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CLIMATIC CHANGES AS MIRRORED BY CARBONIFEROUS AND PERMIAN FLORAL DISTRIBUTIONS

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ABSTRACT: Three major intervals in Late Palaeozoic time, i.e. Mississippian, Pennsylvanian and Permian, are discussed as successive greenhouse, icehouse and greenhouse climatic intervals with different floral compositions. It is emphasised that the record is incomplete due to a strong preservational bias favouring wet lowland basins with reducing environments. Continental configuration is mentioned in relation to a South Polar ice cap, influencing precipitation patterns; and also various other conditioning factors in regard to floral distribution and composition at different times. The palaeobotanical record in the Iberian Peninsula is mentioned in particular.
KEY WORDS: Mississippian, Pennsylvanian, Carboniferous, Permian, floral distribution.

RESUMEN: Dentro del Paleozoico Superior (Misisípico, Pensilvánico, Pérmico) han sido considerados tres grandes intervalos climáticos: cálido-glaciar-cálido, con composiciones florísticas diferentes. Queda patente que el registro fósil tiene un fuerte sesgo hacia floras de zonas pantanosas preservadas en medios reductores. Se aborda también la configuración de las masas continentales en relación a un casquete de hielo en el polo sur (Pensilvánico), el patrón de precipitaciones, así como la influencia de varios factores que han condicionado la distribución de las floras y su composición en distintas etapas. Se ha hecho hincapié en el registro paleobotánico de la Península Ibérica.
PALABRAS CLAVE: Misisípico, Pensilvánico, Carbonífero, Pérmico, distribución de floras.

GENERAL CONSIDERATIONS

Recognition of two subsystems of the Carboniferous system implies recognition of two different periods in time marked by important differences in global climate. Indeed, the Carboniferous Period as instituted by Conybeare (in CONYBEARE & PHILLIPS, 1822 – see RAMSBOTTOM, 1984) refers to the presence of coal deposits in Europe and thus to what is nowadays called the Pennsylvanian Subsystem. The Carboniferous Limestone below the coal-bearing succession carries quite different connotations, and belongs to the Mississippian Subsystem. These two subsystems, originally described as separated systems in North America, are separated by a widespread discontinuity in the Appalachians and American Mid-continent, a discontinuity that is associated with a global fall in sea level and consequent regression and halt in sedimentation in low-lying platform areas. The reason for the global fall in sea level at the Mississippian-Pennsylvanian boundary is generally ascribed to the rapid build-up of a continental ice cap in the South Polar region, which then coincided with part of the Gondwana Supercontinent. It is known from the Recent, which only differs from the Pennsylvanian situation by a different configuration of continental areas, that the continental underpinning of a polar ice cap is a necessary condition for the accumulation of a large thickness of ice. A substantial polar ice cap produces the icehouse conditions, which drive ocean currents and air currents, and thus provide a vital control on the volume and distribution of rainfall. Although the detail of worldwide distribution of temperature and precipitation owes much to another conditioning factor, the continental configuration, it is a fact that icehouse conditions lead to an overall differentiation of temperature according to latitude. The terrestrial floral distribution reflects this differentiation, which becomes even simpler when it is taken into account that the geological record does not include the so-called alpine floras of high altitude. Although the preservation of high altitude floras may be possible in the intramontane basins occurring in high mountain chains, these are to be regarded as impermanent records likely to be destroyed as mountain chains are being worn down by erosion. The more permanent geological records are those preserved at low altitudes, generally not far above sea level. Low altitude subsident basins are the key to the geological record of terrestrial floras. Another factor of considerable importance for the preservation of floral remains is the presence of reducing conditions. Desert plants are unlikely to be preserved. The fossil floras are therefore strongly biased towards low altitude communities that lived under humid conditions; this consideration being valid to a more limited extent for windblown pollen, but this is only a minor proportion of Carboniferous palynomorphs, which are heavily biased towards spores distributed by water.

