvithola</i>		
				Stage 5	APP4		<i>P. rugatus</i>
							<i>D. ericianus</i>
							<i>D. granulata</i>
				Stage 4	APP3	Unit VI	<i>M. villosa</i>
	Unit V	<i>P. sinuosus</i>					
	Artinskian	Stage 3	APP2	Unit IV	<i>M. trisina</i>		
					<i>S. fusus</i>		
				Unit III	<i>P. pseudo.</i>		
	Sakmarian	Stage 2	APP1	Unit II	<i>C. confl.</i>		
Stage 1							

Fig. 9. Correlation of eastern and western Australian palynostratigraphic schemes, after Kemp *et al.* (1977), Foster (1979), Balme (1980), Backhouse (1991) and Price (1983, 1997).

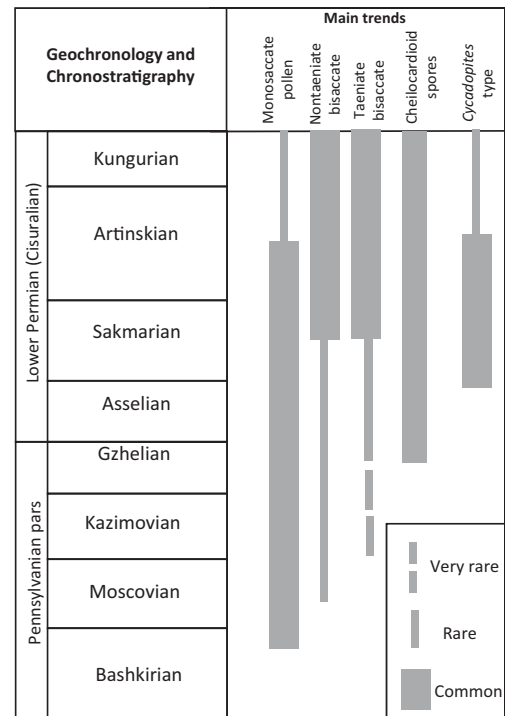
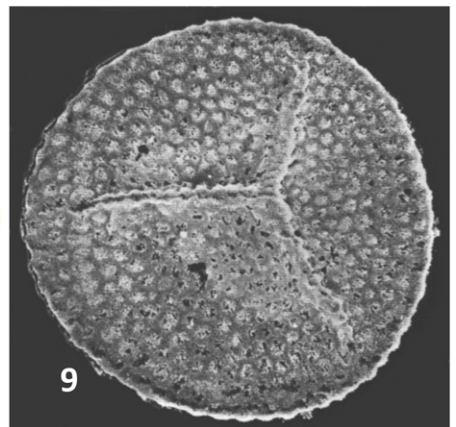
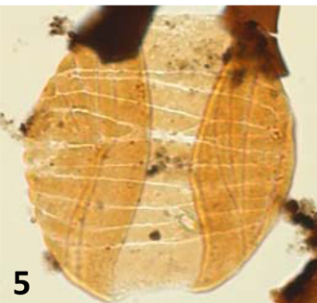
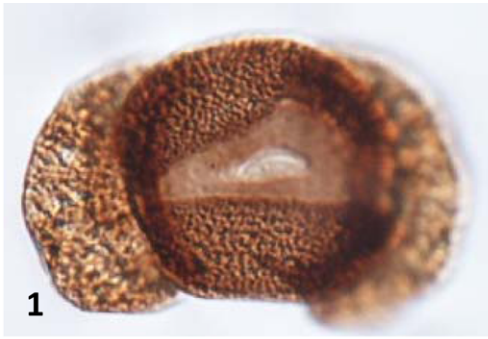


Fig. 10. Main trends in palynomorph types across the Gondwana phytogeographical province from the Pennsylvanian to the Cisuralian, after Stephenson (2008a). Correlation of events to the international scale is approximate.

