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Peltasperms in the Permian of India and their bearing on Gondwanaland reconstruction and climatic interpretation

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ABSTRACT

We report on the first find of peltasperms in the Permian of Gondwana. Well-preserved leaf compressions and reproductive structures of these plants came from the Lower Permian Barakar Formation of Satpura Basin, central India, where they co-occur with diverse glossopterids. The Indian peltasperm record is evidence of floristic exchanges between Laurasia and Gondwana in the Early Permian involving a dominant group of North American–European arboreal vegetation of the time. The phytogeographic differentiation, leaf micromorphology and stratigraphic occurrence of Permian peltasperms suggest a thermophilic group appearing in central India during the transition from humid peat forming to seasonally dry redbed environments. Therefore peltasperms are unlikely invaders to high-latitude cool-temperate zone postulated for Early Permian Australindia. Instead their Satpura occurrence assigns the Indian subcontinent in the equatorial zone of mixed Laurasian/Gondwanan floristic assemblages.

1. Introduction

Gondwana is a mid-XIX century paleogeographic concept much preceding the Wegenarian mobilism, although later incorporated in the continental drift and plate tectonic theories. Initially it was based on the supposed floristic unity of southern continents plus India, having arboreal plants with *Glossopteris* type leaves as their dominant vegetation element. At the same time, a broad floristic realm north of Palaeotethys was covered with peltasperm vegetation spreading from Arizona to the Urals (Read and Mamay, 1964; Meyen, 1984; DiMichele et al., 2005).

Peltasperms are an order of Late Paleozoic gymnosperms having fern-like foliage as in archaic seed ferns from which they descended, but with ovules borne on peltate cone scales as in the major groups of modern gymnosperms. The cone scale morphology is critical for peltasperm classification, being fan-like in the Early Permian representatives, but polygonal with pendant ovules in the derived forms. Both leaves and cone scales are thickly cutinized, leaving well-preserved compressions. The epidermal topography and stomatal structures are important for recognition of the group. Peltasperms were not hitherto reported from the *Glossopteris* realm, allegedly penetrating southern lands only after the assembly of Pangea.

Separation by sea barriers is commonly considered to be the major cause of floristic differentiation, whereas the intercontinental floristic exchanges are attributed to land bridges, convergence of land masses or long-distance rafting of tectonic terranes. Potentially these mechanisms provide for essential congruence of plate tectonic and paleofloristic approaches to paleogeographic reconstructions. Plate motions controlled by a system of spreading ridges, subduction zones and transform faults are traceable back in time to a pre-drift re-assembly of land masses and pre-disjunction plant ranges. Yet the geometry of plate motions is not unequivocally resolved for Gondwanaland, because regional paleomagnetic evidence varies in regard of pole positions (e.g. Geuna et al., 2010). Incidentally, peninsular India is the most controversial part of Gondwana alleged to the virtually unconstrained displacements between Africa, Australia, Antarctica and the mainland Asia (e.g. Scotese, 1984; Cleal and Thomas, 1991).

On the other hand, the potentialities of long distance plant dispersal depend on the growth habits and reproductive biology of plant species involved in floristic exchanges, as well as on saturation of recipient plant communities, and above all on climatic differentiation. Zonal climatic differentiation is an obligatory, although variously expressed, feature of terrestrial biosphere, in principle providing a common denominator of different approaches to paleogeographic reconstructions. Yet in the case of Gondwana the validity of climatic inference from paleobotanical data is still a major problem.

It will be shown in the following discussion that the Indian peltasperm occurrence is relevant to the problems of long distance dispersal and climatic differentiation, as well as potential congruence of plate tectonic landmass reassemblies and phytogeography.