Mississippian floras are generally admitted to be fairly uniform over most of the world. It is also true that Mississippian floral remains are much less common than the more ubiquitous Pennsylvanian floral assemblages, this being readily explained by the higher sea level in Mississippian times when the continental shelf areas were widely flooded. The global fall in sea level at the end of the Mississippian as a result of the rapid growth of a south polar ice cap, resulted in a widespread regression from the continental shelves that became the site of extensive swamps in palaeoequatorial regions with a high rate of precipitation. The icehouse conditions of Pennsylvanian times also produced a marked floral differentiation in accordance to palaeolatitude, with the greater floral diversity corresponding to the palaeoequatorial belt, and a sharply diminished diversity at the higher palaeolatitudes. The floral differentiation according to palaeolatitude continued into the Permian, but the global rise in temperature at the end of the Pennsylvanian allowed the outward migration of palaeoequatorial thermophile elements and the consequent enrichment of floras at the higher palaeolatitudes. Eventually, the floral differentiation according to latitude faded with time as the Permian progressed and graded into the generally warmer, more equitable Mesozoic climate.

MISSISSIPPIAN FLORAS

These floras are characterised by the presumed progymnosperms *Rhacopteris, Triphyllopteris* and similar genera. Lycopsids are generally represented by small trees, such as *Lepidodendropsis* and the isoetalean *Eoacanthocarpus*, with different genera recorded generally as *Lepidodendron (sensu lato)* coming in later in the Mississippian, i.e. in Serpukhovian times. Ferns are well represented and so are the pteridosperms, but not yet in the numbers and variety as found in the Pennsylvanian. *Archaeocalamites* with pith casts showing the ribs continuing across the nodes, and characteristically forked leaves, is the emblematic sphenopsid. In the Iberian Peninsula the Mississippian floras are found only in Sierra Morena, with the older floras, attributed to late Tournaisian, being recorded almost exclusively from the small pull-apart basin of Valdeinfierno and at Cerrón del Hornillo near Puebla de los Infantes (Seville province). The later Mississippian floras, of Serpukhovian (early Namurian) times, are found in a larger number of localities, mainly in the province of Córdoba (see WAGNER *et al*., 1983, and WAGNER, 2001).

An analysis of Mississippian floras around the globe shows only minor variations and no sharp differences in composition. However, this observation is only valid for what may be regarded as a wide belt of low palaeolatitude regions (broadly speaking a palaeoequatorial belt). Data from the high palaeolatitude Gondwana area on the southern hemisphere are few and far between, but recent records such as from the Paracas Peninsula in Perú (IANNUZZI & PFEFFERKORN, 2002 and References therein) show a rather similar floral composition as in the palaeoequatorial belt, with differences particularly in the lycopsids. The high palaeolatitude area of Angara (Siberian region) shows the Mississippian floras (Lower Carboniferous in the Russian sense) to be dominated by lycopsids (Lepidophyttalean assemblages I-IV – for a summary see the chart of Fig. 75 in WAGNER *et al*. (1996) "The Carboniferous of the World", vol. III, p. 196), which occur together with fernlike foliage of uncertain affinity, and *Cordaites*. The lycopsids belong to local genera such as *Tomiodendron, Lophiodendron, Abacodendron*, and *Siberiodendron,* not known from the palaeoequatorial belt, some of which possess air bladders instead of the parichnos canals found in a majority of the "classical" lycopsids of the palaeoequatorial belt. The singularity of the Angara area is maintained for the Pennsylvanian assemblages (*op. cit.*).