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non-taeniate bisaccate pollen is subordinate. In Stage 2 above, small triangular fern spores (cheilocardoid spores) and *Cycadopites* become common; while, around the bases of Stage 3, taeniate and non-taeniate bisaccate pollen become common. In Stage 4, a diversity of pollen and spores develops, including distinctive colpate pollen such as *Praecolpatites sinuosus*; while Stage 5 is partly characterized by the very distinctive spore genus *Dulhuntyispora*, which is distinguished by expanded blister-like exoexine in each of the inter-radial areas.

Antarctica. Early work in Antarctica was carried out by Balme & Playford (1967) and Kemp (1973). Kyle (1977) erected two informal palynological biozones from study of a wide range of Antarctica localities. Her *Parasaccites* Zone is dominated by monosaccate pollen, along with rare bisaccate taeniate pollen, and, locally, high frequencies of *Microbaculispora tentula* and *Cycadopites cymbatus*. According to Truswell (1980), this biozone compares closely with the upper part of Stage 2 in Australia. The succeeding *Protohaploxypinus* Zone of Kyle (1977) is distinguished by abundant bisaccate pollen, including many taeniate taxa. In gross composition and species content, this biozone resembles Stage 4 assemblages from eastern Australia. Work following that of Kyle (1977) has tended to apply Australian palynostratigraphy to Antarctica, rather than develop more sophisticated local palynostratigraphic schemes (e.g. Farabee *et al.* 1990; Larsson *et al.* 1990; Lindström 1995a, b; Lindström & McLoughlin 2007).

Synthesis of Gondwana palynostratigraphy. It is clear that there are quantitative and qualitative similarities in the late Pennsylvanian and Cisuralian that allow correlation across Gondwana with reasonable accuracy; after this period, however, palynological characteristics of the various parts of Gondwana begin to diverge. For example, Guadalupian and

Lopingian palynological assemblages from Oman and Saudi Arabia are very different to those of Australia. Similarly, the Guadalupian palynology of South America differs considerably to that of Australia. These palynological differences, generated in the late Cisuralian following deglaciation of the Gondwana continent, are probably due to the northwards drift of Gondwana through the Permian, and the different order in which the various parts of Gondwana moved through latitudinal belts.

For the Cisuralian, the main palynological events that can be tracked with reasonable certainty through all basins of Gondwana appear to be the appearance and diversification patterns of: (1) monosaccate pollen; (2) cheilocardoid spores (such as *Microbaculispora*); (3) *Cycadopites* pollen; and (4) taeniate and non-taeniate bisaccate pollen. The precise ages of these events in relation to the international scale are not known, and recent data from radiometric dating are still being collected and assimilated (e.g. Stephenson 2009; Césari *et al.* 2011; di Pasquo *et al.* 2015) (Fig. 10).

Having said this, a high-resolution correlations within Gondwana that involve younger Permian rocks have been possible based on close taxonomic comparison and accurate stratigraphic information: for example, the correlation of the Collie Basin, Western Australia by Backhouse (1991) with the South African biozones of Anderson (1977) (see Fig. 7). Dino & Playford (2002) and Stephenson (2008a) identified taxa that are common to South America and Australia in the Carboniferous–Permian. *Converrucosisporites confluens* occurs across most Gondwana sequences: Australia (Foster & Waterhouse 1988), India (Srivastava & Bhattacharyya 1996), Argentina (Archangelsky & Gamero 1979), Uruguay (Beri & Goso 1996), Antarctica (Lindström 1995b), and Oman and Saudi Arabia (Stephenson *et al.* 2003). *Ahrensisporites cristatus* is considered to have a near-synchronous first appearance in the early Pennsylvanian, while