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2. Material and methods

We collected peltasperm remains from New Sethia open cast mine, Pench Coalfield Satpura Basin (78° 50′ 44″ E: 22° 12′ 49″ N) 7 km east of Parasia Town in Chhindwara district of Madhya Pradesh State, central India (Fig. 1). The Gondwana Series of Satpura Basin comprises the coal-bearing Barakar Formation and the overlying Motur Formation of variegated sandy/shaly alternation followed by a thick sandy redbeds (Fig. 2). The Barakar Formation contains five minable coal seams divided by shaly interbeds. Well preserved fossil plants are recovered from a split in the uppermost coal seam and from a coaly siltstone on top of it. The assemblage contains diverse glossopterid leaves *Glossopteris* and *Gangamopteris*, as well as *Phyllotheca*, *Pachwarophyllum*, *Noeggerathiopsis*, *Euryphyllum*, *Ottokaria*, *Arberia*, *Arberiella*, and *Buriadia*, providing phytostratigraphic correlation with the Karharbari and Lower Barakar formations of Giridih, Auranga, Raniganj and Ib-River coalfields (Maithy, 1969; Srivastava, 1977; Singh et al., 1982; Srivastava, 1992). The coal-bearing deposits have been assigned to the regional Barakar Stage, Early Permian on the basis of coal characteristics and associated geological features (Pareek, 1970; Chandra, 1971; Rai and Shukla, 1979; Raja Rao, 1983; Singh and Shukla, 2004). Palynological correlation indicates the late Early Permian (Artinskian) age of the Barakar Stage (Bharadwaj et al., 1974; Bharadwaj, 1975; Trivedi and Ambwani, 1977, 1984).

The leaves and their associated cone scales from the roof of the upper coal seam are preserved as the easily detachable compressions embedded in the rock matrix. After removing the covering rock with fine needles, the compressions were photographed under the stereo-microscope Leica 320. The cuticles were obtained by the nitric acid–potassium hydroxide treatment and studied with the dissecting microscope Nikon Eclipse or covered with gold and placed under the scanning electron microscope (SEM) EF1 Quanta 200. The SEM photographs were obtained in the mixed scattered electron–back scattered regime.

3. Morphology of Satpura peltasperm remains

The peltasperm foliar remains from the Barakar Formation of Satpura Basin represent the polymorphic digitate or pinnate–digitate leaf blades more than 15 cm long (none is completely preserved) showing dichopodial branching of the broadly webbed rachises that extend as midribs of elongate decurrent pinnules or lobes in the pinnatifid variants (Fig. 3A). The margins of pinnules are entirely with microscopic glands. The midribs are distinct, reaching to the apex. The secondary veins are dense, slender, steeply ascending, upcurved along the margin, meeting the margin at narrow angle, repeatedly forked, without anastomoses (Fig. 4).

Similar leaf morphologies occur in the supaioid North American peltasperms (*Supaia anomala*: White, 1929; DiMichele et al., 2005) and occasionally appear as aberrant morphotypes convergently developing on the basis of pinnate architecture in various groups of northern and southern gymnosperms, including glossopterids and corystosperms. The Permian "comioid" leaf morphotypes *Comia* and *Auritifolia* allegedly related to peltasperms are similar in the pinnules morphology, but differ in the pinnate leaf architecture and fasciculate lateral veins (Chaney et al., 2009).

The leaf blades are amphistomatic with nearly equal stomatal densities over the thickly and thinly cutinized (upper–lower) surfaces. The costal/intercostal differentiation is feebly developed, with an irregular pattern of interlocked flexuous intercostals cells traversed by a few rows of elongate, more regularly filed costal cells. The stomata are

