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Floristical and Palaeoecological implications of the Early Cretaceous sequences of Krishna-Godavari Basin, East coast of India

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ABSTRACT

The Early Cretaceous plant diversity and palaeoecology of the Krishna-Godavari Basin flora is studied. The study is based on the plant fossils collected by the authors during the recent years and published reports of past work. Nature and mode of preservation of the leafy fossils were considered to understand the vegetation relationship. Similarly, Nearest Living Equivalent method and palaeoecological information of diverse plant groups from the published sources, along with sedimentological inputs are adopted to draw the palaeoenvironnement. The results show that the flora was dominated by bennettitaleans. The vegetation includes plant fossils from the parauto- to allo-chthonous sources. The association of the plant fossils with marine fauna indicates the vegetation was growing near to the sea. The phytogeographical correlation of the flora shows its similarity with that of Antarctica and Australia in the generic composition but greatly differ in specific composition. The composite flora indicates the prevalence of warm and humid conditions.

KEY WORDS
Flora,
taphonomy,
palaeoecology,
phytogeography,
Early Cretaceous,
Krishna-Godavari Basin.

RÉSUMÉ

Analyse floristique et implications paléoécologiques des séquences du Crétacé inférieur du bassin de Krishna-Godavari, Côte Est de l'Inde.

La diversité et la paléoécologie de la flore du Crétacé inférieur du bassin de Krishna-Godavari sont étudiées. Ce travail exploite des récoltes récentes et des rapports préliminaires faits par les auteurs. La nature et le mode de préservation des feuilles fossiles sont étudiés afin de comprendre la relation entre les végétaux. Pour reconstituer les paléoenvironnements, des données sédimentologiques et des informations paléoécologiques sur des groupes variés ont été utilisées. Cette étude a aussi été complétée par une approche fondée sur la méthode actualiste. Les résultats montrent que la flore est dominée par les bennittitales. La végétation comprend des plantes d'origines parautochtone à allochtone. L'association de plantes à des éléments de faune marine indique un développement proche de la mer. L'analyse de corrélation phytogéographique montre des similitudes avec l'Antarctique et l'Australie dans sa composition générique, mais cette flore diffère dans sa composition spécifique. Cette flore composite indique une prévalence de conditions climatiques chaudes et humides.

MOTS CLÉS
Flore,
taphonomie,
paléoécologie,
phytogéographie,
Crétacé inférieur,
Bassin de Krishna-Godavari.

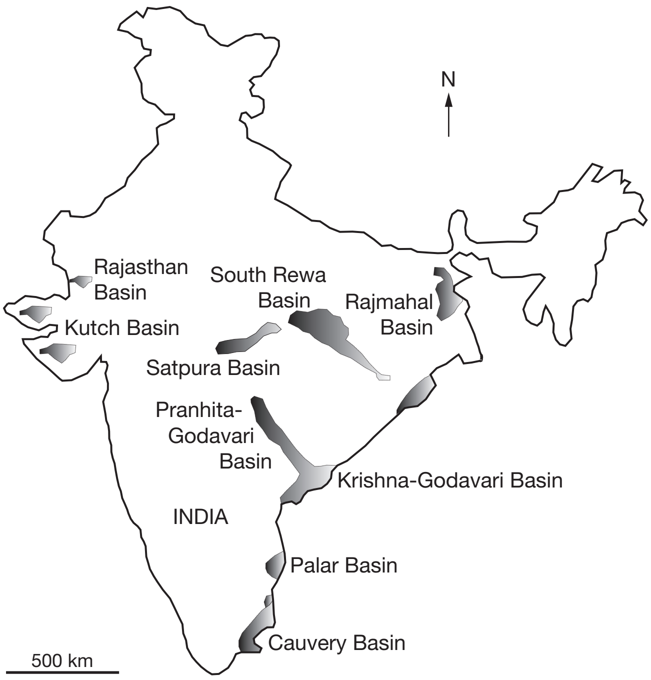

FIG. 1. — Locality map showing the fossil collection sites and the localization of the of the Krishna-Godavari Basin (East Coast of India).

INTRODUCTION

Fluvial-paralic sediments from the East Coast of India host some of the important Early Cretaceous (Neocomian-Aptian) fossil floras recording a range of vegetation types preserved in variety of depositional settings during the rifting event that fragmented eastern Gondwana. Plant fossil studies from these basins (e.g. Mehrotra *et al.* 2012; Rajanikanth & Chinnappa 2016 and references therein) also show that sedimentary basins host information that contributes to our understanding of the southern Gondwana palaeogeography during the Early Cretaceous period (Rao & Venkatachala 1972; Baksi 1977). Geographically and tectonically, these sedimentary units are grouped under 'Coastal Gondwanas', which are distributed in Cauvery (CV), Palar (PL), Krishna-Godavari (KG), Pranhita-Godavari (PG) and Mahanadi (MH) basins (Fig. 1). The segmentation of these East Coast Indian sedimentary basins is owing to the intrinsic subcrustal distinction along the east coast. Each one of the subcrustal blocks behaved differently and mimicked the inherent subcrustal mosaic during the Gondwana period and carved out for itself an exclusive basin of Mesozoic-Cenozoic age. These basins, however, are separated by major tectonic elements. A major fault separates Bengal from Mahanadi; Visakhapatnam high separates Mahanadi from Krishna-Godavari; Nayudupeta high separates Krishna-Godavari from Palar; Chingleput high separates Palar from Cauvery Basins (Lal *et al.* 2009).

The Krishna-Godavari Basin (KG) has received much attention in recent times due to its high petroliferous/hydrocarbon source rock potential (Mehrotra *et al.* 2012). It is one of the most important petroliferous basins of India and occupies an area of 28 000 km^2 on shore and 24 000-49 000 km^2 off shore (Rangaraju *et al.* 1993). The basin has been classified as a major intra-cratonic rift within Gondwanaland until the Early Jurassic period and it later transformed in to peri-cratonic rift basin (Biswas 1992). Sediments co-relatable to those of the Early Cretaceous ('Upper Gondwana') are exposed near the western and northwestern fringe of the Krishna (Budavada and Vemavaram formations) and Godavari (Golapalli and Raghavapuram formations) depressions. The sedimentation in these Cretaceous successions was linked with the faulting of basement blocks as a result of reactivation of NE-SW trending Precambrian faults (Biswas 1992).

Palaeobotanical studies from the Krishna-Godavari basin have been conducted for more than a century (Feistmantel 1879; Seward & Sahni 1920; Sahni 1928; Baksi 1964, 1967, 1968; Bose & Jain 1967; Jain 1968; Mahabale & Satyanarayana 1979; Vagyani 1984, 1985; Vagyani & Zutting 1986; Vagyani & Jamane 1988; Pandya & Sukh-Dev 1990; Pandya *et al.* 1990; Prasad & Pundir 1999; Chinnappa *et al.* 2014, 2015; Chinnappa 2016). These studies were mostly restricted to the taxonomy; however, no attempt has been made to discuss the taphoceonosis, diversity and palaeoecological implications of the flora. Moreover, these studies were restricted either to macro- or microflora.

Macro- or microfloral investigations of ancient sediments can provide a partial picture; both must be considered together to get a complete picture of the vegetation (Chinnappa & Rajanikanth 2017). Therefore, the present study aims to analyze both the micro- and macrofloras from the Early Cretaceous sediments of Krishna-Godavari Basin, to provide a detailed account of taphoceonosis and to determine palaeoecological diversity patterns.

