# = PHYTOGEOGRAPHY =

# Permian Phytogeographic Zonality and Its Implications ' for Continental Positions and Climates

V. A. Krassilov

Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, Moscow, 117868 Russia Received December 15, 1999

Abstract—The traditional Permian phytogeographic divisions do not correspond to separate landmasses. Neither are they floristic divisions for their emblematic leaf genera, such as *Cordaites* or *Glossopteris*, are morphotypes shared by the taxa that are not closely related. A revised scheme of Permian phytogeography is based on the dominant leaf morphologies, taphonomic evidence of seasonality and dead mass (coal) accumulation. It is consistent with climatic zonation including the nemoral, or humid temperate, xerothermic and humothermic zones in the Arcto-Permian realm and their counterparts in the Noto-Permian realm. The Permo-Tethyan realm of mixed Arcto- and Noto-Permian elements corresponds to a global megashear zone of the Permian tropics. This scheme lends no support to either a continental reassembly with submeridional Eurasia, equatorial Euramerian realm (which actually had a Mediterranean type climate) and the Tethys widely open to the east, or a position of the Permian South Pole near Africa (which had a much warmer climate than Antarctica). A westward shear of the eastern Tethyan microcontinents from their pre-Permian position near the Sunda Plate would explain both the constriction of the tropical zone between Tibet and the Himalayas and the origin of mixed floras. The supposedly glaciated areas of Permian tillites supported a diverse arboreal vegetation suggesting a climate totally different from that of Pleistocene glaciation.

# INTRODUCTION

I argued (Krassilov, 1972, 1975, 1997, etc.) that major phytogeographic divisions of the past are vegetational, rather than floristic, for they are based on a few dominant life forms defining the aspects of regional fossil plant assemblages rather than on computed floristic similarities and the ranks of endemic taxa, as is necessary for a proper floristic classification. The Arcto-Tertiary "geoflora" is the first widely accepted division of the kind. It is equivalent to the nemoral, or temperate broad-leaved biome that is recognizable in the Mesozoic (the *Phoenicopsis* realm: Krassilov, 1972, etc.) and, perhaps further back in time. Climatically the nemoral biome corresponds to the humid temperate zone.

South of the nemoral zone there is, and was, a likewise persistent realm of evergreen and deciduous arboreal biomes with a prominent xeromorphic element. The climatic conditions are warm temperate to subtropical of the Mediterranean or Texas types, with a dry summer season. The corresponding vegetation realm in the Miocene of North America was called the Madro-Tertiary flora (Axelrod, 1958). This vegetation type extended over Mediterranean, Central Asia and as far east as northern China. In the Mesozoic the xerothermal zone was marked by the *Cycadeoidea* assemblages with brachyphyllous coniferoids (Krassilov, 1972, etc.).

On the other hand, the relatively dry northern conifer forests and tundras, as well as the tropical rain forests are of a recent origin, related to the Late Cenozoic glaciation, with no equivalents in the Mesozoic ice-free climate, but probably represented during the Late Paleozoic.

In the 1930s the great Permian geofloras were distinguished on the basis of dominant leaf morphologies, such as Callipteris, Cordaites, Gigantopteris and Glossopteris, defining the Euramerian, Angaran, Cathaysian and Gondwana realms respectively (Jongmans, 1936, 1937, Gothan, 1937; Kryshtofovich, 1937; Meyen, 1970). These realms were considered as floristic units corresponding to separate landmasses. As such they played a significant role in the development of the continental drift concept and, later, plate tectonics. To this day they are widely used in paleogeographic reconstructions. However the Permian geofloras are not strictly definable in terms of taxonomic distinctions because of morphological parallelism of their emblematic leaf types that might belong to different, even not closely related, taxa. Thus the Cordaites-type leaves occur in the typical cordaites, vojnovskyaleans and glossopterids (Noeggerathiopsis). Though widely spread in Euramerian, Angaran, Cathaysian and Gondwana floras, this morphotype is poor evidence of floristic affinities. The same is true for the Asiatic and North American gigantopterids, the Gondwana and Angaran representatives of Palaeovittaria-Zamiopteris-Pursongia morphotypes, etc. Glossopteris associates with at least two different types of reproductive organs--cupular, as in *Lidgetonia*, and strobilar, as in *Kendostrobus*. This leaf morphotype might, thereby, belong to at least two groups of Paleozoic gymnosperms, one related to pteridosperms and the other closer to cycadophytes (Surange and Chandra, 1975; Maheshwari and Srivastava, 1992). Taxonomic affinities of Gigantopteris and its morphological allies are still more intricate. Plants



**Fig. 1.** Fertile gigantopterid leaves *Gigantotheca* with marttioid synangia from the Tontseyan Formation, Fujian, Southern China (the material courteously provided by Prof. Yao, Nanjing Institute of Geology and Paleontology, Nanjing): (a)  $\times 10$ ; (b)  $\times 25$ .

with Gigantonoclea-type leaves might have two or more different types of reproductive structures. The typical material from Shansi associates with Jiaochengia, a pinnate microsporophyll with reduced lamina and semisynangiate sporangial clusters (Wang, 1999) while the morphologically similar leaves from Southern China are accompanied by Gigantotheca sporophylls bearing imbricate synangia on unreduced leaf blades (Fig. 1). In the gigantopterid leaves that I collected from the latest Permian (Changhsingian) of Laibin, South China a structurally preserved axis shows tracheids with biseriate bordered pitting similar to those of the Permian conifers and peltasperms (Fig. 2).