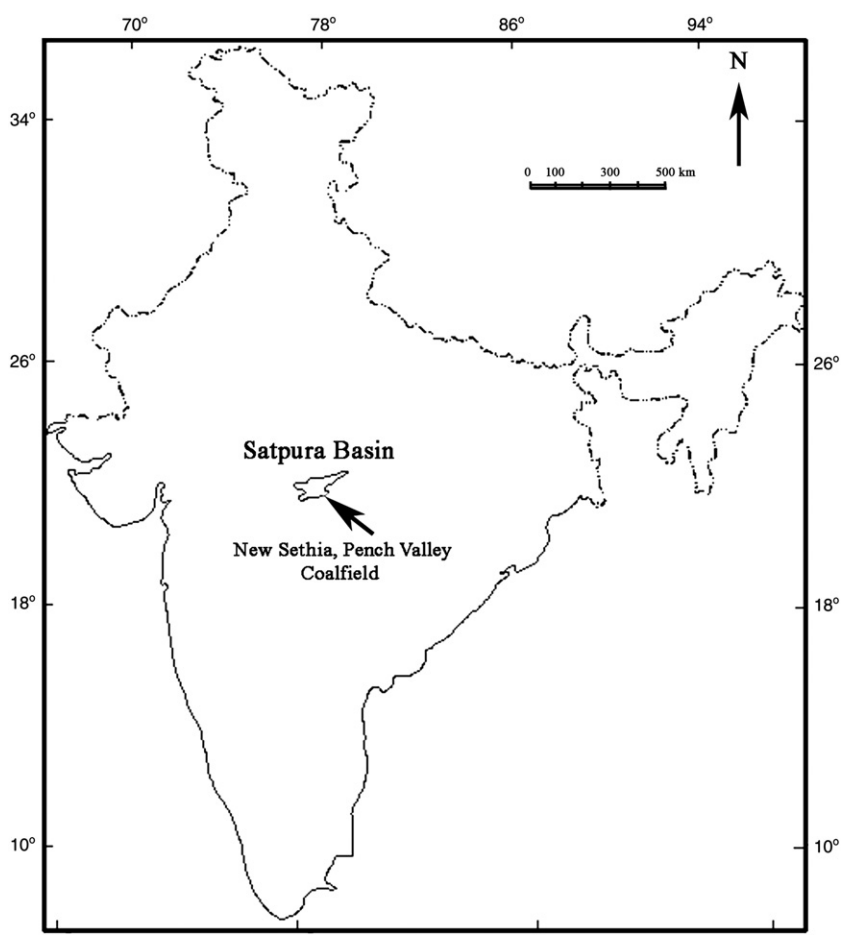

Fig. 1. Peltasperm locality in the Permian of Pench Valley coalfield, Central India (arrow).

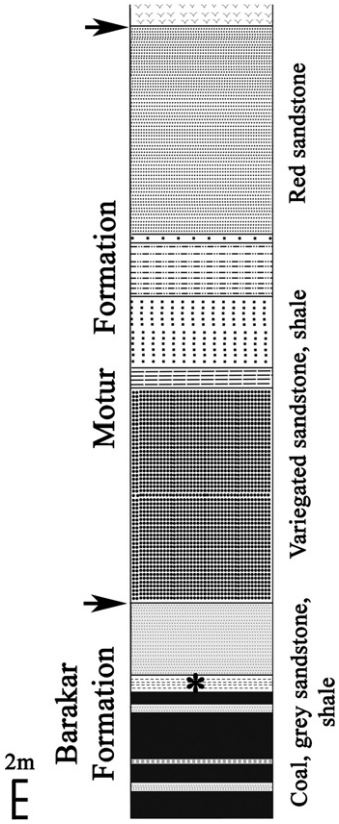

Fig. 2. Generalized geological section of Pench Valley Coalfield; asterisk on fossil plant bed with peltasperm remains.

scattered, often paired, irregularly orientated, sunken in papillate pits, incompletely amphicyclic or (the paired) monocyclic, with 4–6, typically 5 subsidiary cells. In the paired stomata, the subsidiary cells are contiguous and a few encircling cells are shared, arching around the pair. The subsidiary cells are isometric of polygonal, rhombic or trapezoid outlines, thickened over their radial walls and fairly conspicuous against the background of pavement cells, forming a somewhat irregularly lobed corolla around the relatively small stomatal pit — the petal-like configuration characteristic of peltasperms (Fig. 3B).

Stomatal index was calculated as the ratio of stomatal number (S) to cell number (E) plus stomatal number (Salisbury, 1927). S = 115 per E = 1420 were counted for 5 areas of 1 mm^2 over the leaf cuticle, giving SI = 7.496 ± 0.43.