GEOLOGICAL SETTING AND STRATIGRAPHY:

The Krishna-Godavari (KG) Basin contains about 5 km of sediments recording several cycles of deposition, ranging in age from Late Carboniferous to Pleistocene. The basin came into existence following rifting along eastern continental margin of Indian craton in the Early Mesozoic (Sastri *et al.* 1973). Faults penetrating to the basement define the series of horst and grabens cascad down towards the ocean and are aligned NE-SW along Precambrian eastern Ghat trend (Sastri *et al.* 1973, 1981; Rao 2001). The first attempt to describe the geology of the basin was made by Blandford *et al.* (1856), followed by King (1880) who carried out detailed geological studies of the outcrops. Subsequently, these successions were studied in detail by several researchers (Sastri *et al.* 1973, 1981; Rao 1993, 2001; Lakshminarayana *et al.* 1992; Prabhakar & Zutshin 1993; Raju & Misra 1996; Prasad & Pundir 1999; Lakshminarayana 2002). The Early Cretaceous Golapalli, Raghavapuram, Budavada and Vemavaram sediments are exposed towards the western and northwestern fringes of the basin (Fig. 2). These sediments were distributed in two depressions namely Godavari (Golapalli and Raghavapuram formations) and Krishna (Budavada and Vemavaram formations). Lakshminarayana *et al.* (1992) revised

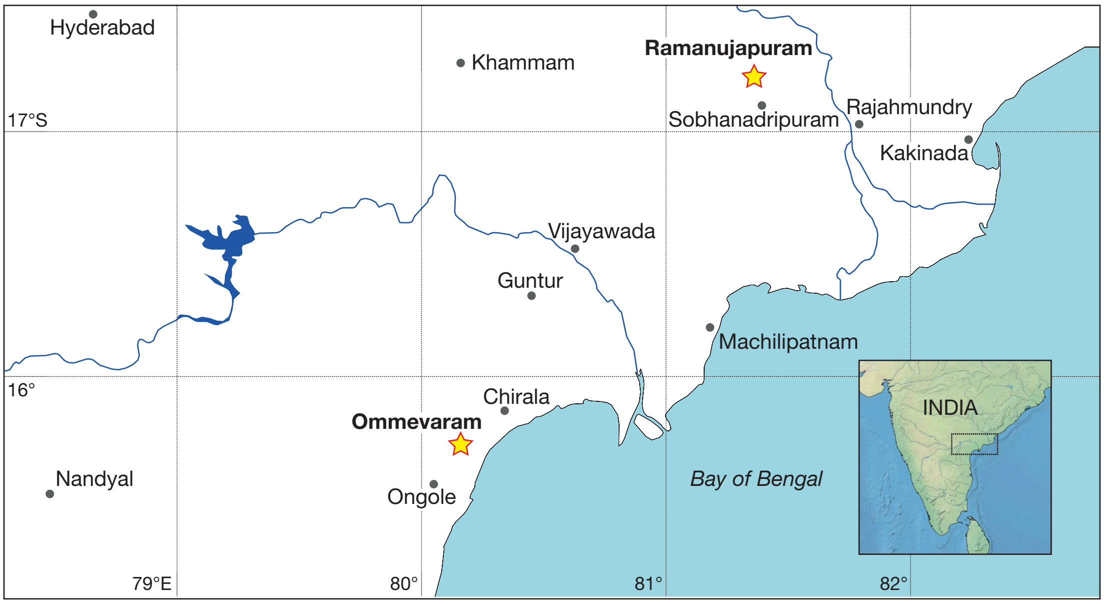

Fig. 2. — Map of the Krishna-Godavari Basin (East Coast of India; after Sastri *et al.* 1973) (map made with http://www.simplemappr.net).

the stratigraphy of these 'Upper Gondwana' sediments of the KG Basin and considered the Golapalli Formation under Kota Formation (Jurassic) at Musnuru, Nehrunagaram and Somavaram areas and similar rocks around Golapalli-Nuzividu areas were included under the Tirupati Formation (Late Cretaceous). However, Prasad & Pundir (1999) and Rao (2001) treated these rocks under Golapalli Formation as originally identified by the King (1880). The tectonic framework and depositional environment of the basin was studied by Sastri *et al.* (1973, 1981), Baksi (1977), Vasudeva Rao & Krishna Rao (1977), Venkatachala & Sinha (1986) and Rao (2001).

The Early Cretaceous sediments exposed in the Godavari Depression are divided into the Golapalli, Raghavapuram and Tirupati formations (Fig. 3A). The Golapalli Formation comprises white to pale white and light brown sandstone with siltstone partings. The Raghavapuram Formation sandwiches between the Golapalli and Tirupati formations, characterized by white pale to reddish shale and red ferruginous claystone, light buff to grayish white, medium grained glauconitic sandstone. The Tirupati Formation overlies the Raghavapuram Formation and composed of purple red to light brown, medium grained sandstone.

The Early Cretaceous sediments exposed in the Krishna Depression are also divided into the Budavada, Vemavaram and Pavaluru formations (Fig. 3B). The sedimentary rocks of Budavada Formation is composed of sandstone. The Vemavaram Formation lies between the Budavada and Pavalur formations and is composed primarily of shale containing carbonaceous matter. The Pavalur Formation comprises of medium to coarse grained clay and lateritic sandstone and it is overlying by the Deccan intertrappeans (Rao 2001).

The Golapalli, Ragahavapuram and Tirupati formations are considered, equivalent to the Budavada, Vemavaram and Pavalur formations respectively (Sastri *et al.* 1973; Venkatachala & Sinha 1986; Venkatachala & Rajanikath 1987). These formations are correlated with each other based on floral and faunal data (Sastri *et al.* 1973) Among these formations Golapalli, Raghavapuram, Budavada and Vemavaram are dated as the Early Cretaceous and Tirupati and Pavalur are Late Cretaceous based on mega and micro-floral and faunal evidences such as ammonites, brachiopods, lamellibranchs, fish scales and mammalian ribs (Spath 1933; Venkatachala & Sinha 1986; Venkatachala & Rajanikath 1987; Prasad & Pundir 1999). The generalized lithostratigraphy of the basin is given in the Table 1.

MATERIAL AND METHODS

Plant fossil material was collected from the mudstone succession of Raghavapuram Formation, exposed as a small hillock at about 1 km towards the South East of the village Ramanujapuram (17°13'27"N, 81°19'11"E), near Jangareddigudam, West Godavari District, Andhra Pradesh, India (Fig. 2). The fossiliferous section is characterized by white pale to reddish mudstone/shale and red ferruginous claystone, and light buff to grayish white, medium grained glauconitic sandstone. Plant fossils were preserved in pale-reddish mudstones/earthy shales (Fig. 3A). The plant fossils were also collected from the Vemavaram Formation, exposed at road cutting near about 0.5 km towards the North West and North East of the village Ommevaram (15°41'17"N, 80°09'01"E), near Ongole, Prakasam District, Andhra Pradesh, India (Fig. 2). These plant fossils were preserved in shale (Fig. 3B). The fossil leaves were preserved as impressions, and cuticules have not been recovered. Examination was done using an Olympus SZH 10 stereo dissecting microscope. All specimens were photographed with Canon SX 150 IS digital camera using either polarized light or low angle lighting to reveal surface details.

Table 1. — Lithostratigraphy and ages of the various lithounits in the KG Basin (data from Sastri *et al.* 1973; Lakshminarayana *et al.* 1992; Prasad & Pundir 1999) .

Group	Formation	Lithology	Age
		Recent alluvium	
Tertiary	Rajahmundry	Red, feldspathic, ferruginous, laterized, crossbedded and conglomeratic sandstone	Miocene-Pliocene
	Infra-Inter-Trappeans	Basaltic lava	Late Cretaceous-Early Paleocene
		Unconformity	
Upper Gondwana	Tirupati/Pavalur	Purple red-light brown sandstone/clay and caleritic sandstone	Late Cretaceous
	Raghavapuram/ Vemavaram	White pale-reddish earthy shale, red ferruginous claystone, light buff-grayish white glauconitic sandstone/shale containing carbonaceous matter	Early Cretaceous
		Unconformity	
	Golapalli/Budavada	White-pale white and light brown sandstone with siltstone partings/sandstone	Early Cretaceous
		Unconformity	
Lower Gondwana	Chintalapudi/Kamthi	Coarse grained feldspaathic sandstone, alternating calcareous claystone	Permain
		Unconformity/Fault	
Proterozoic	Khondalite	Igneous and metamorphic rocks	Precambrian

To isolate spores and pollen, sediments from all the localities that have yielded macrofossils were also treated with hydrochloric, hydrofluoric and nitric acid (HCl-HF-HNO_3) and sieved (mesh width 25 mm). However, only samples from the Raghavapuram were productive. The slides were studied under an Olympus BH 2 microscope, fitted with a digital camera. All samples and slides (BSIP 40156-40192 and 40243-40285) are deposited in the repository of Birbal Sahni Institute of Palaeobotany for future reference.

The taxonomic affinities at family level of the spore/pollen obtained are after Ramanujam & Rajeshwar Rao (1979). Similarly, the taxonomic affinity of the pteridophytic fronds at family level follows Harris (1969) and Barbacka & Bodor (2008). However, the taxonomic affinities at family level are not certain for many gymnosperm taxa; many of these taxa could be related to more than one family. Macro-and microfloral species diversity was analysed separately by considering the total number of taxa known in the flora. The reports of the present study and previous studies are taken into consideration for this purpose. The taxonomic diversity of the flora is presented in pie diagrams as simple percentage representation of each group (at order level), generated by using MS Excel. Similarly, the abundance of the various plant taxa was calculated by counting the number of samples for the given taxa. The difference between the micro-and macroflora is explained with regard to taphonomy and natural variations.