PENNSYLVANIAN FLORAS

These are often called the "coal-measure floras" because of their close association with the coal deposits of Europe and North America, all corresponding to the palaeoequatorial belt that extended from North and Central America (and including Venezuela) through Europe into Central Asia and China (Fig.1). These floras are also referred to as Amerosinian. The environment in which these floras developed was a warm and humid one, of tropical characteristics, and their composition clearly reflects this macro-environment. The most classical "coal-measure" floras are of late Namurian and Westphalian ages and have been described primarily from the Paralic Coal Belt bordering the American craton, which was continued into Scandinavia and the Russian Platform. The total area extends from Alabama, U.S.A., to the Lublin Basin in Poland, and, perhaps, the Donbass, and thus includes the Appalachians of North America (U.S.A.), the Maritime Provinces of Canada, and the European coalfields extending from Ireland and Britain through northern France, Belgium and Germany to Moravia and Poland; and beyond this area into the Donbass region of Russia and the Ukraine on the southern margin of the Russian Platform. Four major groups are represented, viz. the lycopsids, the sphenopsids, ferns and pteridosperms, with the cordaitaleans being fairly common as well. The rhacopterids and other putative progymnosperms are rarely found but occur in strata deposited in the vicinity of basin margins, thus highlighting the ecological bias of the "coal-measure" floras. Walchian conifers are known to have existed at the same time but since these favoured a different habitat, with better drained soils, they are rarely found. An important record of non-coal measure floral elements of (early) Pennsylvanian age is that referring to a Namurian palaeovalley in Illinois (LEARY & PFEFFERKORN, 1977). A different floral habitat is also known from the Paradox Basin, Colorado, where Walchian conifers occur abundantly in Moscovian (Westphalian) strata (LYONS & DARRAH, 1989)

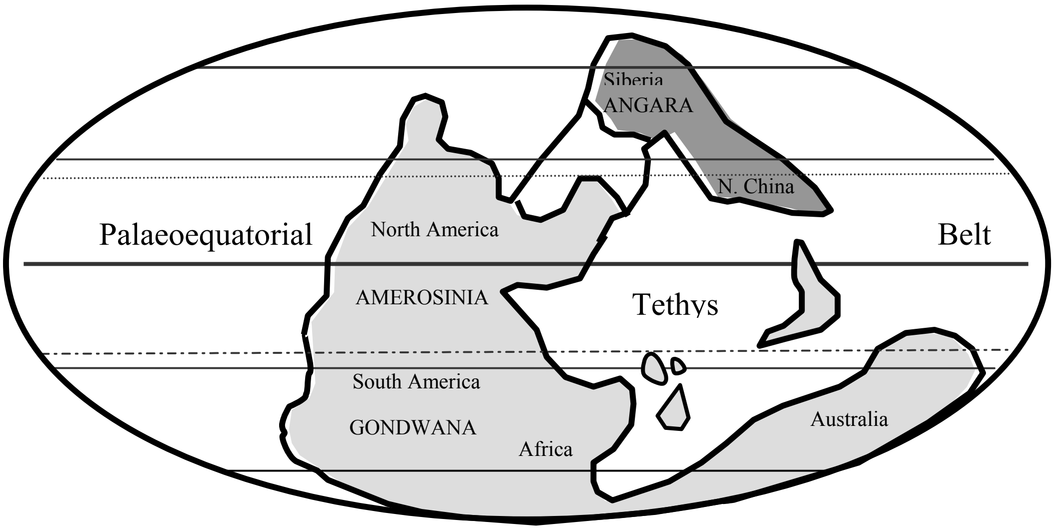

FIGURA 1. Floral realms in Pennylvanian times (after Wagner, 1993)

Pennsylvanian times are subdivided into mid to late Namurian, Westphalian and Stephanian. The latter series used to be exemplified by the intramontane basins of the Massif Central in south-central France, but the historical records from this area are to some extent superseded by the Stephanian floras from coastal, partly marine basins in the Cantabrian Mountains of Northwest Spain, where more continuous stratigraphic successions are found. Most significant is the presence of a gradual transition between Westphalian and Stephanian in the Cantabrian Mountains, such as eluded the classical Stephanian areas of the Massif Central and Saar-Lorraine, the latter being a strike-slip controlled basin extending across the French/German border, and which shows a major gap at the Westpalian-Stephanian boundary. Starting with the highest Westphalian and throughout the lower Stephanian, there is a gradual increase in the abundance and variety of tree ferns, with a concomitant decrease in the diversity and abundance of lycopsid trees. This change in floral composition is accompanied by changes on both the generic and species level of sphenopterid ferns and pteridosperm taxa. The higher Stephanian also witnessed the introduction of sphenophylls of the *Parasphenophyllum* type and the sporadic occurrence of cycadaleans. Walchian conifers are still generally absent because of the environmental considerations mentioned, and putative progymnosperms such as *Rhacopteris* and *Palaeopteridium* are still present but very rarely found, also because of the environmental conditions. *Dicranophyllum* is another rare gymnosperm.