The cuticle is ornamented with diverse trichomes, including the large central papillae on pavement cells, clavate epidermal hairs and conspicuous multicellular glands that are the most distinctive micromorphological feature of the leaves (Fig. 3C, D). The glands are dome-shaped, cutinized, with a broad basement of about 20 tabloid cells and a roof of small columnar cells that are often shed at the apex. These structures are closely comparable with multicellular salt glands of dicotyledonous angiosperms (monocots have a different type of two-celled salt glands) of excessively saline habitats (Faraday and Thomson, 1986). In distinction, hydathodes are multicellular water-excreting glands with stoma-like openings lacking in salt gland.

The seed cones consist of spirally disposed, imbricate fan-shaped coarsely plicate scales of *Autunia–Sandrewia* type (DiMichele et al., 2005) that are heavily cutinized, densely stomatiferous, bearing several pendant ovules (Fig. 5). The stomata are indiscriminately developed over the ribs and their dividing grooves, irregularly amphicyclic, with petal-like subsidiary cells and small deeply sunken guard cells. Although the difference in cutinization between subsidiary and ordinary cells is less conspicuous than in the leaves, the topography and configuration of stomata and trichomes are identical, unequivocally assigning the leaves and their associated cones to one and the same plant.

4. Discussion

The Permian phytogeographic provinciality has developed concomitantly with differentiation of equable Carboniferous climates, enhanced by the Pennsylvanian (Bashkirian–Serpukhovian) glaciation. The Euro-American, Cathaysian, Angarian and Gondwanan floristic realms maintained their distinctness through the Permian owing to segregation of their dominant gymnosperm components, the peltasperms, gigantopterids, vojnovskyids, and glossopterids.

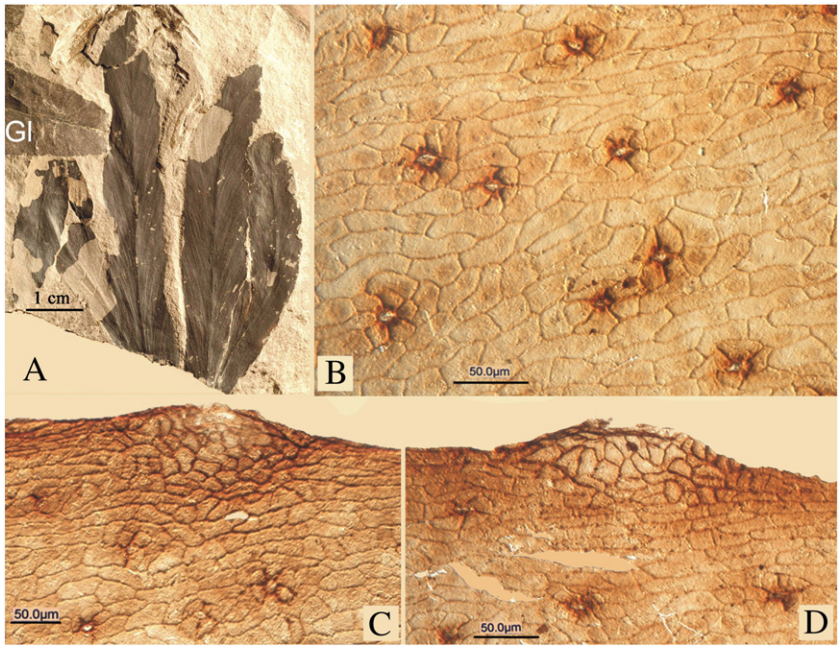

Fig. 3. Peltasperm remains from Pench Valley Coalfield; (A) Digitate supaioid leaf; Gl, an associated *Glossopteris* leaf; (B) Lower cuticle with stomata. (C, D) Multicellular glands.