COMPOSITION OF THE FLORA

The synthesis of macro-and microflora from the Early Cretaceous sequences of the Krishna-Godavari Basin shows that the flora is diverse and composed of bryophytes, pteridophytes, gymnosperms and angiosperms (Appendices 1, 2). The diversity and abundance patterns of these plant groups, however, are not consistent between the macro- and microfloras.

Bryophytes

Macrofossils belonging to this group have not (yet) been recorded to date. In contrast, spores are well represented and constitute members of Anthocerataceae (*Foraminisporis* Krutzsch), Sphaerocarpaceae (*Aequitriradites* Delcourt & Sprumont, emend. Cookson & Dettmann and *Coptospora* Dettmann) and Reillaceae (*Cooksonites* Pocock, and *Staplinisporites* Pocock) (Ramanujam 1957; Kar & Sah 1970; Venkatachala & Sinha 1986; Prasad & Pundir 1999; Mehrotra *et al.* 2012). The qualitative and quantitative composition of the group is less when compared to the other spore producing plants such as pteridophytes (Appendix 2).

Pteridophytes

Pteridophytes are represented in both macro-and microfloras, especially the microflora. Fossil fronds belong to the Marattiaceae, Osmundaceae, Gleicheniaceae and Dicksoniaceae and a few *Sphenopteris* Sternberg type fossils of unknown affinity were recorded (Fig. 4). Many families such as the Lycopodiaceae, Selaginellaceae, Matoniaceae, Schizaeaceae, Marsileaceae, Cyatheaceae and Polypodiaceae are only represented in the microflora. Among these families, the Schizaeaceae and Cyatheaceae display highest species diversity (Fig. 5). The Schizaeaceae include six genera encompassing a total of 17 species and Cyatheaceae constitute 23 species in eight genera (Appendix 2). A few more pteridophytic spore taxa, cannot be assigned to any family with certainty and they are placed in pteridophyte *incertae sedis* (Appendix 2).

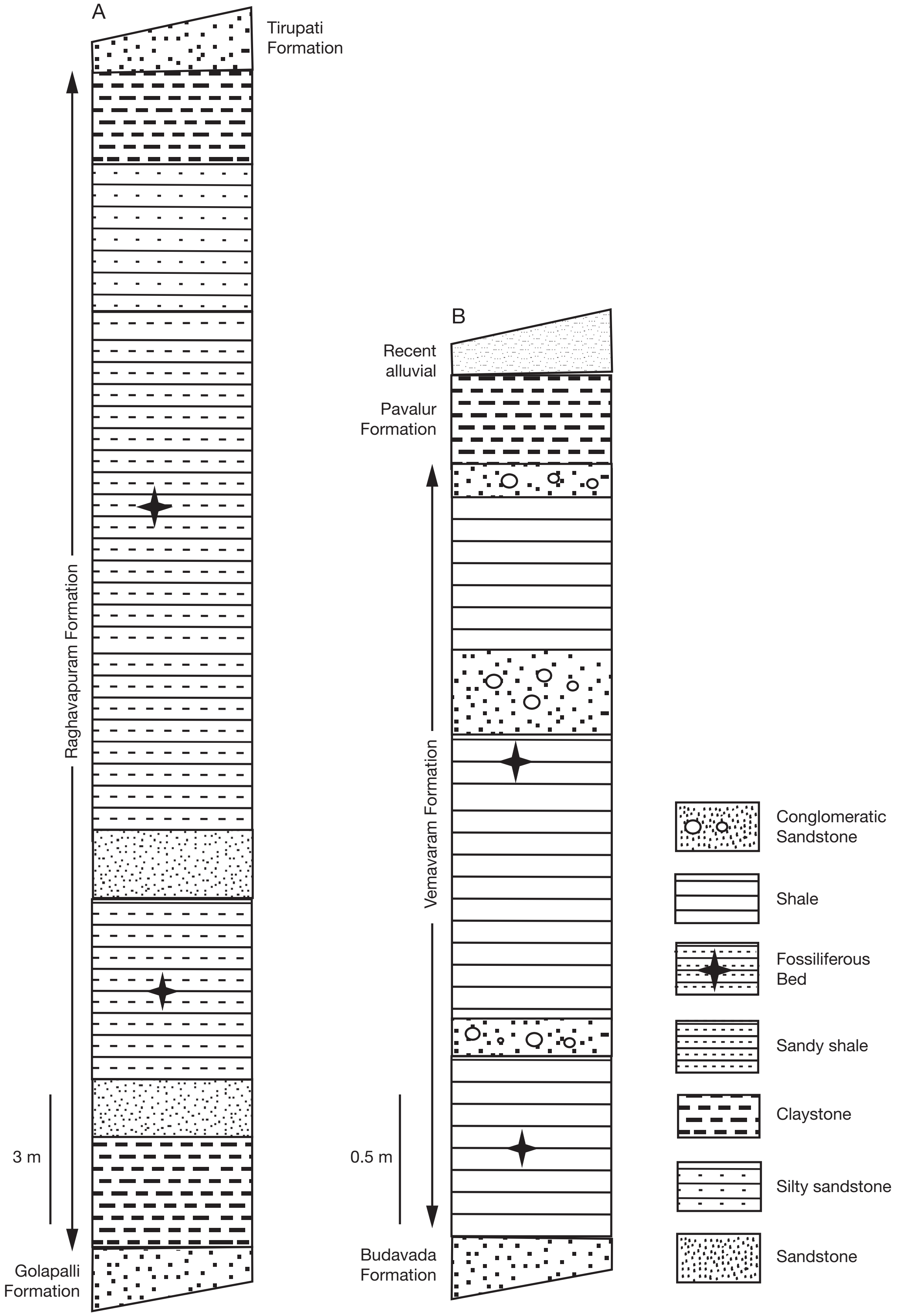

FIG. 3. — Litho-column of fossiliferous sections exposed at Ramanujapuram (**A**) and Ommevaram (**B**), Krishna-Godavari Basin (East Coast of India).

Marattiaceae fossil leaves are rare in the Krisha-Godavari flora, there are only a couple of reports of these fern fronds from the Golapalli Formation (Feistmantel 1876, 1877). The family is represented by a single genus with one species: *Marattiopsis macrocarpa* (Oldham & Morris) Seward and Sahni. Spores related to this family have not been reported.

Macrofossils of Osmundaceae are represented by five species belonging to two genera: *Cladophlebis* Brongniart and *Todites* Seward emend. Harris (Appendix 2). Within the two genera, the former is known from the both Raghavapuram and Golapalli formations but latter is known only from Golapalli Formation (Pandya & Sukh-Dev 1990; Prasad & Pundir 1999). From the Vemavaram Formation the macrofossils of the Osmundaceae are altogether absent. All the species were preserved as pinnae fragments, whole fronds are unknown. Pinnules were well preserved with a distinct venation pattern.

The Krishna-Godavari flora includes spores related to Osmundaceae in four genera – *Baculatisporites* Pflug & Thomson, *Biretisporites* (Delcourt & Sprumont) Delcourt *et al.*, *Osmundacidites* Couper, and *Todisporites* Couper, altogether with five species (Appendix 2). *Osmundacidites* type of spore is known as produced by *Todites* (Naugolnykh 2002). Although, the relationship of rest of the spores with *Cladophlebis* and *Todites* is not known, their spores are considered to be produced by Osmundaceae members (Kustatscher *et al.* 2010).

Gleicheniaceae includes a single genus, *Gleichenia* Smith, with two species (Appendix 1), which are reported from the Golapalli Formation (Feistmantel 1876; Prasad & Pundir 1999). Microfossils are represented by three genera: *Gleicheniidites* Ross, *Ornamentifera* Bolkhovitina and *Plicifera* Bolkhovitina, altogether with seven species.

From Dicksoniaceae a single genus *Onychiopsis* Yokoyama, represented by a single species (Appendix 1) was found from the Golapalli Formation (Prasad & Pundir 1999). The genus corresponds well with the living fern *Onychium* Kaulf in its morphology and spore morphology. Only a fragmentary specimen is known in the studied flora, not enough morphological details were observed hence the specimen is placed under the comparative form *O. psilotoides* Stokes & Webb on the basis of gross morphological similarity (Prasad & Pundir 1999). A number of spore genera are known to originate from Cyatheaceae/Dicksoniaceae and they are the most abundant in the present microflora (Appendix 2).