Why certain leaf morphotypes were so widespread in one geographic realm while rare or lacking in the others remains enigmatic. Phylogenetic parallelism is not a plausible explanation for we are dealing with plant groups that are not even distantly related (e.g., the marattialean ferns and peltasmermous gymnosperms in the case of gigantopterids). A biomic interpretation (Krassilov and Naugolnykh, 2000) appears consistent with a convergence of prevailing leaf morphotypes, as in the present day sclerophyllous vegetation. However, a purely ecological parallelism seems improbable for the morphotypes that, as *Glossopteris*, might have spread over a wide range of biotopes. The most similar recent phenomenon is geographic parallelism as defined by Went (1971) and the reason for it might ha been the same-horizontal gene transfer over the ge graphic realm.

In the above interpretation, the Permian "floras" "floristic provinces" are essentially the "morphocho ons" defined by a few peculiar morphotypes that spre over taxonomic and ecological boundaries. Their cor spondence to floristic or vegetational divisions is not be taken for granted, but is a matter of taxonomic a paleoecological analysis.

# GENERAL ON PALEOVEGETATION ANALYS

Paleovegetation analysis is based on the plant *l* forms rather than taxa. Life forms are groups of orga isms adapted to a certain functional role in the bio community. At the lower hierarchical levels th roughly coincide with species (though conspeci organisms can fill more than one niche depending age, sex, etc.). In extinct plants the life form is esse tially an interpretation of morphological characte Fossil leaves are the most frequent plant macrofoss providing an important life form information, for th morphology relates to their structural position (in t canopy or understorey), habitat, climate, pollinati mode, etc. For the dominant Permian plants we ha also evidence of their shoot morphology, axial an



**Fig. 2.** Anatomy of an axis with attached gigantopterid leaf form the latest Permian of Penlaitan Section, Talung Formation, Laibin, Southern China: (a) specimen no. 4793/106-25, leafy shoot with axis partly preserved as compression,  $\times 10$ : (b) protoxylem tracheid with helical thickenings, SEM; (c, d) metaxylem tracheids with obligue pit-like series between helical coils and secondary xylem tracheids with biseriate pitting-on the radial walls, SEM.

omy, underground organs, reproductive structures and even their pollinators. Seasonal dynamics of plant communities is inferred, in addition to leaf morphology, from the taphonomy of leaf assemblages that, in deciduous forms, accumulate as leaf mats. Coal is a fossilized accumulation of plant dead mass and as such is evidence of highly productive wetland (helophyte) communities.

However this information is useful only in the context of stratigraphic lithofacies sequences. For example, in the above mentioned Late Permian plant locality of Laibin, South China (see Shen et al., 1999 for stratigraphic information), the plant bed occurs on the top of a marine regressive sequence. It is about 50 cm thick consisting, from base up, of a thin coal, a root bed with arthtophyte stems and abundant pecopterid fronds, and a shale with *Gigantonoclea* and fragmentary conifers. The succession means an expansion of the arthrophytepecopterid coastal peatbog community immediately following the retreat of the sea. Later it was replaced by the riparian gigantopterid community. The conifers are rare, but they also occur as a transported material in marine strata downsection suggesting a more distant source at higher elevations.

Fossil plant assemblages are defined by the repeated association of their dominant life forms. In the above example, we have two types of wetland assemblages, of which the fern-arthrophyte one is recognized worldwide, while the gigantopterid one is characteristic of the Cathaysian region. In other regions it was partly or completely substituted by the callipterid, cordaite or glossopterid assemblages. This is a rough picture, but a sufficient one to start with.

The precursory Permian-type assemblages sporadically occur in the Late Carboniferous of both Laurasian and Gondwana landmasses. In Gondwana realm, a decline of the arboreal lepidophyte wetlands is traditionally explained by climatic changes related to glaciation. In the Euramerian realm the coeval vegetational change is, fikewise habitually, ascribed to aridity. However, the change took place worldwide, with humid non-glacial Cathaysia no exception. A drop in ground water levels caused by global regression at about the Carboniferous-Permian boundary might have been critical for lepidophyte wetlands. On evidence of the better-dated tillites, glaciation was restricted by this transboundary interval. New types of wetlands appeared with a subsequent sea level rise in the Artinskian. Owing to the role of wetlands as a major source of fossil plant material, this event is commonly taken as the beginning of the fully developed Permian flora.