The important change in emphasis from a high percentage of arboreal lycopsids characteristic of the swamp habitat in the Westphalian, to an increasing predominance of tree ferns throughout the Stephanian, has also become apparent from an analysis of permineralised plant remains and their spores in coal seams, which has been carried out by PHILLIPS & PEPPERS (1984) in the Illinois Basin of North America. This change, which they equate with the Westphalian-Stephanian boundary, is rather too sudden in their records, almost certainly as a result of a widespread stratigraphic gap at a level just above the Westphalian-Stephanian boundary and which has removed most of the lower Stephanian (and more?) from the North American stratigraphic record. The actual changeover is much more gradual, as the floral records from more continuous successions in Northwest Spain have demonstrated.

Pennsylvanian floras are well represented in the Iberian Peninsula. They are all of classical European type, which is understandable since the Carboniferous equator is supposed to run across south-central France. The Carboniferous terranes that make up the present-day Iberian Massif, were all close to the palaeoequator, and thus belong to the Amerosinian Realm of the palaeoequatorial belt. Upper Namurian floras occur in the Pyrenees (DELVOLVÉ & LAVEINE, 1985). They are also represented, but poorly, in the Cantabrian Mountains (La Camocha coal mine near Gijón, Asturias), whereas lower Westphalian floras occur in Asturias and in the Peñarroya Basin of Sierra Morena, as well as in South Portugal. Upper Westphalian floras are notably present in the Cantabrian Mountains of Northwest Spain (Central Asturian Coalfield and northern Palencia), in the Sierra de la Demanda, and in two localities of northern and southern Portugal, respectively. The Cantabrian Mountains contain the most complete record of Stephanian floras in the world, from Cantabrian Stage to Stephanian B Stage (*sensu* St Etienne) inclusive, with gradual transitions showing the evolutionary changes of floral assemblages within the same general macroenvironment. Three floral zones have been distinguished for this interval. Floras of the Stephanian C (= lower Autunian), the highest stage in the Stephanian Series, are well represented in the Puertollano Coal and Oil Shale Field in the La Mancha region of central Spain. Stephanian floras are also found in different parts of Portugal, in the Pyrenees, and in Cuenca province.

Despite the environmental restrictions which reduce the record almost invariably to lowland alluvial plain and swamp floras, the palaeoequatorial belt area (Amerosinia) furnishes relatively rich assemblages with perhaps up to a thousand species of lycopsids, sphenopsids, ferns and pteridosperms as well as more incidental other groups such as cordaites, cycadaleans, etc. This is in marked contrast to the much poorer record of higher palaeolatitudinal floras. With regard to the southern hemisphere Pennsylvanian Gondwana flora, which is often called the *Rhacopteris-Botrychiopsis* flora, there is a notable absence or near-absence of ferns and pteridosperms (the few records of these groups constitute rarities), and a complete dominance of the putative progymnosperms *Rhacopteris* and *Botrychiopsis*, with presumably allied genera such as *Fedekurtzia*, etc. Lycopsids in this flora include the small tree *Bumbudendron,* which is characterised by air bladders in place of parichnos. Sphenopsids in the Pennsylvanian Gondwana flora are poorly characterised (*Paracalamites*). Other forms include Dicranophyllales and possible cycadaleans. The dominance of *Rhacopteris* (called *Nothorhacopteris* on morphological criteria that seem to have been misinterpreted) has invited comparison with the Mississippian floras of the palaeoequatorial belt, and this has led to the mistaken attribution of the Pennsylvanian Gondwana flora to the "Lower Carboniferous" in the earlier literature (e.g. CHALONER & LACEY, 1973). It is clear that the Pennsylvanian Gondwana flora presents an archaic aspect due to the paucity of ferns and pteridosperms that characterise the Amerosinian Pennsylvanian of the lower palaeolatitudes. Although *Rhacopteris* and other putative progymnosperms are also found throughout the Pennsylvanian of the palaeoequatorial belt (Amerosinia), they occur so very rarely as to constitute oddities. In contrast, they continued to be dominant elements in the Pennsylvanian Gondwana flora, undoubtedly because the evolutionary advances of the palaeoequatorial belt floras did not penetrate into the Gondwana area. The succession of floras in the Pennsylvanian of the southern hemisphere Gondwana area is only known in some detail from areas in west-central Argentina and from eastern Australia, with the lower part of the Pennsylvanian being present in the latter area, and the Pennsylvanian-Permian transition being found in the Argentine (e.g. Sierra de los Llanos in the state of La Rioja). Additional records are more incidental.