GYMNOSPERMS

Gymnosperms are important components of the Mesozoic floral ecosystems, dominating until the Late Cretaceous (Vakhrameev 1991). However, they started to decrease in their diversity and abundance, with the appearance of angiosperms in the Early Cretaceous and their subsequent expansion in the Late Cretaceous (McLoughlin 2001; Friis *et al.* 2011). In the Krishna-Godavari flora, the gymnosperms constitute a major share.

PTERIDOSPERMS

Pteridosperms are rare components in the Early Cretaceous Krishna-Godavari flora and are represented by two genera: *Thinnfeldia* Ettingshausen and *Pachypteris* (Brongniart) Harris with single species in each genus (Appendix 1). Of the two genera the former was reported from the Vemavaram and Raghavapuram formations (Feistmantel 1879; Baksi 1968; Chinnappa 2016) and the latter is known from the Vemavaram and Golapalli formations (Feistmantel 1876; Pandya & Sukh-Dev 1990)

Traditionally, *Thinnfeldia* type leaves reported from the early Cretaceous of India were variously assigned to *Dicroidium* Gothan and *Thinnfeldia* Ettingshausen (Feistmantel 1879, 1882; Lele 1962; Rao & Lele 1963; Baksi 1968; Jain 1968). Many of these specimens were originally described under *Thinnfeldia* by Feistmantel (1879, 1882). Later, however, Lele (1962) and Rao & Lele (1963) re-evaluated these fossil leaf types and transferred them from *Thinnfeldia* to *Dicroidium*. While doing so, Lele (1962) and Rao & Lele (1963) also considered the similar fossil leaves were also in *Dicroidium* despite their origin from the Early Cretaceous succession and morphological variations (Townrow 1957). Subsequently, Baksi (1968) and Jain (1968) also placed the leaf fossils resembling *Thinnfeldia* in *Dicroidium* instead. *Dicroidium* is characterized by dichotomized rachis with frequent sphenopteroid to taeniopteroid venation in the pinnules whereas *Thinnfeldia* lacks the dichotomized rachis and shows frequent odontopteroid and alethopteroid venation. Further, *Thinnfeldia* is considered as geologically younger (Jurassic) than the *Dicroidium* (Triassic). Chinnappa (2016) has considered the leaves described under *Dicroidium* from the Early Cretaceous sediments of India under *Thinnfeldia* based on the morphology and stratigraphic distribution. Recently, Cleal & Rees (2003) considered *Thinnfeldia* as taxonomic synonym of *Pachypteris*; nevertheless, we believe that the Indian specimens referred to *Thinnfeldia* needs a critical re-examination before considering them under *Pachypteris.*

CYCADALEANS

Foliage resembling that of modern-day cycads has long presented palaeobotanists with major problems, especially when dealing with foliage lacking cuticles. *Taeniopteris* Brongniart leaves are one such type that has a poorly understand systematic position (Pott & Launis 2015; Van Konijnenburg-Van Cittert *et al.* 2017; Chinnappa & Rajanikanth 2017). The affinity of leaves of this type can be clarified only when they associated with reproductive structures or preserved with cuticle (Cleal & Rees 2003; Pott & Launis 2015; Van Konijnenburg-Van Cittert *et al.* 2017). However, in the studied locality the leaves are known only as imprints, with no cuticles or associated reproductive structures having been found to date. Leaves of this type are here represented by a single species *Taeniopteris spatulata* McClelland known from all the three litho-units: Vemavaram (Feistmantel 1879), Raghavapuram (Baksi 1968; Chinnappa 2016) and Golapalli (Feistmantel 1876; Pandya & Sukh-Dev 1990; Prasad & Pundir 1999). Because the present leaves are preserved as impressions and there is a large uncertainty regarding the systematic affinity of the genus, we placed them under *incertae sedis* within the gymnosperms as suggested by Cleal & Rees (2003) and Pott & Launis (2015).

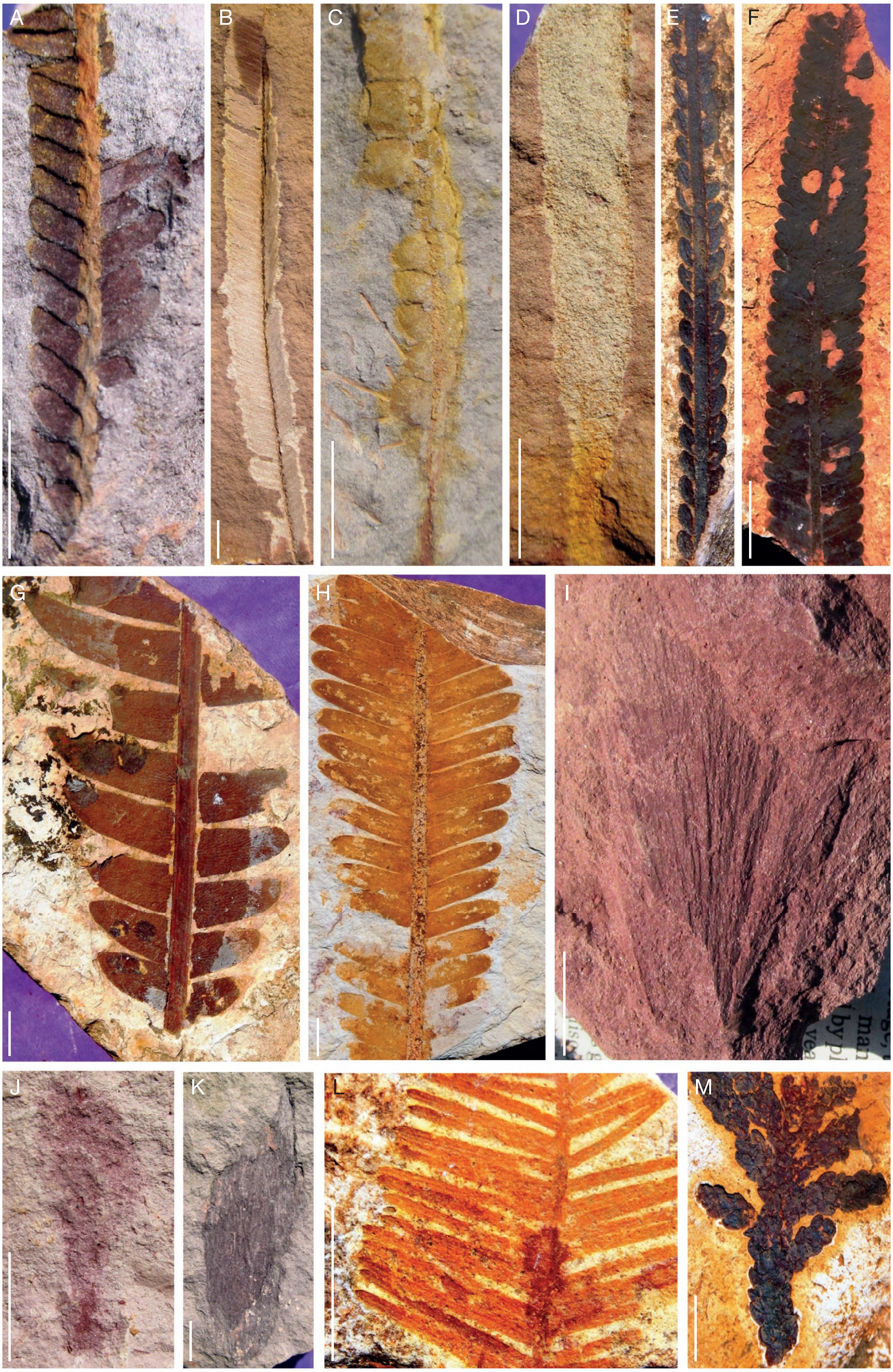

Fig. 4. — Plant material preserved from the KG basin: **A**, *Ptilophyllum cutchense* (Morris) Bose & Kasat; **B**, *Ptilophyllum acutifolium* (Morris) Bose & Kasat; **C**, *Anomozamites* sp.; **D**, *Taeniopteris* sp.; **E**, *Otozamites vemavaramensis* Bose & Jain; **F**, *Ptilophyllum rarinervis* (Feistmantel) Bose & Kasat; **G**, *Dictyozamites ommevaramensis* Chinnappa, Rajanikanth & Rao; **H**, *Dictyozamites feistmantelii* Bose & Bano; **I**, *Ginkgo* sp.; **J**, *Pityospermum godavarianum* Chinnappa, Rajanikanth & Rao; **K**, *Araucarites raghavapurensis* Chinnappa, Rajanikanth & Rao; **L**, *Elatocladus loyolii* Chinnappa, Rajanikanth & Rao; **M**, *Brachyphyllum sehoraensis* Bose & Maheshwari. Scale bars: 1 cm.