# ARCTO-PERMIAN REALM

In most Laurasian localities the fern-arthrophyte peatland communities are associated with gymnosperm wetlands dominated by vojnovskyaleans, cordaites, peltasperms or the related gigantopterids. Despite considerable geographic differentiation, these types of wetlands intergrade in the broad ecotonal zones. Therefore we can speak of the Arcto-Permian realm as analogous to the Holarctic or Arcto-Tertiary.

# Temperate Nemoral Zone

The Permian fossil plant assemblages of northern Asia, known as the Angaran flora or floristic kingdom

(Kryshtofovich, 1937; Meyen, 1970) covered Siberia, Petchora Basin in the northern Fore-Urals, most of Mongolia and northern China north of  $45^{\circ}$  N. The Angaran flora is typically represented in the Kuznetsk Basin, West Siberia, a major coal-producing area in Asiatic Russia. *Cordaites* and the morphologically similar *Rufloria* are the dominant leaf genera often deposited as one-species plant beds.

The Angaran Cordaites (Rufloria)-type leaves might at least partly belong to the extinct gymnosperm order Vojnovskyales (Neuburg, 1965). Phylogenetic relationships of Vojnovskyales to the typical Euramerian cordaites is a matter of discussion (Meyen, 1984). In the present author's opinion (Krassilov, 1997) they are only distantly related. The Vojnovskyales are reported from few localities outside northern Asia, such as Midtkap in Greenland and Mount Dall in Alaska (Wagner *et al.*, 1982; Le Page and Pfefferkorn, 1996; Naugolnykh, this volume). Among the spore-plants an arthrophyte group, the Tchernovskiales appears characteristic of the, but not necessarily endemic to, the Angaran-type floras.

The geographic range of "cordaite flora" was thought to coincide with the borders of Angaraland. However, the Angaran realm is linked with the Euramerian callipterid realm by a broad zone of mixed floras extending over the Urals, Volga Basin and to Arctic Canada (Fig. 3). Many European taxa, such as *Quadrocladus*, have spread over this transitional zone to the Petchora Basin, Taymyr (Sadovnikov, 1997) and further east. Actually, the Late Permian uplift of Uralian Ranges suturing the closed seaway had a minor effect on the position of phytogeographic boundaries that in the Mesozoic maintained nearly the same position as in the Permian (Krassilov and Shorokhova, 1975; Krassilov, 1997).

A popular notion of the Angaran "cordaite taiga" is incompatible with leaf morphology, for the present day typical taiga is formed of evergreen needle-leaved trees. In the dry permafrost areas east of Yenisey River it is replaced by the larch taiga of deciduous needleleaved trees shedding needles from persistent spurshoots. The Cordaites-Rufloria type of broad taeniate leaves with parallel venation commonly occurs in monocotyledonous angiosperms in which they are of a phyllodic origin, derived from inflated petioles with the leaf blade reduced. Phyllody relates to developmental acceleration in turn related to rapid leaf expansion required by a short growth season. In the cordaite realm, the monodominant to oligodominant forests grew on raised peat bogs in which a considerable part of biomass consisted of bryophytes (Durante, 1995). The *Rufloria*-type leaves were shed separately, with clear-cut abscission lines, or clustered on deciduous spur shoots. They formed thick leaf-mats, the commonest type of fossil plant assemblages in the coal measures. Since considerable peat accumulation requires a humid summer-wet climate, a combination of morphological and taphonomic data indicate the presence of



**Fig. 3.** Mid-Permian phytogeographic zones—the major biomes on the present day map (prepared with participation of Naugolnykh: Krassilov and Naugolnykh, 2000). Shading: (1) temperate nemoral, (2) warm temperate meso-xeromorphic, (3) subtropical xero-thermic, (4) subtropical humothermic, (5) Tethyan tropical and mixed. Symbols of floristic composition: 1—Angaran, II—mixed Eurangarian, III—mixed Cathangarian, IV—Eauramerian, V—mixed Euramerian/Cathamerian, VII—Cathamerian, VII—mixed Eurogondwana, VIII—Gondwana. Localities: 1—Midtcap, 2—Petchora, 3—Western Taimyr, 4— Eastern Taimyr, 5—Norilsk, 6—Tunguska, 7—Kuznetsk, 8—Verkhoyansk, 9—Sverdrup, 10—Soyana, 11—Kama, 12—Tchekarda, 13—Karaungir, 14—Fergana, 15—Junggar, 16—Tabun Tologoy, 17—North Korea, 18—Primorye, 19—Appalachian, 20—Cantabria, 21—Orobic Alps, 22—Turingia, 23—Utah, 24—Arizona (Hermit Shale), 25—Kansas, 26—Guadalcanal, 27—High Atlas, 28—Hazro, 29—Saudi Arabia, 30—Iran, 31—Texas, 32—Mexico, 33—Shanxi, 34—Anhui/Henan, 35—Jiangsi, 36—Chubut, 37—Niger, 38—Gabon, 39—Kashmir, 40—Lhasa, 41—Yunnan, 42—Phetchabun, 43—Jambi, 44—Irian Jaya, 45—Transvaal, 46—Handapa, 47—Perth, 48—Bowen, 49—Mount Achernar.

summer-green broad-leaved vegetation ecologically similar to the present-day nemoral zone of the humid temperate climate.