Fig. 11. Photomicrographs of taxa of possible biostratigraphical value between and within phytogeographical provinces of the Permian. (1) *Lueckisporites virkkiae*, F46, V-619, 2187; from the basal Khuff clastics, Saudi Arabia; width of specimen approximately 50 µm. (2) *Lueckisporites virkkiae*, E42, V-619, 2187; from the basal Khuff clastics, Saudi Arabia; width of specimen approximately 50 µm. (3) *Converrucosisporites confluens*, V42, MM-151, 3167, distal focus; from the Al Khlata Formation, Oman; width of specimen approximately 40 µm. (4) *Converrucosisporites confluens*, V42, MM-151, 3167, proximal focus; from the Al Khlata Formation, Oman; width of specimen approximately 40 µm. (5) *Weylandites* sp. slide: 1563, EF: V30.3; from the Lower Karoo sequence, Kalahari Karoo Basin, Botswana; courtesy Alain Le Hérisse; specimen featured in Modie & Le Hérisse (2009); width of specimen approximately 35 µm. (6) *Vittatina* sp., M27, RA-2, 4256; from the Al Khlata Formation, Oman; width of specimen approximately 35 µm. (7) *Vittatina* sp., M27, TL-16, 982, from the Al Khlata Formation, Oman; width of specimen approximately 35 µm; (8) *Scutasporites unicus*, collection number GBA 2010/013/0027 (holotype); single grain preparation, slide No. 404, England-finder K34r; Gröden Formation = Grödnér Sandstein (Arenaria di Val Gardena); courtesy of Prof. Hans Egger; specimen featured in Draxler (2010); width of specimen approximately 50 µm. (9) *Otyinisporites eotriassicus*; Otyin IG 1 borehole, depth 817.5 m; Balic Formation (Lower Buntsandstein), Induan; courtesy of Dr Teresa Marcinkiewicz; specimen featured in Marcinkiewicz *et al.* (2014); width of specimen approximately 400 µm.

the last appearances of *Psomospora detecta*, *Spe-laeotriletes ybertii* and *Rattiganispora apiculata* were also considered to be possibly coeval in both continents (Dino & Playford 2002).

Discussion and conclusions

The purpose of palynostratigraphy, like biostratigraphy generally, is to provide correlation. Correlation helps palynologists, stratigraphers and geologists to relate sedimentary rocks deposited in one place to those in another, and to relate geological resources or events to each other and to other important geological or scientific phenomena.

In the Permian, the most important reasons for correlation related to resource extraction are to describe coal and hydrocarbon resources, to place them into a regional framework, and to help to understand how to find more coal and hydrocarbons. Probably, the bulk of work that has been done on Permian rocks in palynostratigraphy has been in this area. There have been several tens of palynostratigraphy papers published on coal measures stratigraphy in India, South America, Australia and southern Africa, with the result that coal measures sequences (e.g. Foster 1979), and even individual coal seams, can be correlated (e.g. Aitken 1994). Perhaps the work that has led to the highest-resolution palynostratigraphy (in terms of being able to recognize and distinguish the smallest divisions of stratigraphy and time) has been for the hydrocarbons industry, particularly in the Middle East where very large accumulations of oil and gas occur in the Permian. These schemes are capable of biostratigraphically characterizing rock units of only a few metres in thickness across oil and gas fields or even basins (e.g. Stephenson & Osterloff 2002; Penney *et al.* 2008; Stephenson *et al.* 2008a). In Australia also, the work of Price (1983, 1997) has been widely used for Permian onshore oil, gas, unconventional hydrocarbons and coal exploration.

Although these palynostratigraphic schemes related to resource extraction have been very successful, their main shortcoming has been a lack of correlation with schemes outside the basins, coal-fields and hydrocarbon fields that they serve, and chiefly a lack of correlation with the international Permian scale. In the past, a lack of fundamental stratigraphic standards (e.g. GSSPs) for the Permian hampered this kind of correlation, but these now substantially exist (see Henderson *et al.* 2012) and local and regional palynostratigraphic schemes should be fitted into the wider Permian scale.