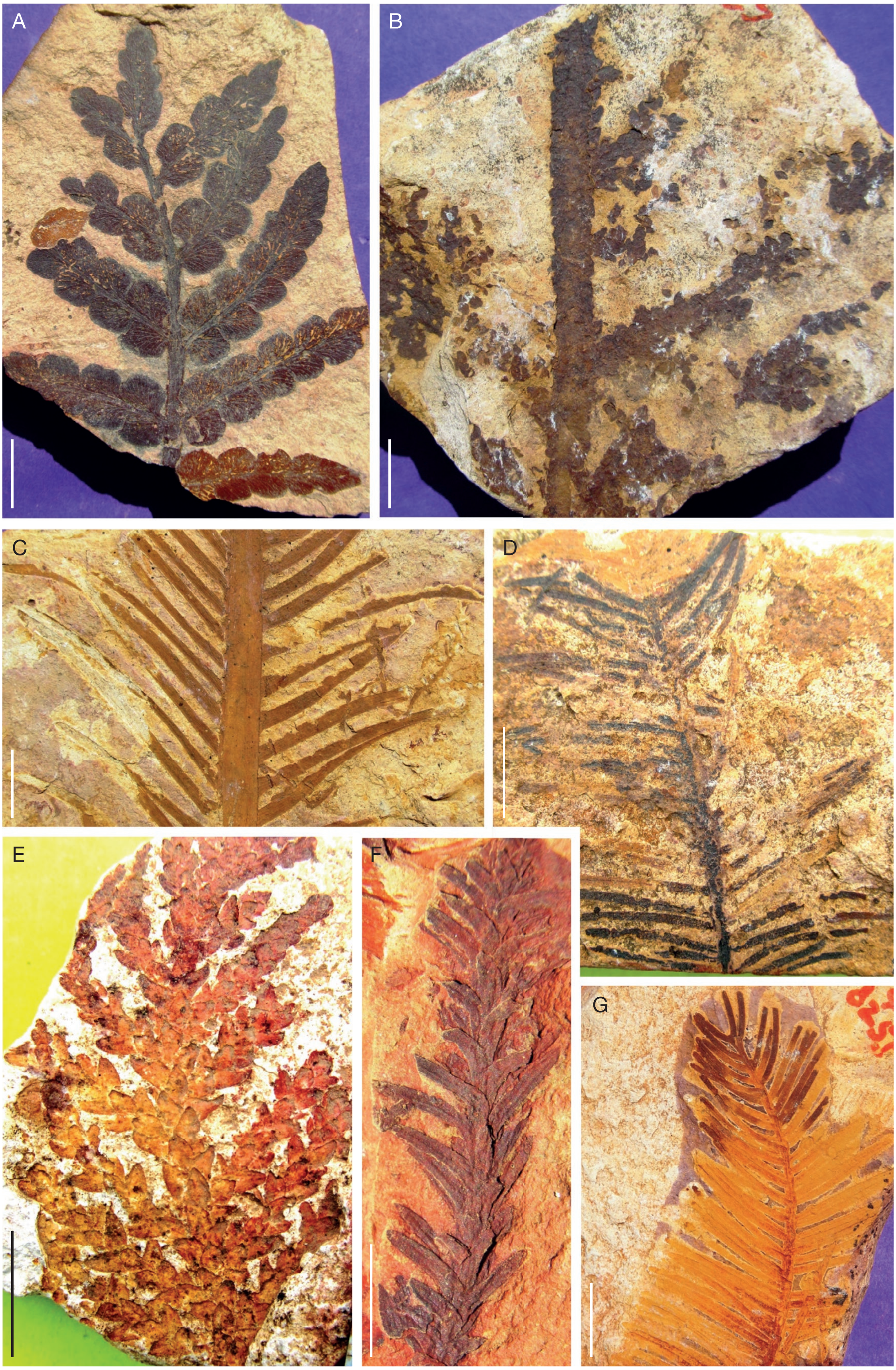

FIG. 5. — Plant material preserved from the KG basin: **A**, *Thinnfeldia vemavaramensis* (Feistmantel) Chinnappa, Rajanikanth & Rao; **B**, *Brachyphyllum expansum* (Sternberg) Seward; **C**, *Pterophyllum footeanum* Feistmantel; **D**, *Elatocladus loyolii* Chinnappa, Rajanikanth & Rao; **E**, *Pagiophyllum ommevaramensis* Chinnappa, Rajanikanth & Rao; **F**, *Pagiophyllum* cf. *rewaensis* Bose & Sukh-Dev; **G**, *Elatocladus loyolii*. Scale bars: 1 cm.

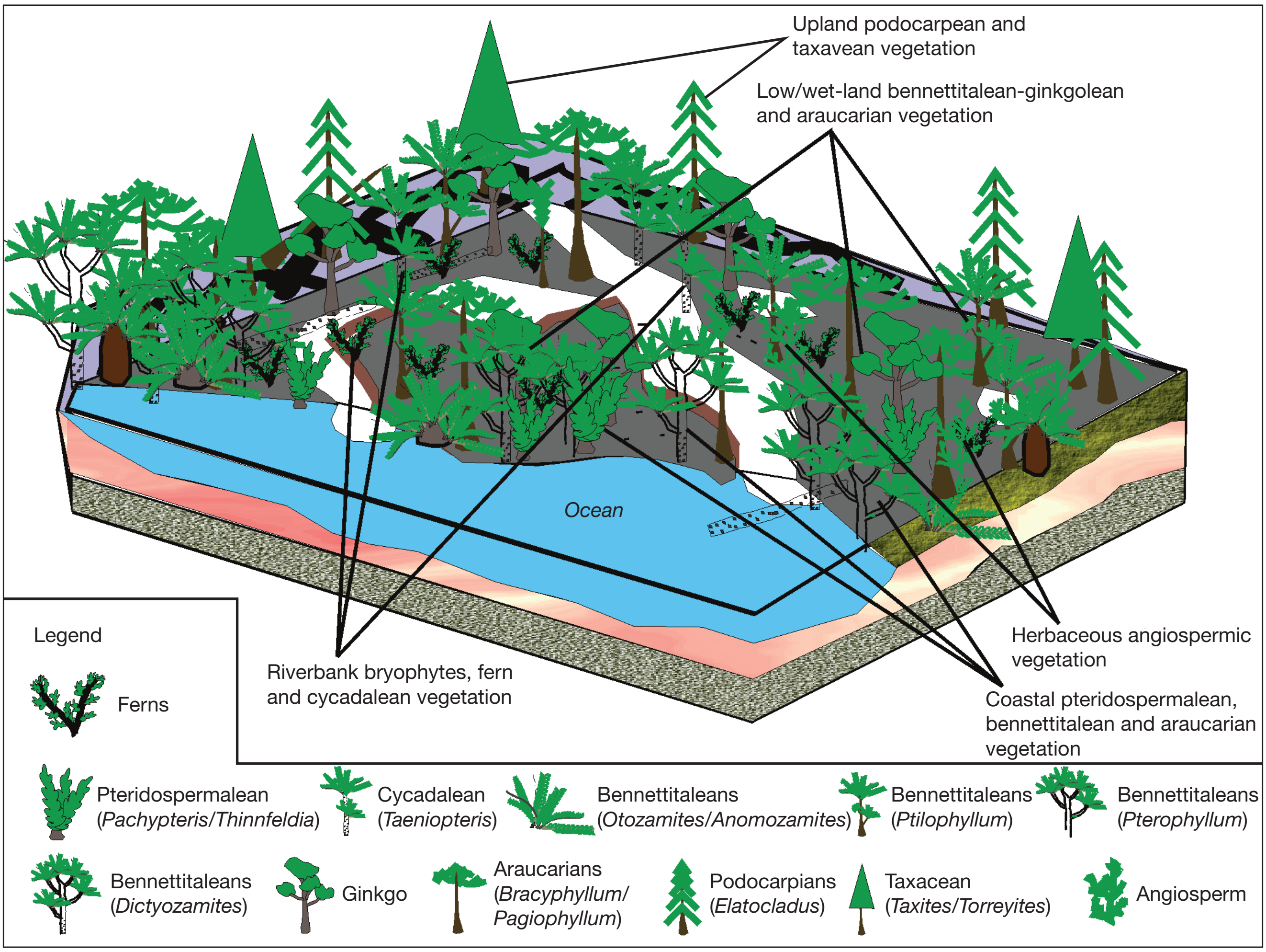

Fig. 6. — The macrofloral diversity of the various plant groups in the Krishna-Godaveri Basin (East Coast of India).

