

Early Cretaceous flora from the Pranhita-Godavari Basin (east coast of India): taxonomic, taphonomic and palaeoecological considerations

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ABSTRACT. The Early Cretaceous flora from the Gangapur Formation (Pranhita-Godavari Basin, east coast of India) was studied. Its plant diversity and abundance patterns were examined, and its palaeoecology and environment were interpreted, based on the micro- and macrofloras and sedimentological inputs. The flora is rich and diverse, and consists of bryophytes, pteridophytes, pteridosperms, gymnosperms and angiosperms. The microflora shows higher taxonomic diversity and abundance than the macroflora. Overall, the study indicated an abundance of conifers, particularly Podocarpaceae. The taphocoenosis of the flora comprises local to regional elements derived from riverbank, floodplain, backswamp and valley settings. Taken together, the data on the flora and sedimentology suggest that warm and humid environments prevailed.

KEYWORDS: microflora, macroflora, taphonomy, palaeoecology, Early Cretaceous, Gangapur Formation, Pranhita-Godavari Basin

INTRODUCTION

The Pranhita-Godavari Basin, named after two well known rivers of Peninsular India (Pranhita, Godavari), is an intracratonic Gondwanic rift basin trending NW-SE. The basin extends to the east coast and plunges into a pericratonic rift basin, the Krishna-Godavari Basin (Lakshminarayana 1996). The Early Cretaceous succession (Gangapur/Chikiala) in the basin has an exposed thickness of ca 525 m (Biswas 2003). It is exposed in and around the village of Gangapur (19°16'N, 79°26'E) in Adilabad District, Telangana, India. Historically these Early Cretaceous outcrops were referred to as “Gangapur beds” and placed in the Kota Group (King 1881), but on the basis of lithology Kutty (1969) separated them from the Kota Group and erected the Gangapur Formation, after Gangapur village. The formation extends

from north of Nowgaon (19°20'N, 79°24'E) to west of Gangapur village (19°16'N, 79°26'E) and to Dharmaram and Paikasigudem in the east (Kutty 1969).

The Early Cretaceous Pranhita-Godavari flora is known from micro- and macrofossil studies (Feistmantel 1879, Sahni 1928, Mahabale 1967, Ramanujam & Rajeshwar Rao 1979, 1980, Rajeshwar Rao & Ramanujam 1979, Bose et al. 1982, Rajeshwar Rao et al. 1983, Ramakrishna et al. 1985, Ramakrishna & Muralidhara Rao 1986, 1991, Prabhakar 1987, Ramakrishna & Ramanujam 1987, Muralidhara Rao & Ramakrishna 1988, Pal et al. 1988, Sukh-Dev & Rajanikanth 1988, Chinnappa et al. 2014, Chinnappa 2016). The diverse flora is composed of bryophytes, pteridophytes, pteridosperms, gymnosperms and angiosperms. Earlier, Rajanikanth (1996) analyzed the micro- and macrofloras of these Early Cretaceous sediments, but without

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attempting to explain differences in the composition of the micro- and macrofloras, nor to assess their palaeoecological implications. Recently, Chinnappa et al. (2014) examined a small macroflora from these sediments and considered its palaeoecology, but did not take into account the associated microflora. Investigations of one or the other component of ancient sediments can provide only a partial picture; they must be considered together to get a complete picture of the vegetation. In the present study we analyzed the micro- and macrofloras from Early Cretaceous sediments of the Pranhita-Godavari Basin, and attempted a detailed account of their taphocoenosis. The stratigraphic significance of the flora and a comparison with other Early Cretaceous floras from India and southern Gondwana have been discussed (Rajanikanth 1996, Chinnappa et al. 2016). Here we focus on its taphocoenosis, the diversity patterns of the vegetation, and the prevailing palaeoecological conditions.

MATERIALS AND METHODS

Plant impressions (Pl. 1, 2) were collected from pinkish mudstone/siltstone in active quarries (RLQ 1 and RLQ 2) located at Ralpet ($19^{\circ}18'N-79^{\circ}25'E$) ca 7 km south of Sirpur-Kaghaznagar ($19^{\circ}21'N-79^{\circ}28'E$), Adilabad District, Telangana (Fig. 1), and from grey to buff mudstone/siltstone exposed on the banks of Butarmal Nala ($19^{\circ}27'N; 79^{\circ}13'E$) ca 13 km west northwest of Asifabad ($19^{\circ}21'N-79^{\circ}17'E$) Adilabad District, Telangana (Fig. 2). Plant fossils were studied under an Olympus SZH 10 dissecting stereomicroscope. All specimens were photographed with a Canon SX 150 IS digital camera using either polarized light or low-angle lighting to reveal surface details.

To isolate spores and pollen, sediments from all the localities that yielded macrofossils were treated with hydrochloric, hydrofluoric and nitric acid (HCl, HF, HNO_3) and sieved (25 mm mesh). However, only samples from Butarmal Nala were productive. The slides were studied under an Olympus BH 2 microscope fitted with a digital camera. All samples and slides are deposited in the repository of the Birbal Sahni Institute of Palaeobotany for future reference.

The family-level taxonomic affinities of the obtained spores/pollen follow Ramanujam and Rajeshwar Rao (1979), and those of the periderphytic leaves

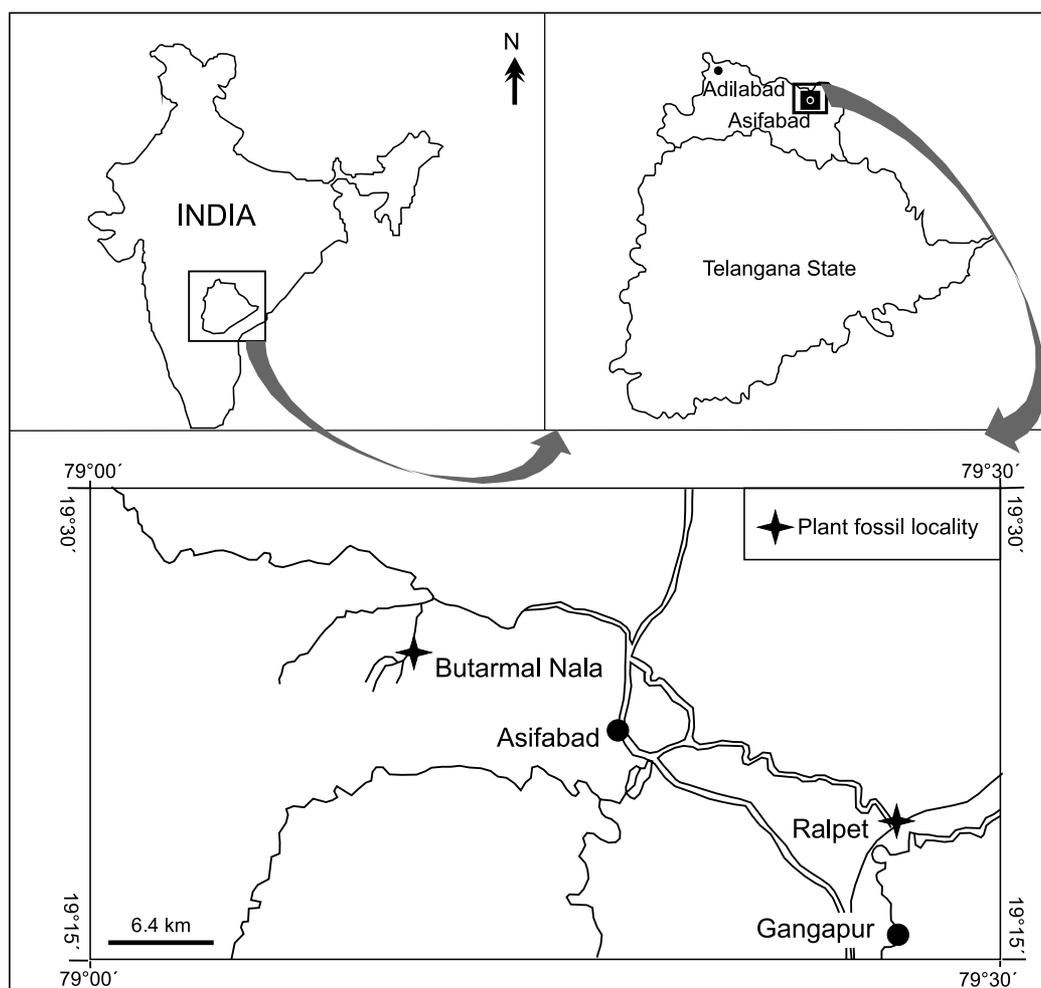


Fig. 1. Locality map of the Asifabad area, Adilabad district, Telangana, showing fossil collection sites