Within the northern hemisphere Angara region three successive floral assemblages have been recognised for the Middle and Upper Carboniferous (which together constitute the Pennsylvanian Subsystem), based in the main on the succession in the Kuznetsk Basin of Siberia (see YUZVITSKY *et al.* in WAGNER *et al*. (1996) "The Carboniferous of the World", vol. III, p. 194). The lowest assemblage, from the Kaezovsky beds, marks a striking change from the lepidophyttalean assemblage IV of the top Mississippian (Lower Carboniferous in the Russian sense), and contains fewer lycopsids and an increased number of cordaitaleans and putative pteridosperms. This is taken to be due to the global fall in temperature at the end of the Mississippian. Most characteristic is the *Rufloria* plant assemblage I from the Mazurovsky beds, which is dominated by cordaitaleans (mainly *Rufloria*) occurring together with a number of putative pteridosperms, some sphenopsids (e.g. *Koretrophyllites*) and rare ferns. Lycopsids still occur (*Angarodendron obrutchevii*), but rarely. The striking predominance of cordaitalean trees has prompted a comparison with the conifer forests (taiga) of the cold temperate regions of the present day. The *Rufloria* assemblage I is poorly diversified, and seems to mark relatively cold conditions associated with the Gondwana Ice Age of late Namurian and Westphalian times. The subsequent Alykaevsky beds, which carry the *Rufloria* assemblage II, apparently mark a fairly substantial climatic amelioration. This assemblage is more diverse, and shows the incoming (through migration?) of some palaeoequatorial (Amerosinian) type plants roughly in the middle of the formation. These include two species of *Sphenophyllum* (including the well known Stephanian index *Sphenophyllum oblongifolium* = *S. kemerovoense* Gorelova), one *Annularia*, and several ferns. *Rufloria* is still well represented, together with *Cordaites*, and some putative pteridosperms. A species of *Dicranophyllum* has been described, as well as *Ginkgophyllum*. All species are still supposed to be peculiar to the Angara region. The change in complexion of the Angara flora within the Alykaevo beds may be correlated tentatively with the steady increase in tree fern taxa in the lower Stephanian of the Amerosinian (palaeo-equatorial) region, which PHILLIPS & PEPPERS (1984) equate with somewhat drier conditions, presumably due to a warming of the climate.

CARBONIFEROUS (PENNSYLVANIAN) PERMIAN CHANGEOVER

If Stephanian times saw already a slight warming, the end of the Ice Age came at the end of the Pennsylvanian when sea level rose again, and the diminished size of the South Polar ice cap and its eventual disappearance brought a change in weather pattern (for a discussion on the influence of continental configuration on the climate and the corresponding distribution of Permian floras, see ZIEGLER, 1990). Although this is likely to have been a more or less gradual process, there may have been a critical mass where the melting of the ice cap accelerated, and the Ice Age proper ended. Geologically speaking, this may have been a fairly sudden event. In terms of floral distribution, it is apparent that the warm palaeoequatorial belt widened with the consequent migration of thermophile plants into southern and northern higher latitudinal areas where conditions had formerly been inimical to such plants. Also, the almost uniformly wet conditions in the palaeoequatorial belt of Pennsylvanian times changed to a situation where drier condition prevailed over substantial areas where the floral record consequently favoured the plants living on better drained soils. This is particularly evident with regard to the Walchian conifers and the peltasperms of the callipterid alliance. Alternating wetter and drier conditions gave rise to two rather different environmentally controlled, floral associations as described by GOTHAN & GIMM (1930) and later authors. The drier conditions became established particularly in Europe and North America, where red beds with caliches are commonly associated with the drier climatic conditions within the lower Permian of the Euramerican Realm. This is commonly described as the Rotliegend facies, after the uppermost Stephanian and lower Permian deposits of this kind which underlie Upper Permian limestones and dolomites with evaporite deposits of the Zechstein sea in Germany, Denmark and the eastern part of the British Isles. The Autunian red beds of the Massif Central in France are quite similar. With time, the climate became even drier and the Upper Permian floras of the Euramerican Realm became more restricted with regard to the number of taxa found.