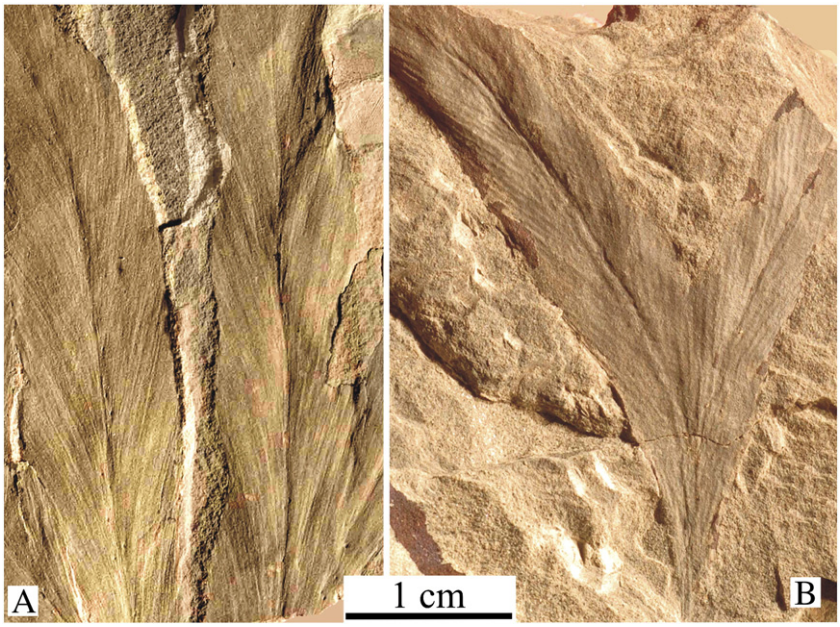

Fig. 4. Peltasperm remains from Pench Valley Coalfield; (A. B) Leaf venation.

Recent studies using modern molecular techniques revealed the role of long distance dispersal in the Gondwanan phytogeographic disjunctions (Givnish and Renner, 2004; Heinrichs et al., 2006; Milne, 2006). For spore plants of interzonal wetland communities like those the Permian fern–arthrophyte assemblages seem to represent, long distance dispersal is less of a problem than for seed plants of zonal vegetation. The central Indian occurrence of peltasperms thus poses a more intriguing paleogeographic problem than the previously reported evidence of floristic exchanges involving spore plants (Banerjee et al., 2009). Moreover, on a consensual plate tectonic–phytogeographic reconstruction (Cleal and Thomas, 1991; Cuneo, 1996), the Indian peltasperms are assigned to a climatic zone that does not seem encouraging for their invasion (Fig. 6).

4.1. Peltasperm phytogeography

The North American–European realm is subdivided into the Cordilleran, Lauroeuropean, and Volga–Uralian provinces, dominated by the supaioid, callipteroid, and tatarinoid peltasperms, respectively (Read and Mamay, 1964; Krassilov, 1972; Meyen, 1984; DiMichele et al., 2005). The callipterids with *Autunia* type cone scales first appeared in