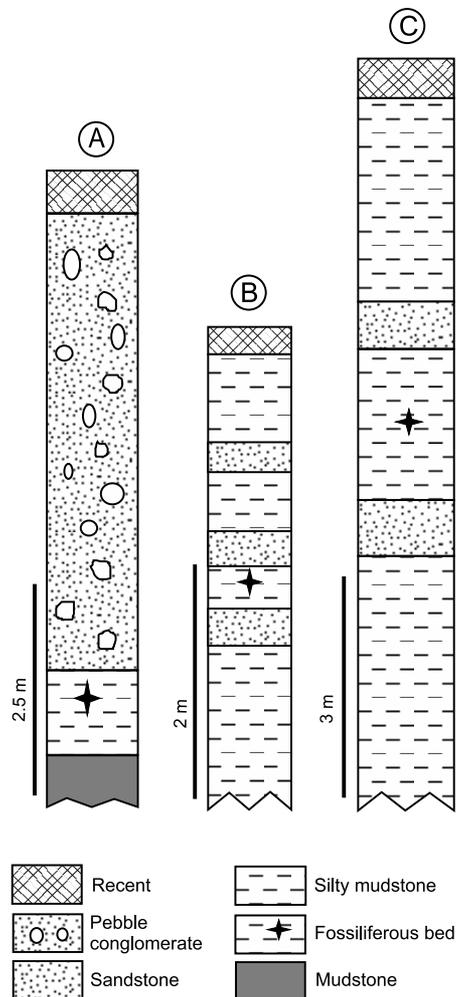


Fig. 2. Lithostratigraphic columns of strata exposed at Butamal Nala (A) and at quarry RLQ 2 (B) and quarry RLQ 1 (C)

follow Harris (1969) and Barbacka and Bodor (2008). However, taxonomic affinities at family level are not certain for many gymnosperm taxa; many of them could be related to more than one family, so they are assigned to order-level only. We analyzed species diversity separately for the micro- and macrofloras, considering the total number of taxa known in the flora on the basis of the present and previous studies. The taxonomic diversity of the flora is presented in pie diagrams (using MS Excel) as simple percentage shares of each group at order level. The abundance of the various plant taxa was calculated from counts of the number of samples for a given taxon. Discrepancies between the micro- and macrofloras are explained in terms of taphonomy and natural variations.

GEOLOGICAL SETTING AND SEDIMENTATION

The Pranhita-Godavari Basin is one of the largest Gondwanan basins of India. It contains an almost complete succession of Gondwana rocks. The sediment in the basin, deposited from the Late Carboniferous/Early Permian to

Cretaceous, is ca 3000 m thick (Biswas 2003). Sedimentation in the Gangapur area took place during the Early Cretaceous after renewed rift activity (Biswas 2003). The Gangapur Formation is 100–250 m thick, and the Chikiala Formation is ca 275 m thick (Lakshminarayana 1996). The formation consists of coarse ferruginous sandstone with many pebble bands, succeeded by an alternating sequence of sandstone and mudstone or siltstone. The Early Cretaceous sequences are in turn covered by Deccan Traps (Kutty et al. 1987, Lakshminarayana 1996). The stratigraphical nomenclature for the Pranhita-Godavari Gondwana Basin has been variously given in the literature; here we adopt the classification given by Lakshminarayana (1996). Table 1 presents the geology, stratigraphy and ages of the entire basin.

Lower Cretaceous plant fossils in the Pranhita-Godavari Basin (Fig. 3) occur within a sequence of alternating sandstone, siltstone and clay/mud shale. Individual beds range from 7 m to 12 m thick. The plant fossils are comparatively abundant in the siltstone/mudstone facies. They include impressions of leafy twigs, cone scales, winged seeds, root traces and woody axes. The sedimentology of the Gangapur Formation indicates fluvial channel deposition (Lakshminarayana 1995, 2001). Fine-grained sediments are characteristic of flood plain deposits laterally associated with channels (Boggs 2006). This plain was formed by almost continuous sedimentation of fine sediments from overbank flooding, and crevasse splays represented by sandstone. Poor sorting and the random orientation of the plant fragments in clay beds may reflect frequent floods in the basin, which would have caused the vegetation to be transported and deposited in turbid floodwater. Based on the convergence of palaeocurrents, it is proposed that sediments debouching from all sides silted (Lakshminarayana 1995).

COMPOSITION OF THE FLORA

The micro- and macrofossil records from the Gangapur Formation of the Pranhita-Godavari Basin indicate a diverse flora that includes bryophytes, pteridophytes, pteridosperms, gymnosperms and angiosperms. The diversity and abundance patterns of these plant groups, however, exhibit great discrepancies in their micro- and macrofloras.

Table 1. Lithostratigraphy and ages of various lithostratigraphic units in the Pranhita-Godavari Basin (data from Kutty et al. 1987, Lakshminarayana 1996 and Sen Gupta 2003)

	Formation	Lithology	Age	
Deccan Traps				
	Gangapur/Chikiala	Coarse ferruginous sandstone, greywhite-pinkish mudstone and silty mudstone/shale	Early Cretaceous	
Unconformity				
Upper Gondwana	Kota	Upper: Sandstone, siltstone and claystone Middle: Limestone Lower: Sandstone with pebbles of banded chert	?Jurassic	
	Dharmaram	Coarse sandstone and red clays	Late Late Triassic	
	Maleri	Red clays, fine-medium sandstone and limestone	Early Late Triassic	
	Bhimaram	Ferruginous/calcareous sandstone, minor red clays	Late Middle Triassic	
	Yerrapalli	Red and violet clays with sandstone and limestone	Early Middle Triassic	
	Lower Gondwana	Kamthi	Upper: Coarse-grained ferruginous sandstone with quartz pebbles Middle: Siltstone Lower: Purple argillaceous sandstone interbedded with sandstone	Late Late Permian- ?Early Triassic
Unconformity				
Kundaram/Barren Measure ('Ironstone shale/'Infra Kamthi')		White-light yellow feldspathic sandstone, ferruginous shale, ironstone and clay/coal bands	Late Early Permian- Late Permian	
Barakar		Upper: Feldspathic sandstone, shale and carbonaceous shale Lower: Feldspathic sandstone, siltstone and coal laminae	Late Early Permian	
Talchir		Diamictite, rhythmite, tillite, greenish shale and sandstone	Early Early Permian	
Unconformity				
Proterozoic		Igneous and metamorphic rocks	Precambrian	

BRYOPHYTES

No macrofossils belonging to this group have been recorded yet. Spores are well represented and belong to members of the Anthocerotaceae (*Foraminisporis* Krutzsch), Sphaerocarpaceae (*Aequitriradites* Delcourt and Sprumont, emend. Cookson and Dettmann, *Coptospora* Dettmann), Reillaceae (*Cooksonites* Pocock, *Rouseisporites* Pocock, *Staplinisporites* Pocock) and Sphagnaceae (*Stereisporites* Pflug) (Ramanujaum & Rajeshwar Rao 1979, Prabhakar 1987). This group is less diverse than the other spore-producing plants such as pteridophytes (Tab. 3), but is well represented quantitatively (Ramanujaum & Rajeshwar Rao 1979, Prabhakar 1987, present study).

PTERIDOPHYTES

Pteridophytes are an important component of the flora, and are represented by micro- and macroremains. Qualitatively and quantitatively the group is better represented in the microflora. Equisetaceae constitute a single genus *Equisetum* Linnaeus, an ancient genus comprising the sole extant representatives of the class Sphenopsida, the only class of the once-abundant and diverse subdivision Sphenophytina

(Scagel et al. 1984). Mesozoic fossils with distinct ridges and grooves which resemble the extant *Equisetum* can be attributed to the fossil genus *Equisetites* Sternberg or *Neocalamites* Halle. No specimens in the material from the Pranhita-Godavari Basin showed details of the leaf sheath or nodal diaphragm, so they are determined as Sphenophyta gen. et sp. The specimens resemble *Equisetites rajmahalense* (Oldham & Morris) Schimper from the Rajmahal Formation. Spores attributable to this family were found but have not been identified yet.