# Warm-Temperate Ecotone

The Permian flora of Fore-Urals and Volga Basin is considered as a broad ecotone of callipterid and cordaite vegetation. It is dominated by Euramerian peltasperms, conifers and their derived forms (Zalessky, 1927; Naugolnykh, 1998). The latest Permian assemblages of this area constitute the so-called *Tatarina* flora named after a highly polymorphic leaf-genus of peltasperms the lobate variants of which resemble both the European *Callipteris* and American *Supaia* (Gomankov and Meyen, 1986). "*Tatarina* flora" can be seen just as a local variant of the "*Callipteris* flora." The Angaran ruflorias and representatives of the fern – tchernovskian wetland communities formed a significant, yet subordinate element. To the east the ecotonal vegetation extended to Kazakhstan (Karaungir locality that yielded seeds similar to Euramerian *Salpingostoma*: Krassilov, 1999), Central Asia and northern China. On palynological evidence, the warm-temeprate vegetation zone can be traced to Greenland and Arctic Canada (Utting, 1994).

In China, the Permian floras of Junggar–Khingan (Hinggan) latitudinal area are considered as belonging to Angaran realm (Li and Wu, 1996; Li, 1997; Huang and Ding, 1998). Actually they are of ecotonal aspect, with the Volgian *Tatarina* and *Phylladoderma* admixed by the Cathaysian taeniopterids (Wang and Wang, 1986). This zone is traced to southern Mongolia and Primorye in the Russian Far East were the dominant *Rufloria–Cordaites* morphotypes associate with gigan-topterids, a feature shared with floras of North Korea, Anhui and adjacent provincies in eastern China (Mei *et al.*, 1996) and perhaps typical of the Pacific coastal areas. Notably the marine faunas of fusulinids and bra-

chiopods from the same latitudues are also of a mixed boreal/tropical aspect (Sih and Zhan, 1966).

#### Xerothermic Zone

The Permian plant assemblages of Central-Western Europe and eastern North America are dominated by callipterids (peltasperms with the *Autunia*-type strobili) and conifers, with a highly diverse fern–arthrophyte components. The boundary with Cathaysia over southern Xinjang and along the northern border of Tarim Basin to the Lesser Khingan (Li, 1997) was easily surmountable for these components that were also widespread in Gondwana floras (see below).

The Euramerian peltasperms and conifers had xeromorphic leaves with thick cuticles that are usually associated with dry climates. However leaf xeromorphism is also a typical feature of wetland (helophytic) habitats. Preservational features of xeromorphic Permian plants suggest their proximity to deposition sites. Their remains often occur in paralic facies indicating a coastal, perhaps mangrove, community.

Another type of wetland vegetation, with abundant pecopterids and calamites, is here designated as the fern-arthrophyte marsh community. These two types might intergrade in the marginal habitats. Yet in stratigraphic sequences they often alternate, with the fernarthrophyte plant beds mostly confined to regressive parts of sedimentary cycles. The peltasperm-conifer assemblages typically came from estuarine deposits (e.g., the cuticle beds of Nedubrovo: Krassilov *et al.*, 1999), whereas the fern-arthrophyte assemblages more commonly occur in deltaic deposits. Their stratigraphic recurrence might have been related to sea level fluctuations.

The Euramerian plant localities commonly associate with red or variegated beds that are traditionally conceived of as evidence of arid climate. Typical redbeds are molassoids of the Hercynian foldbelts that served as a source of ferruginous clastic material. A change from ferrous to ferric oxides (green to red beds) relates to frequent fluctuations of ground water level reflecting not so much a low mean precipitation, as a seasonal dryness of a widely variable duration. Marginal variants of redbed facies associate with either evaporites or coals. On the sum of evidence, the climate of the Permian xeromorphic zone might have been close to the modern Mediterranean climate.

# Humothermic Zone

Gigantopterids and emplectopterids are characteristic of the Permian plant localities in China, Korea, Japan and Laos constituting the Cathaysian flora. To southeast they extend to Thailand, Malaysia, Indonesia and New Guinea. Typical of gigantopterid vegetation are also large taeniopterid leaves and diverse pecopterids, at least partly shared with the xerothermic zone, lobatannularias and other arthrophytes. Their Asiatic range consists of a number of tectonic blocks at one time or another separated by seaways. The widely scattered Middle East localities (Wagner, 1962; El Khayal *et al.*, 1980 mark, its western extension, while the western North American plant assemblages have close Cathaysian affinities owing to *Cathaysiopteris* and taeniopteroid fertile leaves with marginal ovules (Mamay *et al.*, 1988; Mei *et al.*, 1992). On the other hand, *Supaia*, the emblematic North American genus, has been recently recorded from China (Wang, 1997). Therefore, the so called Cathaysian flora was actually Cathamerian.