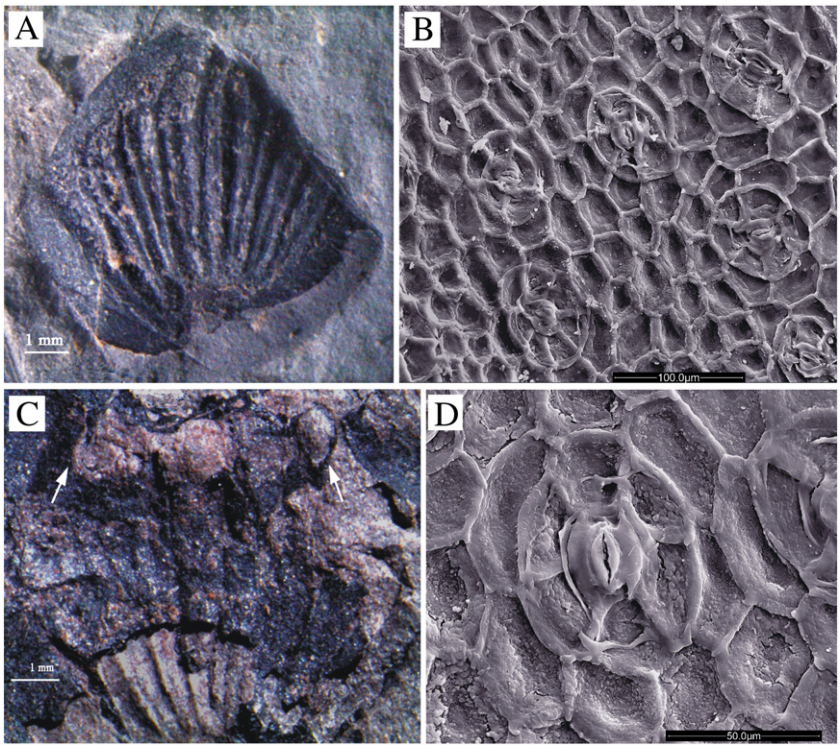

Fig. 5. Peltasperm remains from Pench Valley Coalfield: (A) Cone scale, ribbed upper surface. (B) Upper cuticle with stomata, SEM. (C) Cone scale with seed scars (between arrows). (D) Stoma, interior view, showing sunken guard cells and the petal-like subsidiary cells, SEM.

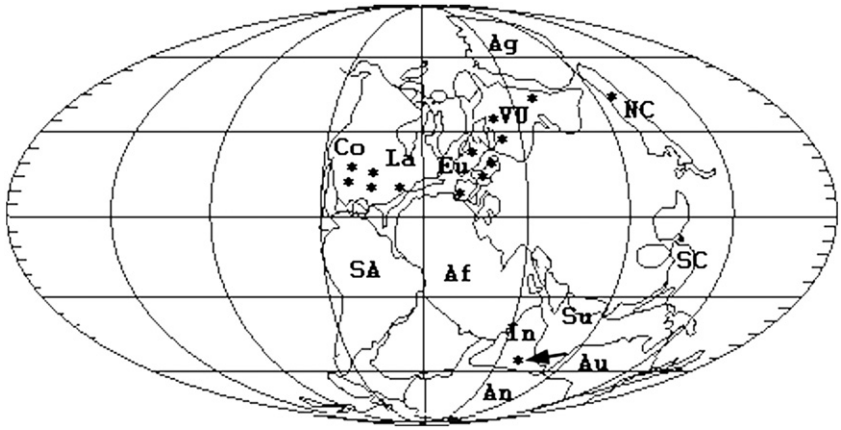

Fig. 6. Late Early Permian (Artinskian–Kungurian) paleogeographic map after (Cleal and Thomas, 1991) simplified, showing peltasperm occurrences (asterisks); arrow at new Indian locality. Af, Africa, Ag, Angarida, An, Antarctica, Au, Australia, Co, Cordilleran province of North America, EU, western–central Europe, La, Laurentian province of North America, NC, Northern Cathaysia, Su, Sundaland, VG, Volga–Uralian Region.

the Late Carboniferous of central Europe and became dominant over the Early Permian Lauroeuropean landmass (DiMichele et al., 2005). Their derived forms with strongly peltate *Peltaspermum* type cone scales are recorded from the late Early Permian of the Volga–Uralian province (Naugolnykh and Kerp, 1996) giving rise to the *Lepidopteris* leaf floras that persisted over the Permian–Triassic boundary spreading worldwide with Triassic climate warming.

In the Cordilleran province of southwestern North America, peltasperms co-occurred with gigantopterids, a phylogenetically allied group of mainly equatorial distribution. Gigantopterids constituted a dominant vegetation element of the trans-equatorial Cathaysian realm divided into northern and southern provinces and involved in floristic exchanges with Gondwana. However, peltasperms penetrated the northern Cathaysian land rather late during the end-Permian regression (Wang, 1997; Huang and Ding, 1998).

Over the eastern border, the Volga–Uralian peltasperms have mixed with the vojnovskyid gymnosperms ("Siberian cordaites") of the temperate Angarian realm extending from northern Asia to Greenland and Arctic Canada (Wagner et al., 1982; Utting, 1994; LePage et al., 2003). After closure of Uralian seaways, this boundary still remained fairly distinct, marked by the mixed occurrences of *Lepidopteris* and *Phoenicopsis*, the dominant leaf genera of European redbed and Siberian coal measure assemblages. Peltasperms scarcely penetrated the core area of the Angarian–Siberian realms (the comioids are not here considered as bona fide peltasperms).