Osmundaceae, with a global distribution during the Palaeozoic and Mesozoic, played an important role in the ancient flora (Tidwell & Ash 1994). Members of the family were the primary elements of the forest floor and contributed a major share of the total species diversity of ferns during the Mesozoic. The single genus *Cladophlebis* Brongniart and 5 species were recorded here as macrofossils (Tab. 2). All the species were preserved as small pinnae (Pl. 1, fig. 1); whole leaves are unknown. Pinnules were well preserved, with a distinct venation pattern. The microflora suggests relatively high taxonomic diversity and includes 5 genera: *Baculatisporites* Pflug and Thomson, *Biformaesporites* Singh, *Biretisporites* Delcourt

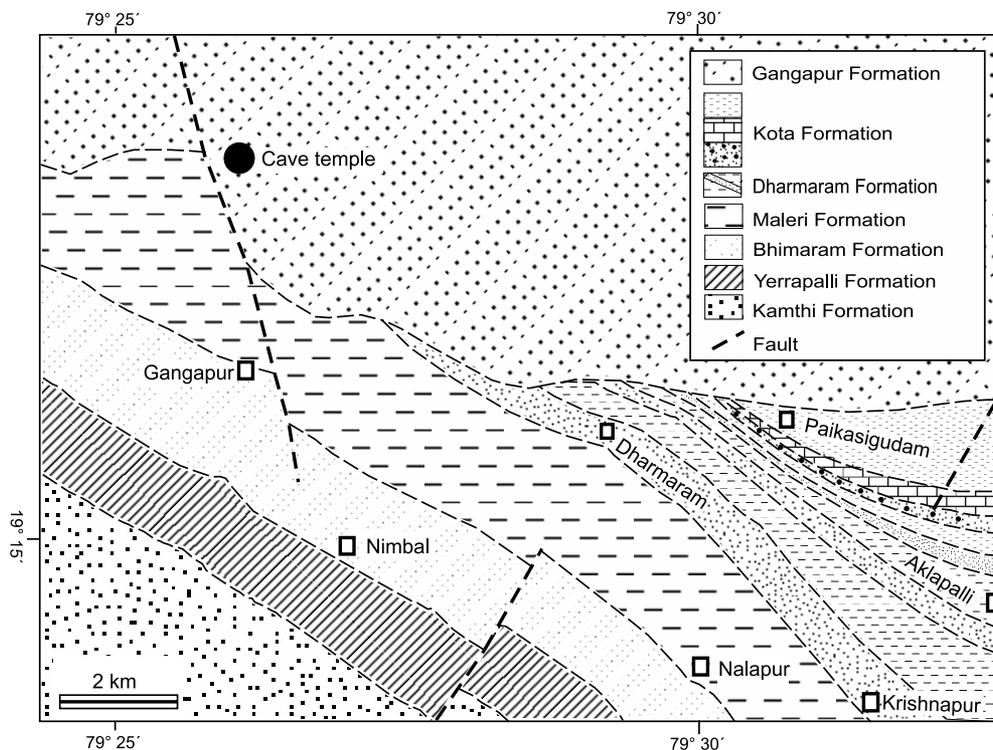


Fig. 3. Geological map of Pranhita-Godavari Basin around Gangapur village (after Kutty 1969)

and Sprumont) Delcourt et al., *Osmundacidites* Couper, and *Todisporites* Couper, with 7 species altogether (Tab. 3). Gleicheniaceae is another important Mesozoic fern family, here represented in the macro- and microfloras. The macroflora comprises the single genus *Gleichenia* Smith and 5 species. Microfossils are represented by 4 genera: *Concavisporites* Pflug, *Gleicheniidites* Ross, *Ornamentifera* Bolkhovitina and *Plicifera* Bolkhovitina, with 7 species altogether. Dicksoniaceae is represented by a single fragmentary specimen with partly preserved pinnules of the genus *Coniopteris* Brongniart, of unknown species affinity (Chinnappa 2016).

Many families such as Lycopodiaceae, Selaginellaceae, Ophioglossaceae, Schizaeaceae, Marsileaceae, Cyatheaceae and Polypodiaceae are only represented in the microflora. Among these families, Schizaeaceae and Cyatheaceae show the highest species diversity (Tab. 3, Fig. 5). There are a few more pteridophytic spore taxa which cannot be placed in any family with confidence; they are placed under incertae sedis of pteridophytes (Tab. 3).

GYMNOSPERMS

Gymnosperms are important components of the Mesozoic floral ecosystems, dominating until the Late Cretaceous (Vakhrameev

1991), but they began to decrease in diversity and abundance with the sudden appearance of angiosperms in the Early Cretaceous and their subsequent radiation in the Late Cretaceous (McLoughlin 2001, Friis et al. 2011). The group forms a major share of the studied flora.

PTERIDOSPERMS

Pteridosperms are rare components of the flora, with only the single genus *Pachypteris* (Brongniart) Harris and 4 species: *P. gangapurensis*, *P. specifica*, *Pachypteris* cf. *specifica* and *Pachypteris* sp. (Tab. 2). The cuticle in *P. gangapurensis* Sukh-Dev and Rajanikanth (1988) shows papillate and highly cutinized epidermal cells with sunken stomata, restricted to the lower surface of the leaf, and the cuticle is thicker on the upper side of the leaf. The microfossils of this group have not been identified yet.

CYCADOPHYTES

Taeniopteris leaves are one of the most common elements of the Early Cretaceous floras of India and southern Gondwanan localities (Sahni 1948, Harris 1962, Drinnan & Chambers 1985, Howe & Cantrill 2001). They have been reported from almost all Early Cretaceous sequences of India (Bose & Banerji 1981). The systematic position of such leaf types is often

Table 3. Taxonomic composition of Early Cretaceous macroflora from Pranhita-Godavari Basin

PTERIDOPHYTES	GYMNOSPERMS	
Equisetaceae	Pteridospermaleans	Coniferales
<i>Equisetites</i> sp.	<i>Pachypteris gangapurensis</i>	<i>Elatocladus andhrii</i>
Osmundaceae	<i>Pachypteris specifica</i>	<i>Elatocladus bosei</i>
<i>Cladophlebis denticulata</i>	<i>Pachypteris</i> cf. <i>specifica</i>	<i>Elatocladus confertus</i>
<i>Cladophlebis indica</i>	<i>Pachypteris</i> sp.	<i>Elatocladus heterophylla</i>
<i>Cladophlebis kathiawarensis</i>	Bennettitaleans	<i>Elatocladus jabalpurensis</i>
<i>Cladophlebis</i> sp.	<i>Cycadolepis</i> sp.	<i>Elatocladus kingianus</i>
<i>Cladophlebis</i> sp. A	<i>Dictyozamites gondwanensis</i>	<i>Elatocladus plana</i>
<i>Cladophlebis</i> sp. B	<i>Otozamites</i> sp.	<i>Elatocladus sehoraensis</i>
Gleicheniaceae	<i>Pterophyllum medlicottianum</i>	<i>Elatocladus</i> sp.
<i>Gleichenia bosahii</i>	<i>Ptilophyllum acutifolium</i>	<i>Pagiophyllum burmense</i>
<i>Gleichenia gelichenoides</i>	<i>Ptilophyllum cutchense</i>	<i>Pagiophyllum marwarensis</i>
<i>Gleichenia nordenskioldii</i>	<i>Ptilophyllum distans</i>	<i>Pagiophyllum peregrinum</i>
<i>Gleichenia rewahensis</i>	<i>Ptilophyllum horridum</i> Roy	<i>Pagiophyllum rewaensis</i>
<i>Gleichenia</i> sp.	<i>Ptilophyllum rarineris</i>	<i>Pagiophyllum spinosum</i>
<i>Gleichenia</i> sp. A	<i>Ptilophyllum</i> sp.	<i>Pagiophyllum</i> sp.
Dicksoniaceae	<i>Ptilophyllum</i> sp. A	<i>Allocladus bansaensis</i>
<i>Coniopteris</i> sp.	<i>Nilssonia</i> sp.	<i>Araucarites cutchensis</i>
<i>Coniopteris</i> sp. A	? <i>Anomozamites</i> sp.	<i>Pagiophyllum minutus</i>
<i>Onychiopsis psilotoides</i>	Cycadophyta Incertae sedis	<i>Araucarites</i> sp.
Incertae sedis	<i>Taeniopteris kutchense</i>	<i>Brachyphyllum sehoraensis</i>
<i>Actinopteris</i> sp.	<i>Taeniopteris spatulata</i>	<i>Brachyphyllum</i> sp.
<i>Sphenopteris</i> sp.	<i>Taeniopteris</i> cf. <i>daintreei</i>	Incertae sedis
	<i>Taeniopteris</i> sp. A	<i>Conifero-caulon rajmahalense</i>
	<i>Taeniopteris</i> sp.	<i>Conites sripermatorensis</i>
	Taxaleans	<i>Harrisiohyllum lanceolatus</i> n. sp.
	<i>Arthrotaxites feistmantelii</i>	<i>Pityospermum</i> sp.
	<i>Taxites lanceolata</i>	Angiosperms
	<i>Torreyites sitholeyi</i>	<i>Sahniophyllum indica</i>

problematic, especially when they are known only from impressions. *Taeniopteris* leaves have been attributed to several groups such as pentoxylaleans, cycadaleans or bennettitaleans (Sahni 1948, Vishnu-Mittre 1957, Harris 1962, Bose et al. 1985). Such leaves have also been shown to belong to pteridophytes (Webb 1983). When these leaves are found to be associated with pentoxylean reproductive material of *Cornocnites*, they are placed in the same group (e.g. Howe & Cantrill 2001). When they are preserved with cuticle it is possible to show their relation to other plant groups (Harris 1962). In material from the studied locality the leaves are known only as impressions, with no cuticles or associated reproductive structures having been found to date.