In general, also, standards of recording of palynological data and accessibility of data are higher, allowing easier comparison between palynostratigraphic schemes. Some problems still exist in the

precision of taxonomic classification in different areas such that the utility of potentially useful widely correlateable palynological taxa are reduced (e.g. *Lueckisporites virkkiae*).

The benefits of a better integrated general palynostratigraphy are very great scientifically because there are numerous events of global scientific interest in the Permian: for example, the timing and order of deglaciation events across the continent of Gondwana that can, arguably, only be established through a Gondwana-wide palynostratigraphic scheme (see Stephenson *et al.* 2007), large-scale patterns of floral migration across continents, and the detailed characteristics and timing of mass extinction events within the Permian and at the Permian–Triassic boundary.

Perhaps the most important generalization that can be made about the palynostratigraphy of the Permian is that phytogeographical provinciality is strong throughout the Permian and particularly from the Guadalupian onwards, as predicted by palaeobotanical studies. This makes correlation between regional palynostratigraphic schemes difficult. These differences appear to be more than could be accounted for by differing taxonomic concepts, although these may contribute to the extent of the apparent differences between phytogeographical provinces. For these reasons, it is unlikely that a single comprehensive palynostratigraphic scheme for the Permian globally will ever be developed, or at least not one that contains inherent precision that will be valuable for resolving Earth events. This paper does not, therefore, suggest such a scheme, nor even suggest unified schemes, for the phytogeographical provinces of the Permian.

What are likely to be possible are high-resolution palynostratigraphic schemes for regions (which substantially already exist) that can be linked by tie points. These tie points will be provided by precise assemblage-level quantitative taxonomic comparison or by the use of single well-characterized palynological taxa ('bridging taxa') that occur across Permian phytogeographical provinces.

Perhaps the most important of these taxa for the Permian include (Fig. 11): (1) *Scutasporites* spp., *Vittatina* spp., *Weylandites* spp. and *Lueckisporites virkkiae* (for correlation between the Euramerican and Angaran provinces); and (2) *Vittatina* spp., *Weylandites* spp. and *Lueckisporites virkkiae* (for correlation between the Euramerican and Gondwana provinces). Correlation between the Cathaysian and other phytogeographical provinces remains a problem because few 'bridging taxa' have been identified. This may represent a lack of effort in palynological studies in linking Cathaysian and other phytogeographical provinces, and the isolation of much Chinese palynology in that it is published only in Chinese.

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None of the Permian GSSPs involve palynological definitions, which may be problematic given the importance of palynology in correlation in the commercial and academic worlds. However, there appear to be taxa that occur at GSSPs or well-dated boundary sections that could be used to correlate those boundaries. For example, *Aratrisporites* spp. and *Otynisporites eotriassicus* may be useful to correlate the Permian–Triassic boundary into non-marine sections or sections without radiometric dates. *Converrucosporites confluens* may be useful in correlating the Carboniferous–Permian boundary (Fig. 11).