Floristic exchanges between the northern and southern landmasses are documented for the Permian fossil plant localities of Primorye in the Russian Far East, New Guinea, Malaysia, Thailand, Kashmir, Tibet, Middle East, northern Africa and elsewhere over the coasts and insular landmasses of the Paleotethys (Wagner, 1962; Kon'no, 1963; Zimina, 1967; Broutin, 1977; Asama et al., 1975; El-Khayal et al., 1980; Pant et al., 1984; Broutin et al., 1995; Rigby, 1996; Li and Wu, 1996; Singh et al., 2006; reviewed in Krassilov, 2000). Such mixed floras are interpreted as fragments of a transitional floristic zone (ecotone) or assigned to tectonic terranes rafted from Gondwana mainland (Li and Wu, 1996). Peltasperms have been recently reported from the "mixed" Permian floras of Sumatra (Booi et al., 2009) and Venezuela (Ricardi-Branco, 2008), both belonging to the Paleotethys realm.

Floristic exchanges have involved in the first place the fern–arthrophyte assemblages of supposed Laurasian origin. Their non-uniform distribution over the western and eastern Gondwana gave rise to phytogeographic differentiation of the western and eastern Gondwanan realms (Maheshwari, 1992; Archangelsky, 1996; Li, 1997) that were further subdivided into the Main South American, Patagonian, African, Australoindian and Antarctic provinces (Cuneo, 1996). The glossopterid phytogeography is insufficiently studied, their regional distinctions in leaf dimensions and morphological diversity being probably conferred by climatic differences. The glossopterids shortly survived over the end-Permian crisis, being eventually substituted by the corystosperms with *Dicroidium*-type dichotomous leaves first appearing in the Late Permian of Paleotethys realm (Kerp et al., 2006). The Indian supaioids reported here represent the first so far documented wave of peltasperm invasion to Gondwana mainland, followed by *Lepidopteris* in the Triassic (Zamuner et al., 1999; Retallack, 2002).

4.2. Peltasperm paleoecology

Both the divergence of related plant taxa (Srivastava and Agnihotri, 2010) and floristic mixing are controlled by climatic differentiation in the first place. The Permian peltasperm floras are currently interpreted as tropical–subtropical of seasonally dry "redbed climate" (DiMichele et al., 2006). Peltasperms rapidly decreased in diversity and abundance with temperization of climate and vegetation toward the higher latitudes and through time. The acme of their expansion falls at the Triassic thermal maximum, but even then they failed to intrude the temperate Siberian realm (Krassilov and Karasev, 2009).

The Jurassic peltasperms of *Pachypteris* type are no longer a dominant group, but are locally abundant over the habitats that are interpreted as coastal mangrove-like swamps (Harris, 1964). Mangrove adaptations are not unlikely in the Permo-Triassic peltasperms as well, although a great variety of life forms is postulated for the group (DiMichele et al., 2006).

The Indian peltasperm assemblage from the roof of the upper coal seam has replaced a peat-forming glossopterid–arthrophyte assemblage of the coal split down the stratigraphic sequence. The peltasperm leaves are fairly abundant, outnumbering the regionally dominant *Glossopteris* and *Gangamopteris*. The cuticles are better preserved in peltasperms than in the associated glossopterid remains. The depositional environment of chaotically amassed leaf and cone scale compressions embedded in silty rock matrix indicate rapid burial in anoxic environment under massive influx of clastic sediment. Such an occurrence may suggest a profuse single-species growth over a flooded peat-bog buried under channel deposits.

The Indian peltasperm leaves display epidermal characters of edaphic adaptation to a highly mineralized waterlogged habitat, such as the amphistomatic leaf blades, small sunken stomata, thick cutinization and diverse trichomes, in particular the multicellular glands. Similar salt glands occur in *Avicennia*, *Aegialitis*, *Limonium* and *Tamarix* and other angiospermous thermophilic xerohalophytes of mangrove swamps, coastal salt marshes or inland evaporation basins (Thomson et al., 1969; Faraday and Thomson, 1986; Drennan et al., 1987).