In China, the Cathaysian (Cathamerian) flora is presently subdivided into the northern and southern provinces supposedly confined to disjunct Cathaysian terrains on the eastern periphery of Tethys. The northern Cathaysian flora occurs on the Sino-Korean–Tarim block bound from the south by the latitudinal Kunlun – Ginling fault zone traceable to Central Japan (Li, 1997). However the floristic differences between the northern and southern provinces involve a few endemic genera, such as *Emplectopteridium* and *Gigantotheca* (Li et al., 1996; Li, 1997). More significant are quantitative distinctions, with Otofolium, Gigantopteris and *Rajahia* common in the south in contrast to the predominantly northern *Cathaysiopteris*, *Emplectopteris*, large Taeniopteris and Yuania. Such distinctions suggest climatic differentiation rather than isolation. The Permian flora of Xu-Huai-Yu region in eastern-central China (at the junction of Jiangsu, Anhui and Henan provinces) is considered as a separate floristic subprovince (Mei et al., 1996), but is, in a sense, transitional between the northern and southern Cathaysian floras, having both *Cathaysiopteris* and *Gigantopteris* as equally common elements. A palaeobotanical standpoint would hold that the northern and southern Chinese blocks had already collided by the Devonian (Li et al., 1996; Li, 1997).

In the Early Permian, the typical Cathaysian flora of Shansi (Shanxi) Formation with Lobatannularia and *Emplectopteris* replaced the essentially lepidophyte flora of the conformably underlying Taiyuan Formation. This rather abrupt floristic change at about the Asselian/Sakmarian boundary (Li, 1997) might reflect a substitution of cosmopolitan lepidophyte wetland community by the newly appearing arboreal wetlands dominated by taeniopterids, emplectopterids and gigantopterids. In the Lower Shihhotse these assemblages occur in the coal measures that in the Upper Shihhotse are replaced by redbeds with Gigantonoclea (Wang, 1999). In the latest Permian the Northern Cathaysian province was invaded by European conifers and peltasperms (also by the Gondwana glossopterids, see below), while the typical gigantopterid flora survived in the southern Cathaysia alone.

In the American southwest, the Proto-Cordillera Province was already differentiated by the Late Pennsylvanian (Reed, 1947). Here, as elsewhere, the fernarthrophyte marshes expanded at the expense of lepidophyte communities (Reed and Mamay, 1964). The Permian plant assemblages of Texas and Oklahoma are of a "Cathaysian" aspect owing to the commonly occurring gigantopterid and taeniopterid morphotypes, the fertile variants of which bore marginal ovules (Mamay *et al.*, 1988). Of the gigantopterids, *Cathaysiopteris* and *Gigantonoclea* morphotypes are formally shared with northern Cathaysia (though probably convergent), while the other three, *Gigantopteridium*, *Delnortea* and *Zeilleropteris* are endemic. The North American gigantopterid province borders on xeromorphic vegetation of Utah and Arizona with *Supaia* and *Walchia* and of Kansas with *Glenopteris* (Reed and Mamay, 1964).

Thus xeromorphic vegetation penetrated both the Cathaysian and North American parts of gigantopterid realm. Floristic exchanges of the latter with xerothermic zone indicate similar climatic conditions. However a widespread coal accumulation suggests a relatively humid climate of Cathaysia in the Early Permian. The *Dadoxylon*-type fossil woods from this area show vaguely marked growth rings (Sze, 1952). Apparently, the Northern Cathaysian and Euramerian realms had similar temperature conditions but differed in precipitation as the present day arid and humid subtropical areas. In the Late Permian their climatic differences became less pronounced. Xeromorphic vegetation eventually replaced the native gigantopterid communities by the end of the Permian.

The gigantopterids and emplectopterids, prominent in the Cathaysian-type assemblages of eastern Asia and western North America, are characterized by a composite nature of their fronds in which the entire or simply pinnate leaf blades were formed by marginal fusion of the ultimate and penultimate segments, with the original segmentation betrayed by the conservative venation pattern (Asama, 1960; Krassilov, 1995). The hierachial areolate venation of such leaves owes its origin to meristematic fusion zones acting as plate meristems (Krassilov, 1995). This leaf morphology is evidence of prolonged marginal meristematic activity characteristic of megaphyllous life forms of equable climates. An advanced Gigantopteris morphotype, some variants of which showing clearly defined drip-tips (Yao, 1986) occur in Southern Cathaysia the tropical climate of which is also indicated by the tree ferns *Psaronius* and Lepidodendron surviving from the Carboniferous.