Leaves of this type are represented here by 5 species (Tab. 2). Among them, *T. spatulata* McClelland was considered to belong to the pentoxyleae (Vishnu-Mittre 1953). In a revision of the Indian species of *Taeniopteris*, Bose and Banerji (1981) considered all those species to be cycadophytes. This determination cannot be considered fully valid because the cuticular morphology is unknown. There is another species which resembles *T. daintreei* known from

Australia (e.g. Drinnan & Chambers 1985), Antarctica (Cesari et al. 1998, Howe & Cantrill 2001), where it was placed in the Pentoxylales. However, the treatment of *Taeniopteris* under pentoxyleae from Australia and especially from Antarctica is equivocal because the anatomical features of the material from these localities have never been interpreted (Sharma 2001). Because the presently studied leaves are preserved as impressions, the systematic affinity of the genus is uncertain; it is safer to treat them under incertae sedis within the gymnosperms.

BENNETTITALEANS

Bennettitaleans are major components of Early Cretaceous floras. Harris (1969) and Watson and Sincock (1992) proposed a number of criteria to distinguish bennettitalean foliage types, according to which 3 genera were identified in the Pranhita-Godavari Basin: *Ptilophyllum* Morris, *Pterophyllum* Brongniart and *Dictyozamites* Oldham. Among these, *Ptilophyllum* foliage is commonest and 5 species have been recorded to date (Tab. 2), of which *P. acutifolium* (Morris) Bose and Kasat,

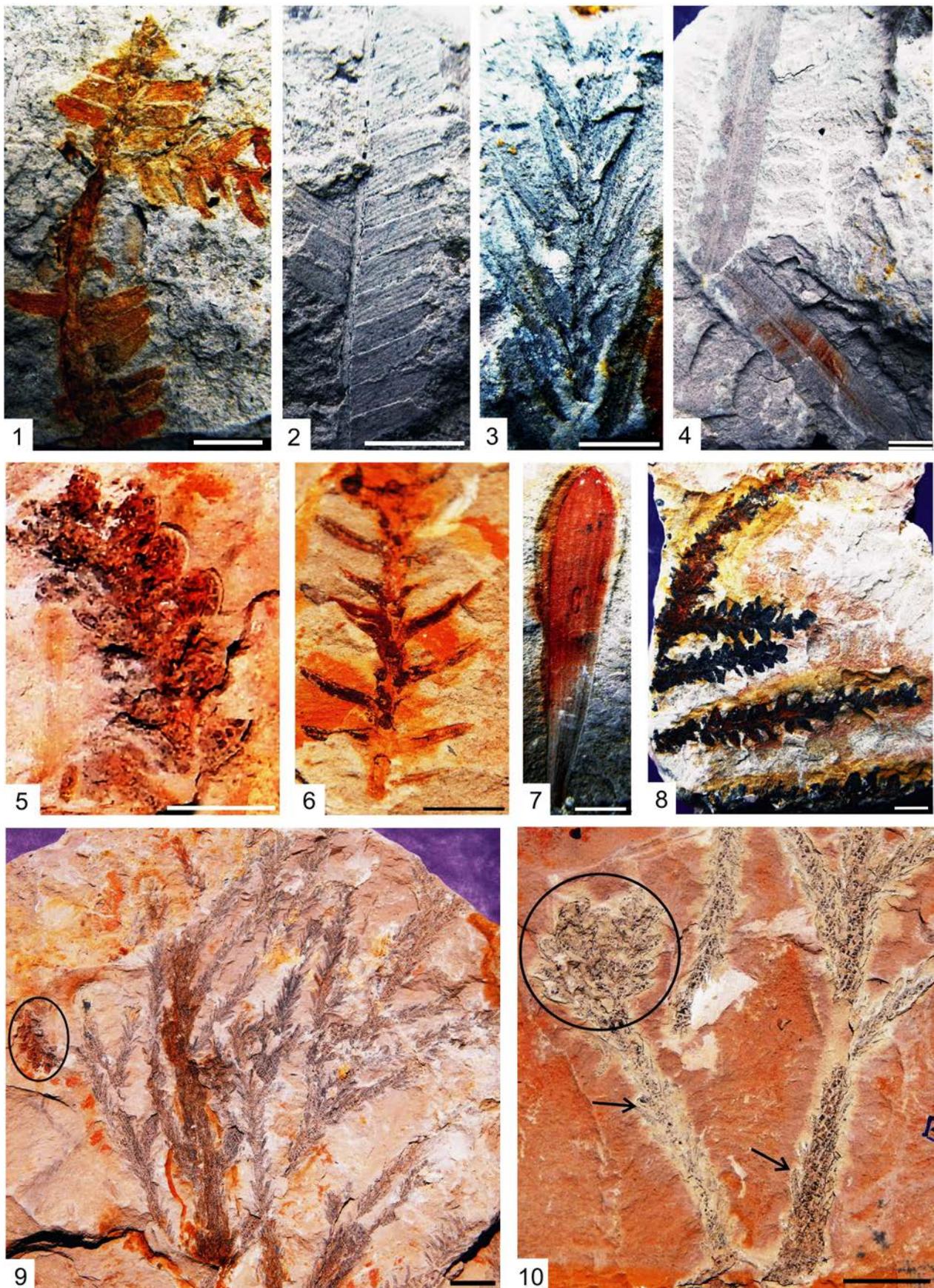


Plate 1. 1. *Ptilophyllum acutifolium* (Morris) Bose & Kasat; 2. *P. cutchense* (Morris) Bose & Kasat; 3. *Taxites lanceolata* Ganju; 4. *Taeniopteris spatulata* (McClelland) Bose & Banerji; 5. Detached strobili; 6. *Pagiophyllum marwarensisi* Bose & Sukh-Dev; 7. *Harrisiophyllum* sp.; 8. *Pagiophyllum* cf. *burmense* Sahni; 9. *Elatocladus andhrensensis* Chinnappa et al.; 10. *Elatocladus andhrensensis* with strobili. Scale bars 0.5 cm

and *P. cutchense* (Morris) Bose and Kasat are more frequent. It has been a common practice to assign specimens lacking cuticles but showing acute or round pinnae apices to *P. acutifolium* and *P. cutchense*. This biased taxonomic treatment of many specimens probably has led to underestimation of the taxonomic diversity of the genus. *Dictyozamites* and *Pterophyllum* are represented by single species each. Specimens belonging to these genera are rarely encountered and are represented in the flora by only a few fragmentary leaves (Ramanujam et al. 1987, Sukh-Dev & Rajanikanth 1988).

The other bennettitalean foliage known in the flora consists of isolated and partly preserved leaves referred to ?*Anomozamites* sp. (Bose et al. 1982), *Cycadites* sp. (King 1881) and *Otozamites* sp. (Tripathi 1975), but their identification was uncertain. The figured specimen of ?*Anomozamites* sp. is a very poorly preserved fragmentary leaf of *Taeniopteris*. Tripathi (1975) listed *Otozamites* sp. and *Nilssonia* sp., but did not describe or figure them. The records of *Otozamites* sp. and *Nilssonia* sp. are doubtful and may have been misidentified, as suggested by Ramanujam et al. (1987).

Epidermal structures are known in specimens of *Ptilophyllum distans* (Feistmantel) Bose and Kasat, *P. horridum* (Roy) Bose and Kasat (Bose et al. 1982) and *Dictyozamites gondwanensis* Sukh-Dev and Rajanikanth (1988). These foliage types are characterized by slightly sunken hypostomatic stomata, subsidiary cells that are slightly more cutinized than normal cells, and epidermal cells with trichomes and papillae.

Little fertile bennettitalean material is known from Gondwana floras to date (Cantrill 2000). A report of *Cycadolepis* sp., generally considered to represent a bract from the base of a female cone (Harris 1969, Cantrill 1997), is the only reported fertile bennettitalean material from the present flora (Pal et al. 1985).

CONIFERS

Conifer remains are a significant component of the flora and constitute 10 genera: *Allocladus* Townrow, *Araucarites* Presl, *Brachyphyllum* Brongniart, *Pagiophyllum* Heer, *Elatocladus* Halle, *Arthrotaxites* Unger, *Torreyites* Seward, *Coniferocaulon* Fliche, *Conites* Sternberg and *Pityospermum* Nathorst (Tab. 2). Leafy axes belonging to *Elatocladus* of Podocarpaceae

predominate in terms of diversity and abundance. Nine species have been identified in the genus (Tab. 2); among them, *E. confertus* (Oldham & Morris) Halle is extremely rich. This foliage type is one of the most common in the Early Cretaceous of the Southern Hemisphere (Cantrill 1997, Rees & Cleal 2004, McLoughlin 1996, Chinnappa et al. 2014). Leaf shoots of *E. confertus* and *E. andhrensensis* Chinnappa et al. with attached fertile strobili are of special interest (Bose et al. 1982, Sukh-Dev & Rajanikanth 1988, Chinnappa et al. 2014). The spirally borne, loosely arranged strobili of *E. confertus* were considered to represent female organs (Sukh-Dev & Rajanikanth 1988), whereas the strobili in *E. andhrensensis* are considered to be male organs on the basis of their structure and arrangement (Chinnappa et al. 2014). Attempts to isolate pollen from these strobili have failed, but these strobili suggest podocarpaceous affinity, at least for the Indian material. In addition to strobili with organic connection, a large number of isolated strobili were found (Pal et al. 1988, Sukh-Dev & Rajanikanth 1988, Chinnappa et al. 2014, 2015). Similar foliage with attached fertile cones is also known from the President Head flora, but these cones are taxodiaceous (Cantrill 1997).