In the late Early Permian (Artinskian) time of deglaciation and sea level rise, coal accumulation extended over the broad longitudinal belt from Antarctica to Australia, India, Cathaysia and Angarida. Entry of xerothermic forms in the Permian wetlands of Satpura basin at the end of peat accumulation signals transition to a drier climate conveyed by the variegated-redbed sequence of the Motur Formation. Brackish waterlogged habitats locally appeared over the peat-forming landscape, providing a vacant ecological niche for invasion of pre-adapted xerohaline forms.

Climate change was also heralded by the increasing morphological diversity of glossopterids under seasonally dry subtropical redbed climate: 43 morphospecies in a single redbed locality of the Mahanadi Basin, central India (Chandra and Singh, 1992). In contrast, an apparently single-species stand of deciduous *Glossopteris* trees was reported from Antarctica (Taylor et al., 1992).

The Gondwanaland glossopterids are a heterogeneous group of gymnosperms that might have included both thermophilic and temperate components. However, their diversity is higher and the leaves are larger in the Barakar Formation and stratigraphic equivalents in India than in the roughly contemporaneous Antarctic and Australian floras (Retallack, 1980; Taylor et al., 1992; McLoughlin, 1994). The prevailing leaf size categories in high latitude forests are nanophylls or microphylls, while *Glossopteris* leaves from India are mesophylls of Raunkiaer's (1934) classification, the most common leaf size in tropical and paratropical forests.

In addition, the fern–arthrophyte component is meagerly represented in Antarctica in comparison with Australia and India (Srivastava, 1992; Banerjee et al., 2009). These distinctions make improbable the extrapolation of cool-temperate climatic conditions, inferred for Antarctica, to Australia and India (McLoughlin, 1994; Cuneo, 1996) that apparently belonged to a different climate zone.

The available phytogeographic and ecological information thus characterizes peltasperms as a thermophilic group of conservative climatic preference through about 100 million years, which makes them the least likely intruders in the cool-temperate "Australoindia" as it is reconstructed for the late Early Permian (Cleal and Thomas, 1991; Cuneo, 1996). The possibility of peltasperm invasion during an episodic greenhouse warming (Retallack, 2009) is not confirmed by the leaf stomatal index that is even higher than previously reported for the Permian peltasperms (Retallack, 2001; Uhl and Kerp, 2005; Vording and Kerp, 2008; Krassilov and Karasev, 2009).

5. Conclusion

After being swept by the Permian–Triassic turnover and the spread of equable climates in the Early Triassic, the salient features of Permian phytogeography have been recovered, with the dominant late Mesozoic pentoxylean gymnosperms and later by the proteaceous angiosperms closely following the ranges of Permian glossopterids over the southern lands and India. Owing to such a remarkable persistence of phytogeographic patterns against the ever changing configuration of landmasses, present still is the key to the past.

India is and was through geological times a crossroad of north–south floristic exchanges. The Indian record of peltasperms, a dominant group of North American–European arboreal vegetation of the time, suggests persistent occurrence of this landmass in the equatorial–subequatorial Palaeotethyan zone of mixed floras, extending over the present day biogeographic regions of Austalasia, Indomalaya and Trans Himalayas to the Mediterranean. The available phytogeographic and ecological information characterizes peltasperms as a thermophilic group of conservative climatic preference through about 100 million years. Their involvement in floristic exchanges might have been enhanced by the rapid change from humid to seasonally dry climate over the Early–Middle Permian transition and the ensuing potentialities for thermophilic and xerohaline forms.

Peltasperm phytogeography and paleoecology make these plants the least likely intruders in the cool-temperate Australoindia of the late Early Permian landmass re-assembly (Cleal and Thomas, 1991; Cuneo, 1996), thus adding paleoclimatic constrains to plate tectonic reconstructions.

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