Thus, in the Arcto-Permian realm, we can preliminary recognize the climatically defined zones of the temperate nemoral, xerothermic and humothermic subtropical vegetation. The thermophilic assemblages of Southern China actually belong to the Permo-Thetyan Realm (below).

# NOTO-PERMIAN REALM

In the 1920s the apparently uniform Late Paleozoic *Glossopteris* flora of India and southern continents prompted the idea of Paleozoic supercontinent Gond-

wanaland separated by the latitudinal Tethys Ocean from the Laurasian landmass in the north. This scheme has encouraged such eminent paleobotanists as Florin and Meyen to develop separate phylogenies for the "northern" and "southern" gymnosperms. Subsequent discoveries of *Glossopteris* or related leaf morphotypes north of Himalayas were considered as evidence of either episodic trans-Tethyan land connections or the larger Gondwanaland comprising Tibet, Iran, Anatolia, etc. (which, incidentally, would place the Tethys-Himalayas inside the Gondwanaland).

The classical Gondwana flora came from the Narmada–Son–Mahandi graben system that transects the peninsular India. Boulder beds occur at the base of their basinal sedimentary fill followed by coal measures that contain the bulk of the flora. Himalayan occurrences are scattered from Kashmir to Assam, with a few outliers in Tibet, Yunnan and the "mixed" floras of Indonesia and New Guinea. A number of well-defined species are shared by the Indian and Australian floras, but other parts of "Gondwanaland" are floristically less similar (Archangelsky, 1990, 1996; Maheshwari, 1992).

A primitive glossopterid morphotype Gangamopteris lacking distinct midrib appears in the pre-tillite deposits already. The early Gangamopteris plants are commonly envisaged as growing in sparse vegetation patches of a glacial landscape. However the fossil plants assemblages found immediately below and above the Dwykka Tillite in South Africa, Bacchus Marsh Tillite in Australia and Talchir boulder beds in peninsular India suggest a less dismal picture, with a number of Carboniferous survivors (Chandra et al., 1992; Pant, 1996). The leaf morphology gives no support to either the "Gangamopteris tundra" or "Gangamopteris taiga." Gangamopteris is linked to Zamiopteris-Cordaites via Palaeovittaria and Noegerrathiopsis implicating similar climatic conditions, i.e., temperate, of the nemoral zone.

The emblematic morphotype Glossopteris emerged and diversified in the period of widespread coal accumulation. Some variants of its highly polymorphic leaves show distinct abscission scars, the others had drip-tips, a character of rain-forest foliage. Such morphological diversity obviously suggests a wide range of habitats (Pant, 1996) which is confirmed by taphonomic data (Retallack, 1980). Glossopterids are sometimes preserved as leaf mats containing spur-shoots shed with clusters of intact leaves, as in deciduous riparian trees. A constant association of *Glossopteris* with Vertebraria, an aerenchymatous underground organ, suggests a peat bog habitat. The coriaceous lingulate leaves, as in the modern mangroves, and the uniquely preserved seedlings (Pant and Nautiyal, 1987) are also consistent with a helophyte life form of a warm temperate to subtropical climate. The maximal morphological diversity of Glossopteris (42 species from a single locality) is reported from the redbed Late Permian of Handapa, Mahandi Basin (Chandra and Singh, 1992).

An impression of the floristic integrity of Gondwana is due primarily to ubiquitious glossopterids that are conspicuous and often numerically dominant fossils. However, the uniformity of glossopterids is only valid at higher taxonomic levels; regional species compositions might have been highly endemic (McLoughlin, 1994). Other components show less uniform distribution, with significant differences between the eastern and western Gondwanalands (Maheshwari, 1992) or the Notoafroamerican, Australoindian and Palaeoantarctic provinces of Li (1997).

The differentiation primarily pertains to pecopteridarthrophyte assemblages of the European-Cathaysian affinities. Thus floras of Niger in Africa and Chubut in South America have a considerable "Euramerian" component of thermophilic pteridophytes (Archangelsky, 1990, 1996) indicating climatic conditions not too different from those in the northern xerothermic zone of Europe and eastern North America. Fossil woods from Chubut often lacks distinct growth rings (Archangelsky, 1996). Notably, a thermophilic Southern Cathaysian *Pectinopteris* or a closely allied form occurs in South Africa and elsewhere (Wan and Basinger, 1992). At the same time, the widespread coal accumulation in India and Australia (Retallack, 1982; Balme et al., 1995) suggests a relatively humid variant of warm temperate to subtropical climate, similar to that of Northern Cathaysia.