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Appendix A

Species names and authors

- Ahrensisporites cristatus* Playford & Powis, 1979
Alisporites cf. *nuthallensis* Clarke, 1965
Alisporites plicatus Jizba, 1962
Alisporites splendens (Jizba) Foster, 1979
Anapiculatisporites concinnus Playford, 1962
Aratrisporites cf. *yunnanensis* Ouyang & Li, 1980
Aratrisporites saharaensis Loboziak *et al.*, 1986
Barakarites rotatus (Balme & Hennelly) Bharadwaj & Tiwari, 1964
Brevitriletes cornutus (Balme & Hennelly) Backhouse, 1991
Cedripites priscus Balme, 1970
Circumstriatites talchirensis Lele & Makada, 1972
Cladaitina kolodae Utting, 1994
Converrucosporites confluens (Archangelsky & Gameiro) Playford & Dino, 2002
Cordaitina uralensis (Luber) Samoilovich, 1953
Corisaccites alutas Venkatachala & Kar, 1966
Crassispora kosankei (Potonié & Kremp) Bharadwaj, 1957
Criminalites sabinensis Utting, 1994
Crucisaccites ornatus (Samoilovich) Dibner, 1971
Cycadopites cymbatus (Balme & Hennelly) Segroves, 1970
Distriatites insolitus Bharadwaj & Salujah, 1964
Endosporites ornatus Wilson & Coe, 1940
Falcisporites zapfei (Potonié & Klaus) Leschik, 1956
Florinites luberae Samoilovich, 1953
Florinites? balmei Stephenson & Filatoff, 2000
Hamiapollenites bullaeformis (Samoilovich) Jansonius, 1962
Hamiapollenites tractiferinus (Samoilovich) Jansonius, 1962
Horriditriletes ramosus (Balme & Hennelly) Bharadwaj & Salujah, 1964
Horriditriletes tereteangulatus (Balme & Hennelly) Backhouse, 1991
Kingiocolpites subcircularis Tiwari & Moiz, 1971
Klausipollenites schaubergeri (Potonié & Klaus) Jansonius, 1962
Kraeuselisporites wargalensis Balme, 1970
Leiotriletes virkkii Tiwari, 1965
Leptolepidites jonkeri (Jansonius) Yaroshenko & Golubeva, 1991
Limatulasporites fossulatus (Balme) Helby & Foster in Foster, 1979
Limitisporites monstruosus (Luber & Valtz) Hart, 1965b
Lueckisporites virkkiae (Potonié & Klaus) emend. Clarke, 1965
Lunatisporites pellucidus (Goubin) Helby ex de Jersey, 1972
Lunatisporites transversundatus (Jansonius) Fischer, 1979
Lycospora pusilla (Ibrahim) Somers, 1972
Microbaculispora tentula Tiwari, 1965
Naumovasporea striata Jansonius, 1962
Otynisporites eotriassicus Fuglewicz, 1977
Platysaccus queenslandi de Jersey, 1962
Playfordiaspora cancellosa (Playford & Dettmann) Maheshwari & Banerji, 1975
Praeocolpatites sinuosus (Balme & Hennelly 1956) Bharadwaj & Srivastava, 1969
Protohaploxypinus amplus (Balme & Hennelly) Hart, 1964
Protohaploxypinus limpidus (Balme & Hennelly) Balme & Playford, 1967
Protohaploxypinus perfectus (Naumova ex Kara-Murza) Samoilovich, 1953
Protohaploxypinus uttingii Stephenson & Filatoff, 2000
Pseudoulatispora pseudoreticulata (Balme & Hennelly) Bharadwaj & Srivastava, 1969
Psomospora detecta Playford & Helby, 1968
Pteruchipollenites indarraensis (Segroves) Foster, 1979
Rattiganispora apiculata Playford & Helby emend. Playford, 1986
Reduviasporonites chalastus (Foster) Elsik, 1999
Scutasporites nanuki Utting, 1994
Scutasporites unicus Klaus, 1963
Scutasporites xinjiangensis (Hou & Wang) Ouyang *et al.* 2003
Spelaeotriletes triangulus Neves & Owens, 1966
Spelaeotriletes ybertii (Marques-Toigo) Playford & Powis, 1979
Striasulcites tectus Venkatachala & Kar, 1968
Striatoabieites multistriatus (Balme & Hennelly) Hart, 1964
Striatoabieites richteri (Klaus) Hart, 1964
Striatopodocarpites cancellatus (Balme & Hennelly) Hart, 1964

Striatopodocarpites fusus (Balme & Hennelly) Potonié, 1958
Sverdrupollenites agluatus Utting, 1994
Thymospora opaqua Singh, 1964
Vittatina costabilis Wilson, 1962
Vittatina saccata (Hart) Jansonius, (1962)
Weylandites cincinmatus (Luber ex. Varyukhina) Utting, 1994
Weylandites lucifer (Bharadwaj & Salujah) Foster, 1975
Weylandites striatus (Luber) Utting, 1994

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