Cuticles are known in specimens of *Elatocladus kingianus* Bose et al. (1982) and *Elatocladus* sp. A Sukh-Dev and Rajanikanth (1988). The former has cuticles of almost the same thickness on both sides of the leaf, but in the latter it is thicker on the upper side. Stomata are hypostomatic in both species and the guard cells are thinly cutinized; they are sunken in *E. kingianus* but exposed in *Elatocladus* sp. A.

Pollen allied to the Podocarpaceae is known under 5 genera: *Callialasporites* Sukh-Dev, *Microcachrydites* Cookson, emend. Couper, *Platysaccus* Naumova, emend. Potonié, *Podocarpidites* Cookson, emend. Couper and *Podosporites* Rao. Both qualitatively and quantitatively, it forms a large part of the microflora. *Callialasporites* with 14 species shows the highest diversity. The quantitative representation of the genus is also very high, accounting for more than 20% of the pollen spectra (Prabhakar 1987). Followed by this are the genera *Podocarpidites* (6 species) and *Platysaccus* (4 species) and the other genera are represented by single species (Tab. 3).

The next important conifer components of the flora are *Brachyphyllum* and *Pagiophyllum*,

two typical and widespread Early Cretaceous foliage types. *Pagiophyllum* is more frequent and includes 6 species (Tab. 2). Specimens of *P. marwarensis* Bose and Sukh-Dev are also known through cuticles (Bose & Sukh-Dev 1972). The cuticle is equally thick on both sides of the leaf, the stomata are amphistomatic and sunken, and the guard cells are thinly cutinized. A hypodermis is present on both sides of the leaf. Foliage of *Brachyphyllum*, which includes 3 species, does not occur consistently in the flora (Tab. 3). Among the 3 species, *B. sehoraensis* Bose and Maheshwari shows the cuticular structure. The cuticle is thicker on the lower than on the upper side of the leaf, the stomata are restricted to the lower side and are deeply sunken, the guard cells are thinly cutinized, and the subsidiary cells are slightly more cutinized than normal cells. Both of these foliage types are usually found associated on the same slab along with *Ptilophyllum* foliage, and rarely with *Elatocladus* (Chinnappa et al. 2015).

The taxonomic relation of *Pagiophyllum* and *Brachyphyllum* is somewhat unclear at family level. The majority of the species in these genera have been shown to fall within the Podocarpaceae and Araucariaceae (Harris 1979), but a few species of these fossil genera have been connected to the Cheirolepidiaceae (see Tosolini et al. 2013). Bose and Maheshwari (1975) placed the Indian records of these genera under the Araucariaceae; this seems plausible, as these leaf axes were frequently found associated with cone scales (*Araucarites*) of Araucariaceae (Sukh-Dev & Rajanikanth 1988). However, the presence of Cheirolepidiaceae pollen *Classopollis* in the same association (Prabhakar 1987, Ramanujam et al. 1987) complicates the issue. One explanation is that the leaf types of *Pagiophyllum* and *Brachyphyllum* possibly pertain to both families. Given the range of morphological similarities between the Cheirolepidiaceae and Araucariaceae, detailed SEM studies of the cuticles are required to properly distinguish the families. Here we tentatively place these taxa under Araucariaceae after Bose and Maheshwari (1975).

Other taxa from the presently studied flora that can be considered under the Araucariaceae are *Allocladus bansaensis* Sukh-Dev and Zeba-Bano (Sukh-Dev & Rajanikanth 1988), *Araucarites cutchensis* Feistmantel and *A. minutus* Bose and Maheshwari. The fossil genus

Araucarites is considered to represent an ovuliferous cone scale of Araucariaceae. Ovuliferous scales with a single ovule/seed and free distal ligule indicate affinity with the Araucariaceae (Cleal & Rees 2003). Although the specimens in the studied flora do not show any ligule, they show clear traces of the presence of a single ovule/seed. The lack of a ligule is probably due to the preservational limitations. Pollen belonging to the Araucariaceae is known under *Araucariacites* Cookson and includes 3 species (Tab. 2).

The Cheirolepidiaceae form an important component of the flora but is known here only by pollen of *Classopollis* Pflud emend. Pocock and Jansonius and *Classoidites* van Amerom. These pollen are abundant in the Early Cretaceous sequence of India (e.g. Ramanujam & Rajeshwar Rao 1979, Venkatachala & Sinha 1986) and other Gondwanan and non-Gondwanan land masses (Vakrameev 1991). Here they are represented by 6 and one species respectively (Tab. 2). *Classopollis*-like pollen is known to be produced by a wide variety of fossil taxa such as *Pagiophyllum* and *Brachyphyllum*, both non-frenelopsid (e.g. *Otwayia*) and frenelopsid (e.g. *Frenelopsis* and *Pseudofrenelopsis*) (Kendall 1949, Couper 1955, Venkatachala 1966, Srivastava 1976, Tosolini et al. 2013). The Cheirolepidiaceae affinity of foliages of non-frenelopsid type and frenelopsid type, and of a few forms of *Pagiophyllum*- and *Brachyphyllum*-type, is well established (see Tosolini et al. 2013). Nevertheless, many species of *Pagiophyllum* and *Brachyphyllum* are placed under Podocarpaceae and Araucariaceae (Harris 1979). Records of *Classopollis* are rich in Early Cretaceous sediments of India, but nothing is known about their parent plants. The pollen has been recovered mostly from the same sediments from which the species of *Pagiophyllum* and *Brachyphyllum* are known (Ramanujam & Rajeshwar Rao 1979), but in India such pollen has never been recovered from *in situ* cones attached to *Pagiophyllum* or *Brachyphyllum*. In light of the uncertainties about the taxonomy of this foliage in India (see discussion above), further evidence is required to establish the parent taxa of *Classopollis* pollen in India.

Taxaleans are comparatively rare in the present floras of *Arthrotaxites*, *Taxites* and *Torreites*, each represented by a single species (Tab. 2). Like the living genus, *Athrotaxites* can be referred to the family Cupressinaceae

by some authors but the affinities are not quite clear, and its assignment to the Taxodineae must be regarded as provisional (Sahni 1928). Vegetative shoots bearing spirally disposed and distichously placed linear leaves, resembling in habit those of *Taxus* and other taxalean members, are generally placed under *Taxites* and *Torreyites* (Seward 1919), but Seward also stated that in the absence of reproductive organs it is impossible to determine the precise position of shoots of this common form, and these generic names do not imply any direct relation with extant members. The records of taxalean woods (taxaceoxylon) in India during the Mesozoic (Rajanikanth & Sukh-Dev 1989) suggest such relations. Hence we believe that *Arthrotaxites*, *Taxites* and *Torreyites* were possibly produced by the Taxaleans as suggested by Sahni (1928).

There are 4 coniferoid taxa with unknown affinity: *Conites sripermatorensis* Sahni, *Coniferoaulon rajmahalense* Gupta, *Harrisiophyllum* sp. and *Pityospermum* sp. A specimen of *Coniferoaulon rajmahalense* is preserved as a long axis with irregular grooves and ridges, and is assumed to represent the stem of a coniferous plant (Sukh-Dev & Rajanikanth 1988). It is 150 mm long and 130 mm wide, suggesting a shrubby habit for the parent plant. Similarly, the exact affinities of the other taxa are not certain. The detached fructifications of *Conites* undoubtedly belonged to conifers (Sahni 1928). *Pityospermum* with a basal seed and attached wing resembles Abietineous seeds (Seward 1919). With the available information, the placement of this fossil-genus within the conifers in a broad sense is justified, although it is not possible to confirm its relation with the Pinaceae. The foliage type of *Harrisiophyllum* is generally believed to be produced by conifers (Pant et al. 1983).

ANGIOSPERMS

Angiosperm macrofossil remains have not been reliably reported to date from the Early Cretaceous sequences of India, although there have been a few claims (Sahni 1932, Sharma 1997, Banerji 2000); later studies rejected their affinity with the angiosperms (Bose & Sah 1954, Srivastava & Krassilov 2012). However, the reports of pollen of angiosperms from Early Cretaceous sequences of India clearly indicate their occurrence (Mehrotra

et al. 2012). The Early Cretaceous macrofossil assemblages from the Pranhita-Godavari Basin include a single species, *Sahniophyllum indica* (Chinnappa 2016), with ribbon-shaped leaves and parallel venation indicating their affinity with the monocotyledons.