BENNETTITALEANS

Bennettitalean leaves are most common in the Early Cretaceous Krishna-Godavari floras. Six genera: *Anomozamites* Schimper, *Dictyozamites* Oldham, *Otozamites* Braun, emend. Watson & Sincock *Pterophyllum* Brongniart, *Ptilophyllum* Morris, and *Dictyozamites* Oldham were identified following the criteria given by Harris (1969) and Watson & Sincock (1992).

Among these, *Ptilophyllum* fronds are the most common and widely distributed throughout all the three formations. Twelve species have been reported to date (Appendix 1), of which six are assigned to the comparative forms such as *P. distans* (Feistmantel) Bose & Kasat, *P.* cf. *institacallum* Bose, *P. amarjolense* (Bose) Bose & Kasat, *P.* cf. *gladiatum* Bose & Sukh-Dev, *P.* cf. *horridum* (Roy) Bose & Kasat, *P.* cf. *jabalpurense* (Jacob & Jacob) Bose & Kasat (Appendix 1). *Ptilophyllum acutifolium* (Morris) Bose & Kasat, and *P. cutchense* (Morris) Bose & Kasat are most common in the studied plant assemblage. The identification of these species based only on the gross morphology. To date, cuticle has not been prepared from the Krishna-Godavari floras. *Dictyozamites* and *Otozamites* leaves are nearly as common as *Ptilophyllum*, but being mostly found in Vemavaram Formation (Feistmantel 1879; Chinnappa *et al.* 2015; Chinnappa 2016). These genera are represented by six species each (Appendix 1). Specimens belonging to *Dictyozamites* are rarely observed in the Raghavapuram and Golapalli formations and are represented in the flora by only a few fragmentary leaves (Baksi 1964; Pandya & Sukh-Dev 1990). *Otozamites* is altogether absent from Golapalli Formation. The other bennettitalean foliages such as *Anomozamites* and *Pterophyllum* are comparatively less common. From each of these genera three species are documented (Appendix 1). The former is reported only from the Vemavaram, whereas the latter known from all the three areas (Feistmantel 1879; Chinnappa *et al.* 2015).

Little fertile bennettitalean material has been described from Gondwana floras to date (Cantrill 2000). However, a few specimens of *Cycadolepis* Saporta and *Williamsonia* Carruthers are present in the flora studied here (Seward & Sahni 1920; Baksi 1968; Pandya & Sukh-Dev 1990). *Cycadolepis* is generally presumed to represent the bract from the base of a female cone (Cantrill 1997a), while *Williamsonia* is considered to be a bennettitalean strobilus (Harris 1969) and they are represented here by two species each (Appendix 2).

GINKGOALEANS

Members of the Ginkgoales are most commonly encountered from the Krishna-Godavari Basin; however, they are restricted to the Raghavapuram Formation (Feistmantel 1877; Baksi 1967, 1968; Vagyani 1985; Chinnappa *et al.* 2015). This indicates that the plants were growing in abundance in the basin. Mesozoic leaves resembling modern ginkgo leaves are usually placed in the genus *Ginkgo* Linnaeus or *Ginkgoites* Seward. Seward (1919) and Tralau (1967) maintained the distinction between the two genera based on the nature of lobes in leaf. Leaves of *Ginkgo* are divided into two or more lobes by shallow notches which never reach the basal part of the lamina, whereas in *Ginkgoites* leaves are deeply and symmetrically divided into narrow segments (Tralau 1967). However, Harris & Millington (1974) considered these distinctions are not applicable in reality as trees of *Ginkgo biloba* can produce many deeply divided leaves. Chinnappa (2016) merged all the Indian specimens previously described under *Ginkgoites* with *Ginkgo*, thus considering the recommendations of Harris & Millington (1974). The genus here represented by four species which gives 5% of species diversity in the Krishna-Godavari basin (Appendix 1). The pollen grain *Ginkgocycadophytus* Samoilovitch (with two species) is the only possible genus represented in the Krishna-Godavari flora probably produced by ginkgoaleans (Appendix 2).

CONIFERALEANS

Although the abundance of the conifer remains is low in the flora they show considerable taxonomic diversity (Appendices 1, 2). Eight genera are represented by macroremains: *Araucarites* Presl, *Brachyphyllum* Brongniart, *Pagiophyllum* Heer, *Elatocladus* Halle, *Torreyites* Seward, *Conites* Sternberg, *Harrisiophyllum* Pant, Srivastava & Pant, and *Pityospermum* Nathorst. The number of species identified within each genus is given in Appendix 1.

The genus *Araucarites*, belonging to the Araucariaceae, includes four species (Appendix 1) and is distributed to all the three formations: Vemavaram (Feistmantel 1879) Raghavapuram (Chinnappa *et al.* 2015) and Golapalli (Feistmantel 1876). The genus *Araucarites* is based on an ovuliferous cone scale that resembles those of recent Araucariaceae. Ovuliferous scales with a single ovule/seed and a free distal ligule are indicative of its affinity with the Araucariaceae (Cleal & Rees 2003). Our specimens of *Araucarites* are preserved with a woody bract and a centrally fused seed mark.

Leafy axes belonging to *Brachyphyllum* and *Pagiophyllum* are common among the conifer remains in the Krishna-Godavari flora (Sahni 1931; Baksi 1968; Pandya & Sukh-Dev 1990; Chinnappa *et al.* 2015). These genera both encompass five species each (Appendix 1). The taxonomic relationship of *Pagiophyllum* and *Brachyphyllum* is a unclear at the family level (see Chinnappa & Rajanikanth 2017). These taxa are herein provisionally placed under the Araucariceae after Bose & Maheshwari (1975). Pollen belonging to the Araucariaceae is known as *Araucariacites* Cookson and *Callialasporites* Sukh-Dev (Appendix 2).

The other significant conifers found in the flora are taxa belonging to *Elatocladus* where the genus is represented by six species (Appendix 1). Among them *E. plana* (Feistmantel) Seward is common and widely distributed. The specimens of the genus from Vemavaram show comparatively large sized leaves compared to material from the Raghavapuram and Gangapur. In the Krishna-Godavari flora, the genus is represented only as impressions of vegetative leafy twig, the cuticles and reproductive structures have so far not been recovered. Therefore the precise taxonomic affinity of the genus is unclear. Since the genus *Elatocladus* from India has already been related to Podocarpaceae (Chinnappa & Rajanikanth 2017), it is treated here under the same family i.e., Podocarpaceae. Pollen allied to the Podocarpaceae is known under four genera: *Microcachrydites* Cookson, emend. Couper, *Platysaccus* Naumova, emend. Potonié, *Podocarpidites* Cookson, emend. Couper, and *Podosporites* Rao and constitute a great deal of the microflora, both qualitatively as well as quantitatively. Among them, *Podocarpidites* shows the highest species diversity with eight species (Appendix 2). The quantitative representation of the genus is also very high and alone represents more than 20% in the pollen spectra (Venkatachala & Sinha 1986). Less abundant are the genera *Podosporites* represented by three species respectively. *Microcachrydites* and *Platysaccus* are represented by a single species each (Appendix 2).

The Taxales are comparatively rare with only a single genus and species of macro-remains *Torreyites constricta* Sahni being known only from the Vemavaram Formation (Sahni 1931). A very few plant fossil records can be assigned to this genus with confidence (Sahni 1931). The vegetative shoots bearing spirally arranged and distichously placed linear leaves characterized by two well marked stomatal grooves on the lower surface and absence of distinct midrib resembling in habit those of *Torreya* were usually assigned under *Torreyites* (Seward 1919). However, because the bands represent grooves to which the stomata were confined referral to Torreyites is not always possible when cuticles are not preserved (Seward 1919; Sahni 1931). The only reliable character is absence of a distinct midrib and the characteristic leaf shape. Although the fossil leaves were identified based on the characters of the extant genus, without reproductive organs it is impossible to determine the precise systematic position of shoots of this common form and these generic names do not imply any direct relationship with the extant members (Seward 1919). The records of taxalean woods (*Taxaceoxylon*) in India during Mesozoic times (Rajanikanth & Sukh-Dev 1989) however, suggest their possible existence as suggested by Sahni (1928).