The Permian plant assemblages of Antarctica differ form the rest of Gondwana realm in a lower taxonomic diversity and a scarcity of pteridophytes (Archangelsky, 1990; Cúneo et al., 1993). The latter feature was emphasized by Cúneo et al. (1993) as indicating a lack of undergrowth. As suggested above, the diverse pteridophyte component associates with a special type of fern-arthrophyte wetlands as different from the gymnosperm (peltasperm, glossopterid) wetlands with scarce pteridophytes of a few peculiar species. Incidentally, the Antarctic glossopterid assemblage contains a peculiar fern Skaaripteris, suggestedly aerenchimatous and probably aquatic or semiaquatic (Galtier and Taylor, 1994). Therefore, the Antarctic Permian climates were not too harsh for fern growth in general, but less favorable for the pecopterid-arthrophyte communities than in the other parts of Noto-Permian realm. The Antarctic "fossil forest" is a dense growth of small to medium sized trees with Vertebraria pneumatophores. The Gangamopteris and, later, Glossopteris assemblages are associated with coal seams about 2 m thick containing stems 50 cm in diameters (McLoughlin and Drinnan, 1997). The seams contain clastic dikes that might form upon permafrost veins of palsa mires as in the present day cool temperate areas in Canada (Krull, 1999).

The Glossopteris vegetation thus extended from cool temperate to subtropical climatic zones. In the

present day arboreal vegetation, only some riparian plants, such as willows and poplars, have comparable latitudinal ranges.

# PERMO-THETYAN REALM

The Tetyan phytogeographic realm is a continuous zone of mixed Cathaysian and Gondwana floras extending from southern Spain and Morocco over Middle East and Anatolia and North Africa (Wagner, 1962; Broutin, 1977; El-Khayal *et al.*, 1980; Lejal-Nicol, 1990; Aassoumi, 1994; Broutin *et al.*, 1995) to Tibet, Yunnan, Thailand (Phetchabun), Sumatra (Jambi) and West New Guinea (Irian Jaya). Ecological equivalents of the Southern Cathaysian vegetation might occur on the Gulf coast and over Caribbean. Occasional reports of gigantopterids come from Mexico and Venezuela.

The Cathasian gigantopterids occur in the Permian floras of Anatolia, Thailand, southern Malaysia and New Guinea (Kon'no, 1963; Asama *et al.*, 1975; Wagner, 1962), whereas the Gondwana elements prevail in the mixed floras of Kashmir, southern Tibet (Lhasa) and Yunnan where they associate with the Cathaysian pecopterids, calamites and sphenophylls (Singh *et al.*, 1982; Pant *et al.*, 1984; Rigby, 1989, 1996; Li and Wu, 1996; Chandra and Sun, 1997). The Cathaysian and Gondwana type assemblages sometimes occur in different localities separated by tectonic fault zones and interpreted as separate terraines (Li and Wu, 1996). Alternatively, such differentiation can be ascribed to a mosaic vegetation structure including the glossopterid and gigantopterid communities as distinct ecotypes.

Both macrofossil and palynological data show a combination of the Euramerian, Cathaysian and Gondwana elements in the Permian western Tethys extending over Northern Africa, Middle East, Iran and Pakistan (Aassoumi, 1994; Broutin, 1977; Lejal-Nicol, 1990; Broutin *et al.*, 1995; Utting, Piasecki, 1996; Igbal *et al.*, 1998). In palynological assemblages of Yunnan the Gondwana elements amount to 80% (Gao, 1998).

Glossopterids might penetrate the Cathaysian realm through trans-Himalayan connections over Kashmir-Tibet and along the Pacific coast as far north as Primorye where both *Gangamopteris* and *Glossopteris* were found in a single locality (Zimina, 1967). *Abroptopteris* Mo and the recently found *Laibinopteris* Krassilov from the latest Permian of South China are similar to bracteate fructifications of glossopterids that once more became rather common in the Triassic of northern-central China (Meng, 1995).

#### DISCUSSION

A conclusion from the foregoing review is that the Permian "floristic" divisions could be more consistently described as the ecogeographic vegetational biomes controlled by climatic zonation. At about the Carboniferous–Permian boundary the cosmopolitan lepidophyte wetlands were replaced by new types of

plant communities dominated by various gymnosperms. These vegetational changes are associated with a global climatic change, regression and the lowering of ground water level. Climatic differentiation of new plant communities had defined the aspects of the regional fossil plant assemblages. They are preliminary assigned to the temperate (Angara and Antarctica realms), xeric subtropical (Eurameria and West Gondwana), humid subtropical (North Cathaysia and East Gondwana) and tropical (Tethyan) zones.

These Permian zones are roughly parallel to the present day latitudinal belts thus scarcely compatible with paleogeographic reconstructions in which Laurasia is placed submeridionally, with the Tethys widely gaping to the east (Scotese, 1984, etc.). Actually their position on the present-day geographic maps does not seem anomalous. Thus the Angaran realm roughly corresponds to the zone of northen conifer forests and tundras (which does not mean that they are ecologically equivalent; simply there is a phytogeographic realm of the same extent on the modern map). Its western boundary is oblique to the modern latitudes which does not necessarily means rotation of the continent for the corresponding boundaries are similarly oblique in the Mesozoic (Krassilov, 1972, 1997 and elsewhere), Tertiary and at present even.