FLORAL DIVERSITY

MACROFLORA

The macroflora from the Early Cretaceous sediments of the Pranhita-Godavari Basin comprises 29 genera and 69 species (Tab. 2). The plants represented here are pteridophytes, pteridosperms, gymnosperms and angiosperms. The species diversity of the various plant groups at order/family level is shown in Figure 4. Pteridophytes show high diversity, with 6 genera and 18 species, constituting 28% of total species diversity. Gymnosperms are a dominant component, accounting for 72% of the floral diversity. Conifers contribute a major (40%) share, with 12 genera and 28 species. Other members of the gymnosperms such as possible pentoxylean/cycadalean taxa (*Taeniopteris*) represent 7% of species diversity, with one genus and 5 species. Bennettitaleans form 19% of the flora, with 4 genera and 13 species altogether. Pteridosperms are less represented, with a single genus with 4 species, forming 6% of total species diversity. Angiosperms are minor components of the flora, with a single genus and species, representing 2% of total species diversity.

MICROFLORA

The species diversity of various plant groups represented in the microflora diverges from that of the macroflora. Importantly, bryophytes, which are missing in the macroflora, are known from the microflora in 6 genera and 14 species, representing 8% of total species diversity (Tab. 3; Fig. 5). The taxonomic diversity of various plant groups is well represented overall; that of pteridophytes is especially well represented with 45 genera and 104 species, accounting for 60% of total species diversity (Tab. 3, Fig. 5). Many pteridophytic families such as Lycopodiaceae, Selaginellaceae, Ophioglossaceae, Matoniaceae, Schizeaceae, Marsileaceae, and Polypodiaceae

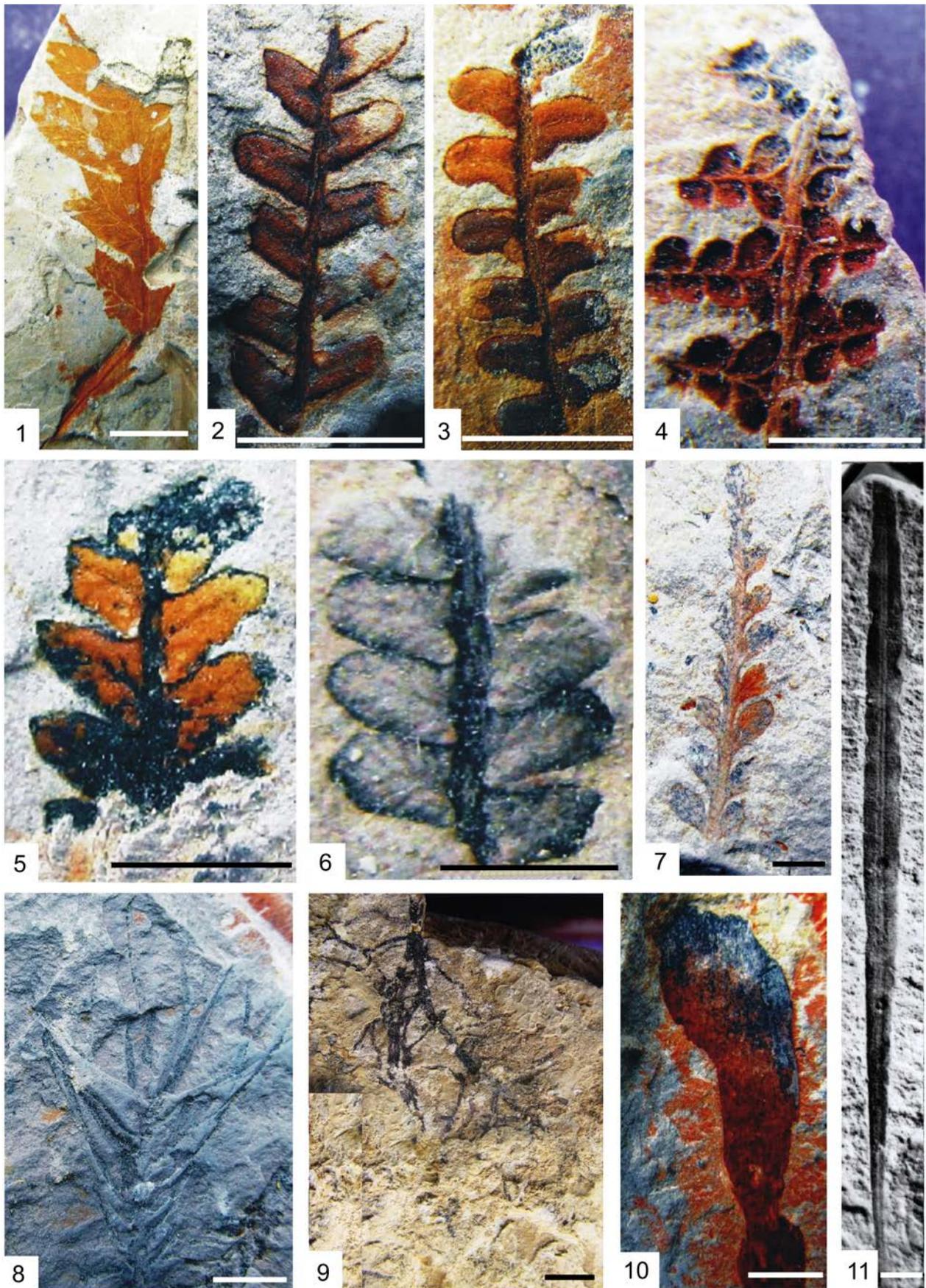


Plate 2. 1. *Cladophlebis kathiawarensis* Roy; 2. *Cladophlebis* sp. B; 3. *Gleichenia rewahensis* Pant & Srivastava; 4. *Gleichenia* sp. A; 5. *Cladophlebis* sp. A; 6. *Gleichenia nordenskioldii* Herr; 7. *Pachypteris* cf. *specifica* (Feistmantel) Bose & Banerji; 8. *Torreyites sitholeyi* Ganju; 9. ?Coniferous root; 10. *Pityospermum* sp.; 11. *Taeniopteris* cf. *daintreei* McCoy. Scale bars 0.5 cm

are added to the flora through their records of microflora. Gymnosperms, with 20 genera and 57 species contributes 33% of total species diversity. The preserved taxa are allied to Cycadophyta, Podocarpaceae, Araucariaceae, and an unknown gymnosperm. Pollen related to the pteridosperms and angiosperms were not recorded.

TAPHONOMY

COMPARISON OF MICRO- AND MACROFLORAS

There is a consistent disproportion between the composition of the microflora and the macroflora drawn from sediments of the geological past. Large discrepancies can be regularly seen in the diversity and abundance patterns of the micro- and macrofloras. The same is true here also, with many families (e.g. Osmundaceae and Gleicheniaceae; also see Tables 2 and 3 for comparison) which are taxonomically well represented in the microflora but are poor in the macroflora. Similarly, while the microflora contains representatives of the Lycopodiaceae, Selaginellaceae, Ophioglossaceae, Matoniaceae, Schizeaceae, Marsileaceae, and Polypodiaceae, they are totally absent from the macroflora. Moreover, within a single flora, the abundance pattern of various members also greatly varies; for example, gymnosperms are well preserved, but pteridosperms and pteridophytes are poorly preserved and bryophytes are absent from the macroflora. Similarly, conifer pollen dominates the pollen spectra quantitatively.

Divergence between micro- and macrofloras can be explained in terms of the diversity and abundance patterns of a flora, and also in terms of the taphonomy and preservation potential of the various plants (Spicer 1991). Our analysis of the studied flora indicates that the differences between the micro- and macrofloras in the Pranhita-Godavari Basin are due largely to taphonomy.

The poor representation of bryophytes in the macrofossil record was once linked to rapid decomposition and low preservation due to the fragility of the plants. Decomposition is high even in bogs, and may result in the loss of over 90% of the total annual productivity of a bog (Reader & Stewart 1972). Experimental studies by Hemsley (2001), however, indicated that the preservation potential of bryophytes is as good as that of vascular plants, as suggested

by the resilient chemistry of their cell walls. Nevertheless, the record of the group is very limited, and its scarcity in the fossil record may be due to difficulties in identification (as experienced in this study), with many examples being mistaken for other plant groups such as various assignments to *Naiadita*, a Triassic liverwort (Harris 1939). Although the group produces characteristic and preservable spores, they are often produced in such a small quantity and so close to the ground that they are rarely found and recognized in pollen analysis (Hartman et al. 2002).