Genera like *Harrisiophyllum* Pant, Srivastava & Pant and *Pityospermum* Nathorst are known from a single isolated specimen each (Chinnappa *et al.* 2015). Although cuticles of the *Harrisiophyllum* were described from Bansa, South Rewa Formation by Pant *et al.* (1983), they did not provide enough information to narrow down the taxonomic affinity of the genus to the family level. Records of *Pityospermum*, a winged seed, are not common from the Early Cretaceous sediments of India. *Pityospermum* sp., from the Sriperumbudur Formation, Palar Basin located in Tamil Nadu, India (Jeyasingh & Kumarasamy 1994) and *P. godavarianum* from the Raghavapuram Formation (Chinnappa *et al.* 2015) were the only reports known to date. The precise taxonomic affinity of the seeds of this type is not clear. The striking resemblance between such seeds and seeds of recent *Pinus* and other Abietineaceae (Seward 1919) suggest their possible affinities with Pinaceae or/and Abietineaceae. However, until more evidence is found it is not possible to confirm their family affinity. Therefore, here we consider them under the broad group Coniferales. Recovery of *Abietineaepollenites* pollen belonging to Abietineaceae from the Krishna-Godavari Basin (Ramanujam 1957) is noteworthy.

Classopollis Pflud emend. Pocock & Jansonius are abundant in the Early Cretaceous successions of India (e.g. Ramanujam & Rajeshwara Rao 1979; Venkatachala & Sinha 1986) and other Gondwanan and non Gondwanan land masses (Vakhrameev 1991). They are represented here by three species (Appendix 1). In spite of rich records of *Classopollis* from the Early Cretaceous sediments of India, nothing is known about their parent plants. The type of pollen is generally presumed to be produced by Cheirolepidiaceae (Venkatachala 1966). However, such pollen is shown to be produced by wide variety of fossil-taxa including *Pagiophyllum* and *Brachyphyllum* type fossils (Kendall 1949; Couper 1955; Venkatachala 1966; Srivastava 1976; Tosolini *et al.* 2013). Such leaf types belong to the Cheirolepidiaceae (Tosolini *et al.* 2013), the Podocarpaceae and Araucariaceae (Harris 1979). In India, *Classopollis* pollen has mostly been recovered from the same sediments yielding the species of *Pagiophyllum* and *Brachyphyllum* (Ramanujam & Rajeshwara Rao 1979). However, it has never been recovered from *in situ* cones attached with *Pagiophyllum* and/or *Brachyphyllum*. The taxonomic affinities of this foliage in India (see Chinnappa & Rajanikanth 2017), and the parent taxa of *Classopollis* necessitates awaiting further evidence.

Conifer remains in the Early Cretaceous Krishna-Godavari flora include two species of detached strobili placed under *Conites* (Appendix 2). Although there can be little doubt that it is a conifer reproductive organ not much is known about their structure and their precise affinity. A number of pollen forms of unknown conifer affinity also occur in the Krishna-Godavari basin. They are listed in the Appendix 2.

Angiosperms

Angiosperm macrofossil remains from the Early Cretaceous sequences of India are rare (Chinnappa & Rajanikanth 2017). Microfossil reports from subsurface and surface data from the Early Cretaceous sequences of India clearly indicate their occurrence by this time (Mehrotra *et al.* 2012). The Early Cretaceous microfossil assemblage from Krishna-Godavari Basin includes about thirteen species of angiosperm pollen (Appendix 2). A small assemblage of megafossils resembling flowering plants were recovered from the Early Cretaceous sequences Krishna-Godavari Basin (Chinnappa 2016). These fossil taxa mostly resemble an aquatic plants with ribbon shaped and dissected leaves.

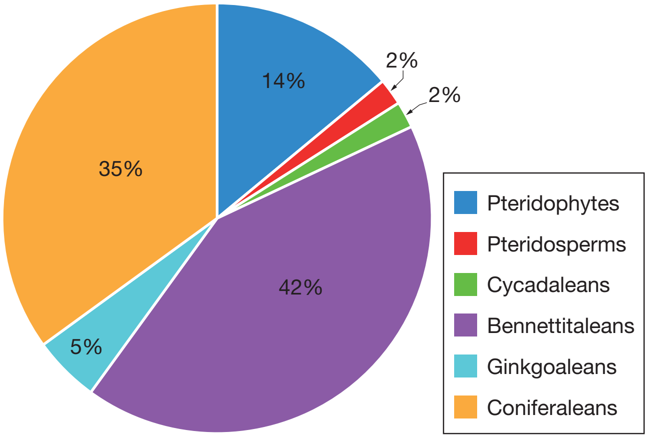

Fig. 7. — The macrofloral diversity of the various plant groups in the Krishna-Godaveri Basin (East Coast of India).

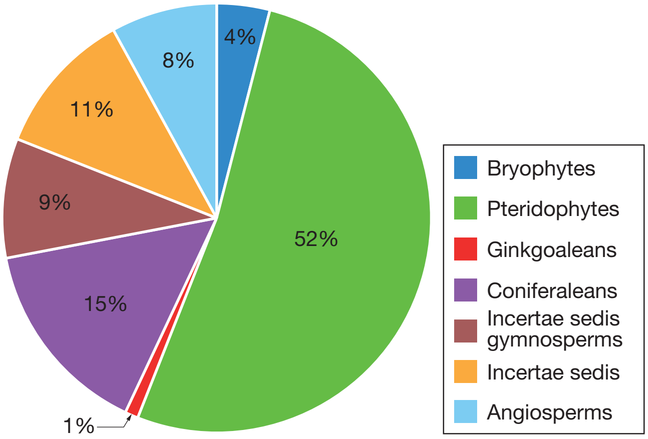

Fig. 8. — The microfloral diversity of the various plant groups in the Krishna-Godaveri Basin (East Coast of India).

FLORAL DIVERSITY

Megaflora

Taxonomic analysis of the megaflora, which includes leaves and cone scales (Figs 4; 5) demonstrate the presence of pteridophytes, and gymnosperms. A total of 81 species under 20 genera have been reported to date. The pteridophytes constitute 11 species under six genera representing 14% in the flora. The gymnosperms are a major element in the flora, they include pteridosperms, bennettitaleans, cycadaleans, ginkgoleans and conifers. With two species and two genera the pteridosperms comprise 2%. The bennettitaleans are dominant elements of the flora and they include 34 species under six genera with 42% of the species share. The conifers constitute 28 species under 8 genera and they represent 35% of the total diversity. The ginkgoleans and cycadaleans are minor components in the flora in terms of diversity. The former include four species under a single genus and make up 5%, and the latter consists of two species and one genus with 2%. Although, the species diversity of the ginkgoleans is less, they are extremely abundant in the Raghavapuram Formation. The percentage share of each group has shown in the Figure 7.

MICROFLORA

The Early Cretaceous microfloras (spore/pollen) from the Krishna-Godavari Basin are rich and diverse (Ramanujam 1957; Kar & Sah 1970; Venkatachala & Sinha 1986; Prasad & Pundir 1999; Mehrotra *et al.* 2010, 2012; and present study). These studies reported a range of taxa affiliated to the bryophytes, pteridophytes, gymnosperms and angiosperms (Appendix 2). Although, the conifer pollen dominates the assemblage, pteridophytes spores are also very abundant. The conifers include 23 species under seven genera and it comprises 15% in the flora. Other gymnospermous taxa include ginkgoaleans and taxa of uncertain affinity (*incertae sedis*). The ginkgoaleans consists of two species under a single genus and make up a small percentage (1%) in the flora. The taxa placed in *incertae sedis* include 14 species in nine genera and represents 9%. The pteridophytes, composed of 82 species, are grouped under 39 genera and occupy 52% of species diversity. The presence of diverse and abundant spores suggests the luxurious growth of the group (Appendix 2). The percentage share of each group is shown in the Figure 8.

The significant contributions of the microflora are the reports of bryophytic spores and angiosperm pollen (Mehrotra *et al.* 2010, 2012). Presence of bryophytic spores suggests existence of the group in the Krishna-Godavari flora, although the megafloral elements have not yet been reported. The bryophyte spores are comparatively rare and they include only seven species in six genera and comprise 4% of species diversity. The records of the angiospermous pollen are of special interest here. They are here represented by 13 species under 10 genera, which occupy 8% of species diversity in the total flora. There are a few more taxa of uncertain affinity, which are here referred to *incertae sedis*, they include 18 species in 13 genera and constitute 11% of species diversity.