The Euramerican area is special with regard to drier climatic conditions becoming apparent from early Permian onwards. However, not everywhere the palaeoequatorial belt lost the humid climate that was so widespread during the Pennsylvanian. This is particularly noticeable in the East Asian Cathaysian area (after Cathay, the medieval name for China) where Stephanian (late Pennsylvanian) floras continued with minor changes into the Permian (Fig.2). The same wet climatic environment continued in the Permian of the Middle East. Also, the southern states of the U.S.A., Texas and New Mexico, show Permian floras characteristic of a wet environment (e.g. READ & MAMAY, 1964). The same kind of flora occurs in Mexico and in the Venezuelan Andes. In most cases, drier environments encroached upon the wet areas as Permian times advanced, thus showing a progressive loss in rainfall over large parts of the palaeoequatorial belt. Most likely, this was the result of a steady waning of the South Polar ice cap.

From early Permian onwards, the area of heavy rainfall seems to have shifted away from the palaeoequatorial belt to the higher palaeolatitudes, a fact that is being reflected in the distribution of coal deposits. Whereas the Pennsylvanian coal deposits arre virtually all concentrated in the palaeoequatorial belt, the Permian coals correspond mostly to the higher palaeolatitudes, both on the Gondwana Supercontinent (South Africa, India, Australia, Brazil), and in the northern hemisphere Angara area (Kuznetsk, Tungusska, and Minnusinsk basins in Siberia). However, Permian coals are also found in North China, which formed part of the palaeoequatorial belt but in an area where humid conditions continued until late Permian times.

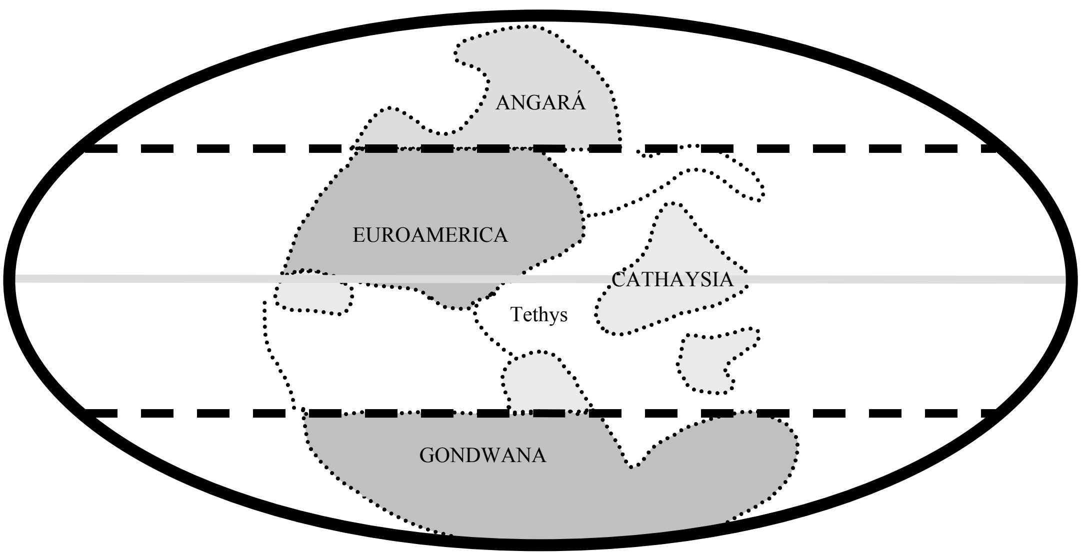

FIGURA 2. Floral realms in Permian times (after Wagner, 1993).