NATURE OF DEPOSITION

The macroflora studied here consists of various plant organs such as roots, leaves, leafy axes, and reproductive parts (cones, strobili, winged seeds). Leaves predominate. The various degrees of destruction and fragmentation of the recovered fossil material suggest that they were transported before their burial (Spicer 1991), but fragmentation in fossil floras also depends on other factors such as water quality, the nature and rate of sedimentation, the presence and number of biological agents, as well as certain characteristics of the leaves themselves (Ferguson 1985, Rich 1989, DiMichele & Gastaldo 2008). *Elatocladus* specimens are the best-preserved plant remains among all the plant taxa. Branched specimens with attached leaves and reproductive cones (Pl. 2, Fig. 10) suggest that this species was less affected by transport. Taxa preserved with cuticles also suggest rapid burial. *Brachyphyllum* and *Pagiophyllum* are largely represented by small fragmentary leaf axes (Pl. 2, Figs 6–8), suggesting a strong effect of transport. *Ptilophyllum* includes specimens with various degrees of fragmentation, but in most cases the leaves are preserved for almost their entire length. A few of the leaves are preserved with petiole and cuticle, suggesting rapid burial with little transport. The ovuliferous cone scales are well preserved as impressions with a clear seed mark and neck, but their ligule is shed, probably due to mechanical damage. Other taxa such as *Allocladus* and *Torreyites* are known only by small fragmentary leaf axes, suggesting long-distance transport. *Taeniopteris* is preserved mostly along its entire length, but often lacking the base and apex. Both parts of leaves broken into two halves were often found

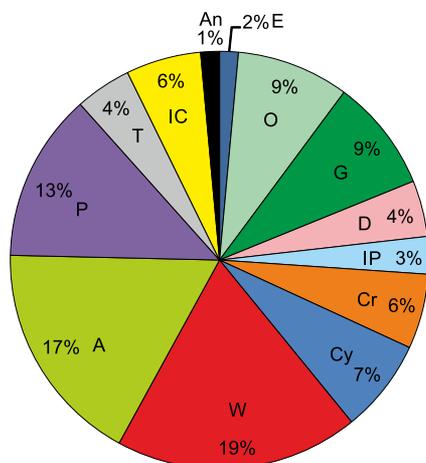


Fig. 4. Diversity pattern of Early Cretaceous macroflora from Pranhita-Godavari Basin (E – Equisetaceae, O – Osmundaceae, G – Gleicheniaceae, D – Dicksoniaceae, IP – Incertae sedis in pteridophyta, Cr – Corystospermaceae, Cy – Cycadaceae, W – Williamsoniaceae, A – Araucariaceae, P – Podocarpaceae, T – Taxaceae, IC – Incertae sedis in conifers, An – Angiosperms)

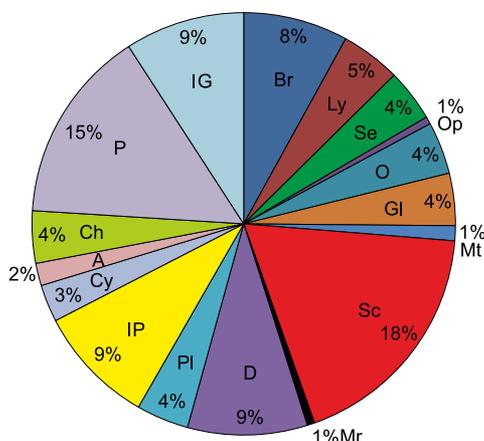


Fig. 5. Diversity pattern of Early Cretaceous microflora from Pranhita-Godavari Basin (Br – Bryophytes, Ly – Lycopodiaceae, Se – Selaginellaceae, Op – Ophioglossaceae, O – Osmundaceae, Gl – Gleicheniaceae, Mt – Matoniaceae, Sc – Schizaeaceae, Mr – Marsileaceae, D – Dicksoniaceae, PI – Polypodiaceae, IP – Incertae sedis in pteridophyta, Cy – Cycadaceae, A – Araucariaceae, Ch – Cheirolepidiaceae, P – Podocarpaceae, IG – Incertae sedis in gymnosperms)

lying close together on the same slab (Pl. 2, Fig. 4), suggesting minimal movement prior to burial, but these leaves were never found preserved with the cuticle. This may be related to their systematic affinities and the possession of very delicate cuticles. Pteridophytes are preserved mostly as isolated fragmentary pinnae. Simple and delicate ferns are more prone to fragmentation even when subjected to slight external force. Experimental observations have indicated that the maximum distance travelled by any given leaf material in fluvial settings is less than 1.5 km (Ferguson 1985, Spicer 1991). Although the vegetation

preserved in fluvial settings is non-indigenous and transported from other sites, the transport distance is particularly critical. Leaves in particular cannot be transported long distances before they are destroyed, so they are generally deposited fairly close to their source (Ferguson 1985, Rich 1989, Gastaldo 1988, Greenwood 1991). The recovered leaves include compound leaves and rachises with intact leaflets, already detached from the stem, suggesting their rapid burial and minimal transport (Krassilov 1975, Ferguson 1985).

The microflora assemblages include spores/pollen of bryophytes, pteridophytes and gymnosperms. Spores and pollen are generally assumed to withstand long-distance transport better than leaves and other macrofossil remains (Behrensmeier et al. 1992, Gastaldo 1992). Saccate pollen in particular can be transported further distances than non-saccate pollen and spores (Hartman et al. 2002). The distance of spores and pollen transport also depends on the height of the parent plant; the greater the height of the parent plant, the greater the advantage in interacting with air currents, leading to spread over a broader area than for spores/pollen of low-growing herbaceous species (Prabhakar 1987, Spicer 1991, Gastaldo 1992). Gymnosperms generally attain greater height. They include large shrubs and trees which can disperse pollen a longer distance. Therefore, some of the pollen-producing plants, particularly the saccate-pollen-producing conifers, can be assumed to have grown a little further away from the depositional site, possibly representing allochthonous components of the flora. In contrast, bryophytes and pteridophytes mostly include herbs and small shrubs; spores produced by them usually are deposited in and around the original site of growth (Prabhakar 1987, Hartman et al. 2002). Even allowing that some fern spores may have been transported from distant areas, the relative abundance of fern taxa indicates that the plants that produced them were indigenous.

The types and states of preservation of these plants allow us to infer the distance between the sedimentary basin and the source area. Based on the above discussion, the distances to which various members of the flora were transported can reasonably be inferred. Within the coniferous taxa, some species of *Elatocladus* found with intact branching and strobili underwent minimal transport

and therefore lived close to the sedimentary basin. Some species found as highly damaged specimens, indicating long-distance transport, probably occupied valley settings. The segregation of *Elatocladus* species into two distinct assemblages, one with a few fern representatives and the other with winged seeds and members of Taxaceae, also supports this conjecture. Other coniferous taxa such as *Pagiophyllum* and *Brachyphyllum*, found as specimens with substantial fragmentation, probably grew some small distance from the depositional site, but the preserved cuticle in a few taxa suggests rapid burial. Similarly, *Ptilophyllum* and *Taeniopteris*, based on their preservation state, probably grew within the depositional basin and mostly are para-autochthonous elements. Ferns are represented chiefly by isolated pinnae but we consider them to be local elements in light of the above-mentioned conditions of taphonomy and preservation. The bryophytes, although absent from the macroflora, are present in the microflora and are considered local elements. We conclude that the flora includes both local and regional components that are para-autochthonous to allochthonous. The presence of root impressions (probably in growth positions characteristic for an undisturbed environment, Pl. 2, Fig. 9) and well-preserved leaves and other organs in abundance, with minimal destruction, supports this interpretation. Ramamohana Rao et al. (2003) sedimentological analysis also suggested short transport and rapid deposition.

PALAEOECOLOGY AND ENVIRONMENT

Bryophytes and pteridophytes mostly preferred to grow near the waterbody, as they needed water or moist conditions for reproduction. Spores and leaves of these groups are mostly found associated with mudstone/carbonaceous shale. This sedimentological association indicates that they preferred overbank or riverbank to swampy habitat (Boggs 2006). The majority of Jurassic-Cretaceous pteridophytes/ferns are considered elements of moist lush vegetation (Harris 1961), often occurring near riverbanks or under forest canopy (Pelzer et al. 1992, Van Konijnenburg-van Cittert 2002, Abbink et al. 2004). These plants are generally thought to attain high abundance under humid conditions. For ferns this is reflected

in a correlation between high spore abundance and lithology indicative of moist environments (Maheshwari & Jana 2004). It is reasonable to conclude that these plants were growing as ground cover near waterbodies and under the shade of large shrubs and trees (Fig. 6).

Species of *Pachypteris* of the Corystospermaeaceae (pteridosperms) are thought to have produced large bushes that may have formed mangrove-like thickets along river mouths inundated by tides (Vakhrameev 1991, Banerji 2004). The presence of a thick cuticle and sunken stomata suggests xeromorphic or halophytic adaptations (Barbacka 1994, Thevenard et al. 2005).