Likewise, the geographic range of *Glossopteris* is fairly similar to that of the present day "Gondwana" family Proteaceae that appeared about 100 Ma after the supposed break up of Gondwanaland. Notably, the mixed Cathaysian-Gondwana flora of New Guinea occurs fairly close to the present day Wallace line.

A widely held biogeographic opinion links such present day geographic features with past distribution of landmasses. But traced back to the Permian they are scarcely compatible with a radical reassembly of the continents.

Neither of the Permian phytogeographic realms was restricted to a separate landmass. Their expansion over the Uralian, Tibetan and Ginling sutures is consistent with intermittent seaways rather than vast oceans. Suturing of the Uralian geosyncline had a minor effect on the Angaran biome that preserved its climatic and vegetational identity far beyond its supposed isolation as a landmass. In fact, the Triassic Siberian realm still coincided with the "Angaraland" (Krassilov and Shorokhova, 1975) and even the later vegetational–climatic boundaries still tracked the familiar outline (Krassilov, 1972; 1997).

In much the same way, the seaways of central and southern China had a little effect on floristic similarity of the northern and southern Cathaysian blocks. Their floristic distinction increased (rather than decreased) in the latest Late Permian owing to expansion of the dry subtropical belt that brought a wave of European migrants to northern China.

The integrity of the Gondwana realm as a continuous landmass is questionable on both phytogeographic and climatological grounds. In a glacial climate, the "Gondwanaland" interiors would experience dry climate, with cyclonic air masses barred from penetration inland by cold atmospheric fronts. Neither coal accumulation nor permanent ice cover would have been sustainable in such conditions. The apparent floristic homogeneity is due primarily to a broad ecological range of glossopterids. However, ecologically the arboreal broad-leaved glossopterid communities had little in common with the Pleistocene to recent periglacial vegetation, suggesting a totally different character of the Permian glacial events. Notably, the Triassic glossopterid "Gondwana" was a redbed zone extending from India to northern China.

The continental reassemblies implying the Permian South Pole near Africa and the Euramerian realm at equator are not compatible with the Permian phytogeography. On both paleovegetational and lithological evidence, central Antarctica experienced a much cooler Permian climate than South Africa or South America which implies the Permian South Pole close to its present day position. From ecological standpoints, the Euramerian plant assemblages had little in common with either humid or arid variants of tropical vegetation. They were oligodominant, of xeromorphic evergreen (rather than deciduous) aspect and with abundant well preserved conifer remains that obviously came from lowland sources (now conifers are lacking in tropical lowlands). There were free floristic exchanges between the Euramerian and the temperate Angaraland realms via a warm-temperate ecotone over Eastern Europe and the Urals.

The Euramerian–Cathamerian–Gondwana "floristic mixing" might result from penetration of interzonal wetland communities (Fig. 4) in disturbed vegetation of the tectonically active Tethys realm. In the high relief areas there might happen also a taphonomic mixing of plant remains coming from different altitudinal belts.

As shown on the modern map, Tethys corresponds to a great shear zone that extends over the Sulaiman Ranges in Pakistan, Karokaram–Nujiang fault zone in Tibet, Arakan Yoma Range in Burma and Andaman– Nikobar Ridge to Sunda Trensh, Timor and the Owen Stanley Range in New Guinea (reviewed in Krassilov, 1985). The Tethyan ophoilites, that are interpreted as obducted remains of oceanic crust, occur in narrow zones bordering numerous blocks of continental crust the larger of which are the Mediterranean (divisible in several minor blocks), Taurian, Arabian, Beshte-Lut in Iran, Helmend in Afganistan, Quangtang in Tibet, Gangdis in India and Sunda in southestern Asia. At the times of Tethyan transgression most of their area might have been covered with epeiric seas. But the Permian floristic mixing is incompatible with the idea of Tethys as a broad ocean between Laurasia and "Gondwanaland", with fragments of the latter rafted and collided to mainland Asia at different times during Mesozoic and early Tertiary, as implied by plate tectonics. Floristic



**Fig. 4.** Schematic zonal distribution of the typical mid-Permian plant communities. Vertical columns represent phytoclimatic zones (biomes): T—temperate, ST—warm temperate, E—equatorial.

links across the ophiolite sutures mean that the Tethyan blocks were parts of a continuous fold belt in the Permian already.

The tectonic style in the western part of this zone is defined by the large-scale right-lateral shear that might brought continental blocks of southeastern Asia to the north of their pre-Permian position close to Sunda plate. A displacement of this kind would explain both the Indo-Australian floristic links and the constriction of tropical zone over the junction of Tibet and Himalayas. In the Earth's rotation stress field the maximal latitudinal shear zone (as reflected in transform faulting of mid-oceanic ridges) corresponds to the equatorial minimum of Coriolis force (Tanner, 1964; Krause, 1970). This consideration supports a tropical position of the Permo-Tethyan realm.

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