With regard to the southern hemisphere Gondwana area, the most characteristic floral element is *Glossopteris,* which sometimes dominates to the exclusion of other forms. The glossopterids, a group of gymnosperm trees with characteristic foliage and separate anther- and seed-bearing strobili, have no known ancestor in the Gondwana area and are most likely the descendants of an immigrant from the palaeoequatorial belt, possibly *Lesleya*, as LEARY (1993) has postulated. *Glossopteris* was an opportunistic tree that used the improved temperature conditions of the higher palaeolatitudes to flourish in the absence of immediate competition. A single species of *Glossopteris, G. anatolica* (ARCHANGELSKY & WAGNER, 1983), migrated back into the palaeoequatorial belt in late Permian times, in a humid area on the edge of the Gondwana Continent, up against the Tethyan Ocean in SE Turkey. This area is in continuity with a more southerly part of the Arabian Shield (Gondwana), at Oman, where BERTHELIN *et al.* (2003) have recorded no less than six species of *Glossopteris* occurring in association with Euramerican and Cathaysian taxa. This was obviously an ecotonal area on the border of tropical/subtropical and warm temperate regions. Within the high palaeolatitude Gondwana area of Australia and Antarctica the floral diversity diminished in the direction of the South Pole, leaving *Glossopteris* as the clear dominant with little or no admixture of other floral elements. Ecotonal floras with a higher degree of diversity are most notably present in northern Patagonia (see CÚNEO, 1996), which transform faulting moved up from lower palaeolatitudes, approximately at the level of Perú.

The Angara flora, already notably enriched in what appears to be the Stephanian equivalent (Alykaeva flora), became even more diverse in the early Permian. Meyen (in VAKHRAMEEV *et al*, 1978, see also MEYEN 1982) distinguished between three different phytochoria (floral regions) in Siberia and the North Urals, centred upon the Siberian area, occupying most of Siberia and including what may have been the North Polar region (apparently without a significant ice cap, probably as a result of a relative lack of precipitation), and fringed by the Pechora/Subangaran and Far Eastern phytochoria. The difference between the Pechora and Subangaran floras is not very great. Together with the Far Eastern area, in the vicinity of Vladivostok, the Subangaran and Pechora floral regions effect the transition with the palaeoequatorial belt. The Subangaran/Pechora floras are continued northwestwards, at what appears to have been the same palaeolatitude, into North Greenland, Arctic Canada, and Alaska (see WAGNER *et al*., 2002; LEPAGE *et al*., 2003, and MAMAY & REED, 1984). These floras show a mixture of Angaran elements (Siberian region) and those of the palaeoequatorial belt. Ferns are quite common, cycadaleans and ginkgoaleans occur, as well as a number of quite characteristic sphenopsids.

CONCLUSIONS

Late Palaeozoic floral composition appears to have been largely climate-controlled, with a preservational bias that favours wet, lowland areas. Within these constraints, which eliminate high altitude and desert floras, palaeoenvironmental conditions make floral elements linked to better drained soils rare finds. A general drop in sea level and icehouse conditions due to a South Polar ice cap make the Pennsylvanian records both widespread and fairly abundant in the palaeoequatorial belt (perhaps some 1,000 taxa), despite palaeoenvironmental constraints.

Floral diversity falls off sharply at higher palaeolatitudes (Gondwana, Angara), to pick up again at the end of the glacial period at the beginning of Permian times. Floral migration becomes an important factor as improved climatic conditions at the higher palaeolatitudes allowed thermophile elements to spread, while the shift in rain belts bring conifer and peltasperm taxa to the fore in part of the palaeoequatorial belt (Euramerian floral facies), with everwet floras being found in East Asia, the Middle East, and Central America (Cathaysian facies). Compositional changes due to evolution can only be detected when climatic/sedimentary conditions remain constant, a case in point being the diminishing role of arboreal lycopsids and the increased dominance of Marattialean tree ferns in Stephanian (Late Pennsylvanian) times. Ginkgoales and Cycadales come to the fore at the same time.

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