The gymnosperms include a range of taxa affiliated with various groups. *Taeniopteris* leaves are recovered mostly from siltstone and in rare cases are associated with massive mudstone/clay beds. These sedimentological associations suggest that the plant bearing *Taeniopteris* leaves mostly inhabited river banks and floodplain areas distal to the river channel. The leaves are thin and broad, suggesting a sufficiency of water. Similar habitats for leaves of this type are also known from Early Cretaceous sediments of Antarctica (Howe & Cantrill 2001).

The bennettitaleans were represented by *Ptilophyllum*, *Pterophyllum*, and *Dictyozamites*, but only the former was common; the others were sporadic. The cuticles of these plants, where available, are rather thick and have sunken stomata, and the epidermal cells possess trichomes and papillae. All these features point to some sort of water stress on the plants. However, sedimentological evidence and palaeoecological considerations do not favour a palaeobotanical interpretation of environmental aridity in the Pranhita-Godavari Basin during the Early Cretaceous. The bennettitaleans are generally thought to grow in lowland where there is enough groundwater for plant growth (Krassilov 1975, Vakhrameev 1991, Pott & McLoughlin 2014, Pott et al. 2014). The sedimentological association of these plants, mostly with laminated siltstone, suggests that these taxa preferred floodplains such as lowland adjacent to the river channel (Fig. 6). A sedimentological study by Lakshminarayana (2001) suggested that there were frequent floods in the Pranhita-Godavari Basin during the Early Cretaceous, which must have occasionally inundated the flora growing in lowland. Prolonged inundation affects the physicochemical properties of the soil and results in flood stress (Junk et al.

2010), which strongly affects plant growth. The hydrological conditions of the floodplain are unfavourable for plant growth, so these taxa tend to exhibit morphological as well physiological adaptations, and many of these adaptations in fact resemble xeromorphic features (Medina 1983, Waldhoff 2003, Waldhoff & Parolin 2010). Seasonal floods with waterlogging (floodplain habitat) may follow a dry season in which the habitat can become extremely arid (Kubitzki 1989, Parolin et al. 2010). Xeromorphic characters may help a plant to cope both with an insufficiency of water during the aquatic phase and with periods of occasional drought in the terrestrial phase (Parolin et al. 2010).

The conifers include members of the Araucariaceae, Podocarpaceae and Taxaceae. The Araucariaceae include *Allocladus*, *Pagiophyllum*, *Brachyphyllum* and *Araucarites*. The epidermal structures in *Pagiophyllum* and

Brachyphyllum show xeromorphic features such as sunken stomata and the presence of a hypodermis, but their association with foliage of *Ptilophyllum* and *Elatocladus* suggests lowland, possibly swampy settings for these taxa (Fig. 6). The xeromorphic traits must have functioned to promote salt tolerance. Evidence from studies by Ramanujam (1980) and Vakhrameev (1991) also indicates that plants bearing leaves of *Pagiophyllum* and *Brachyphyllum* usually grew in lowlands and preferred cooler environments. The sedimentological association of these taxa with siltstone also suggests these plants occupied floodplain areas. Podocarpaceae is represented by *Elatocladus* with both slightly sunken and normal stomata, suggesting that the genus had a diverse distribution. The range of sedimentological associations of the species also suggests the plants inhabited a range of environments. The taxa are found

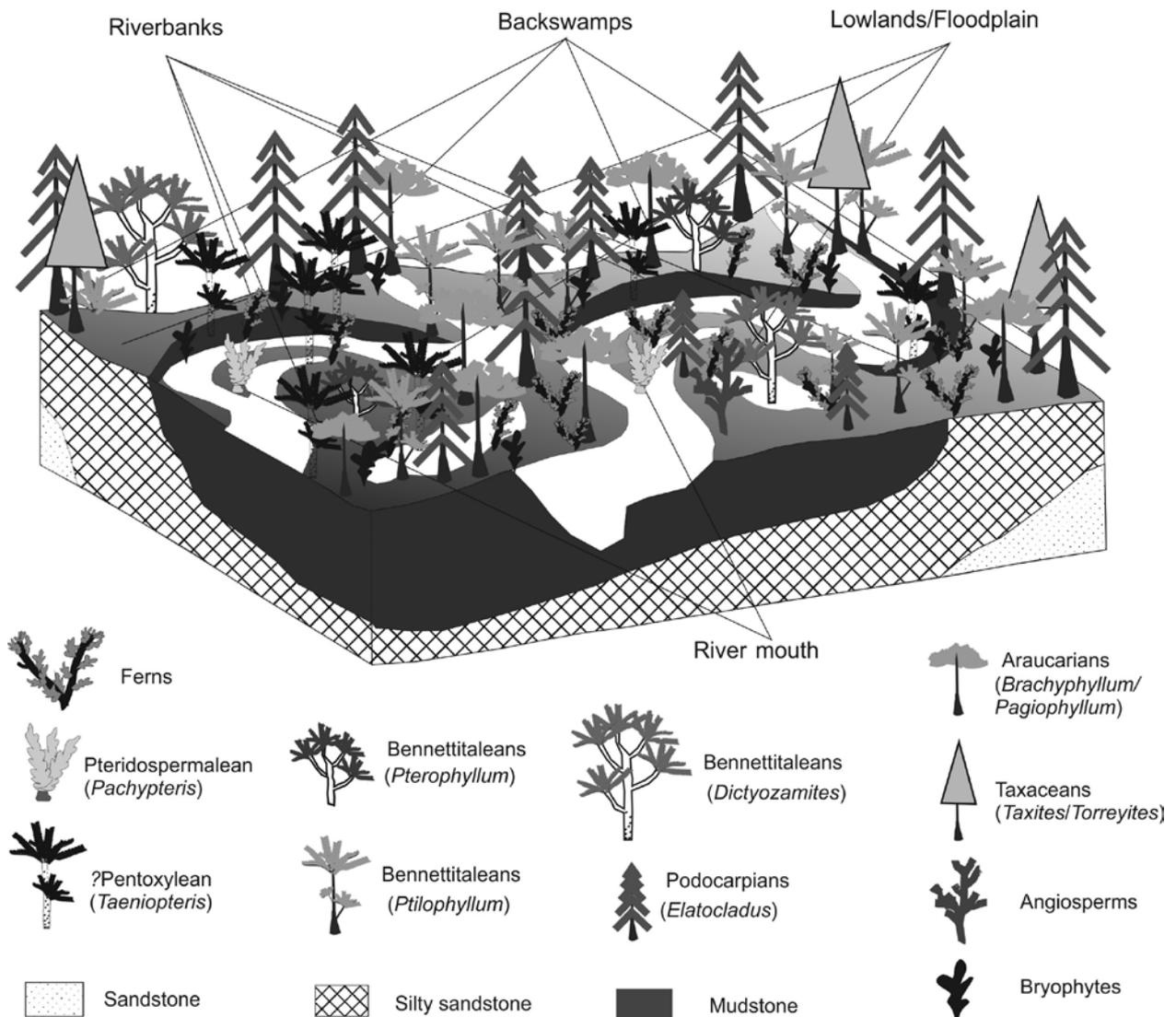


Fig. 6. Palaeoecological reconstruction of Early Cretaceous flora from Pranhita-Godavari Basin

associated with mudstone along with fern components in a few localities, and at other sites are associated with siltstone. Species of *Elatocladus* may have colonized backswamps. Similar habitats for leaves of this type are also known from Early Cretaceous sediments of Antarctica (Cantrill & Falcon-Lang 2001) and Jurassic sediments of southern Hungary (Barbacka 2011). The palaeoecological preferences of *Taxites* and *Torreyites* of Taxaceae are not well understood, due to the paucity of these fossils in the studied area, but the association of these taxa with *Elatocladus* suggests that their habitat preference may be similar to that of the podocarpeans.

Angiosperms are rare components of the flora, only a single taxon having been recorded (Chinnappa 2016). Its ribbon-shaped leaves suggest that it was aquatic and may have occupied stream margins.

Both the sedimentological evidence and the vegetation indicate a relatively humid climate phase; this is also supported by the abundance of spores of bryophytes and ferns. The total flora, with very diverse spores/pollen and foliage of bryophytes, pteridophytes, pteridosperms, gymnosperms, and angiosperms, suggests the prevalence of warm and humid climatic conditions.

CONCLUSIONS

1. An integrated appraisal of the Early Cretaceous micro- and macrofloras from the Gangapur Formation, Pranhita-Godavari Basin, suggests a rich and diverse vegetation that included all the major plant groups.

2. Taphonomic considerations indicate that the flora includes both local and regional components. The regional elements apparently include members of bennettitales and conifers, and the local elements are bryophytes, pteridophytes, pteridosperms and pentoxyleans.

3. Palaeoecological considerations of the various plant taxa suggest that the flora was widely distributed on banks and floodplain areas.

4. Warm and humid palaeoenvironments are inferred on the basis of the composition of the flora and sedimentological information.

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