TAPHONOMIC IMPLICATIONS

The concentration and degree of fragmentation of the plant fossils has been often used as indicative of original vegitational relationship (auto-allochthonous). Plant taphonomic studies by Ferguson (1985), Spicer & Greer (1986), Gastaldo (1988), Spicer (1991) and others suggested that the degree of fragmentation can be related to the distance travelled by a given plant material before its fossilization. This fragmentation determines that leaves in general cannot be transported long distances before their burial and fossilization (Spicer 1991). Additionally, the fragmentation of the plant parts in the fossil floras is also due to other physical and biological factors (Ferguson 1985). Generally, the fossils also get badly mutilated during the process of recovery from sediments like highly cracked and jointed mudstone (Baksi 1968).

The fragmentary nature of the recovered specimens here indicates that the plant fossils were subjected to transportation (Behrensmeyer & Hook 1992). The degree of fragmentation among the various plant assemblages is not uniform, thus suggesting distances travelled by these plant fossils differ. Ferns were mostly recovered as isolated fragmentary pinnules and their concentration is poor. The paucity and fragmentation of the fern leaves can be explained by their delicate structure and poor preservation potential (Gastaldo 1988, 1992; Spicer 1991). However, spores of this group are diverse and abundant suggesting these plants were probably not from the far distance and their source might be close to the depositional site (Venkatachala & Sinha 1986; Spicer 1991).The leaves of *Taeniopteris* are rare and are recovered as isolated fragments (Pandya & Sukh-Dev 1990; Prasad & Pundir 1999; Chinnappa *et al.* 2015) suggesting that perhaps they were produced by plants that did not grow in the immediate vicinity of the depositional environment. The bennettitaleans are common and well preserved in many cases the leaves preserved most of its length (Fig. 4B). These compound leafy rachises with intact pinnae are suggesting their rapid burial and minimal transportation (Ferguson 1985). Therefore, the parent plant that produced these leaves is here considered as a local and was probably growing within or very near the depositional environment. *Ginkgo* leaves are common in the Krishna-Godavari flora and are locally more abundant in the Raghavapuram Formation. These leaf types are well preserved with petioles, however, in a few cases both the base and apex of the leaf are missing (Fig. 4I). This suggests leaves might be exposed to short distance transportation. The pollen of this group is also well preserved. It is rational to consider them as local constituents of the flora based on the preservational attributes.

The conifers in the flora include araucarians, podocarps and members of the Taxaceae. The araucarians constitute moderately preserved leafy axes with branching preserved (Fig. 5B, E), and cone scales with clear seed marks (Fig. 4K). The preservation mode of these taxa suggests considerable transportation before their fossilization, consequently they are considered here as regional elements. The podocarps occur sporadically in the flora; they are mostly represented by isolated fragmentary leaf axes and a winged seed (Figs 4L; 5D, G). They possibly travelled into the depositional site from regional uplands. High frequency of saccate pollen produced by Podocarpaceae is also indicative of its upland habitat (Venkatachala & Sinha 1986; Abbink *et al.* 2004). The saccate pollen must have been flew from the uplands and entered into the depositional sites.

The megafloral records of bryophytes are not known. The presence of the spores such as *Foraminisporis*, *Coptospora*, *Cooksonites* and *Stereisporites* indicates that the bryophytes also constitute as part of the flora (Mehrotra *et al.* 2012). The absence of macrofossil remains is probably because of their poor preservation capacity and taphonomic constraints (Reader & Stewart 1972; Spicer 1991). The bryophytes in general include small herbs with delicate foliages that make them difficult to preserve in fossil record.

The early angiosperms are mostly thought to be herbs and/or small shrubs (Taylor & Hickey 1996; Sun *et al.* 2002; Field *et al.* 2004, 2009). The herbaceous nature might be a possible reason for the dearth of their macrofossils (Spicer 1991), yet their pollen can be preserved. Angiosperms are rare in the Indian Early Cretaceous flora and represented by a few poorly preserved leaves which are ribbon shaped and dissected (Chinnappa 2016). The characteristic shape of these leaves suggest their aquatic nature.

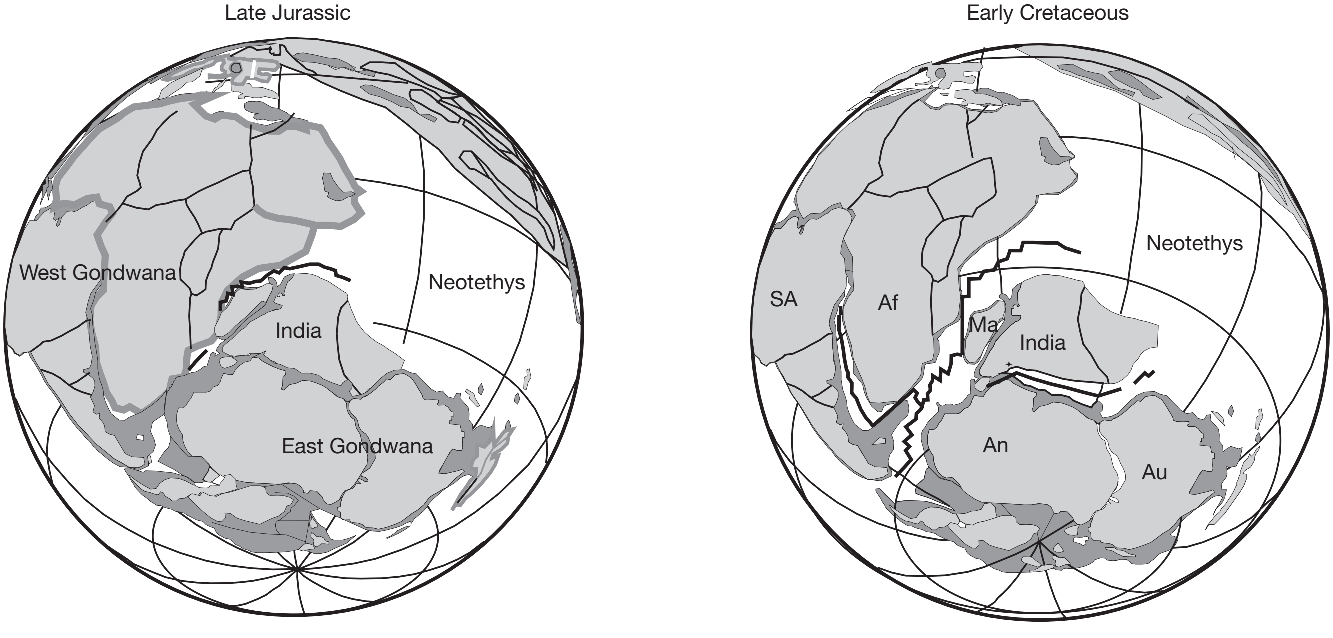

Fig. 9. — Global Palaeogeography map during the Jurassic and Cretaceous periods (after Chatterjee *et al.* 2013).

The above account suggests that many of the plant fossils were most likely exposed to some pre-depositional sorting and abrasion suggesting that perhaps they were produced by plants that did not grow in the immediate vicinity of the deposition environment. This could be the probable reason for the low diversity and low number of specimens in the samples and particularly explain the lack of delicate remnants such as sporangia and frond fragments of bryophytes in the megafossil flora. Nonetheless, the study also indicates the flora is taxonomically less diversified as it is (Chinnappa 2016). Experimental observation of leaf transportation in fluvial systems by Spicer & Greer (1986) indicated that the maximum distance travelled in ideal conditions is less than 1.5 km. Thus, the floral components were probably drifted from local to regional sites. Therefore, the present assemblage is considered to represent parauto- to allo-chthonous elements and the flora mostly includes the local to regional vegetation. It has also been demonstrated that a low energy condition within a fluvial system was inferred on the basis of grain size parameters (Rao 2001). Fluvial settings generally reflect the local flora though the herbaceous component is rare (Burnham 1989).

PALAEOECOLOGICAL IMPLICATIONS

Extant bryophytes mostly grow in moist and shady areas, as they require water to complete their life cycle. Only a few species are known to withstand water stress but even these taxa require water during the reproductive stage (Abbink *et al.* 2004; Schrank 2010). Therefore, this group is here considered to grow at river banks and back-swampy settings as indicated by their association with silt and mud (Boggs 2006). The swampy environments is also supported by an unequal distribution of phytoplanktons (Venkatachala & Sinha 1986)

Ferns have mostly been considered to grow "under moist, rather warm conditions either in marshes, along riverbanks or as understorey in forests" (Van Konijnenburg-Van Cittert 2002). Only a few taxa (e.g. *Gleichenia* [Gleicheniaceae], *Phlebopteris* and *Weichselia* [Matoniaceae]) can tolerate full sunlight and are able to adapt to the stress related conditions (Van Konijnenburg-Van Cittert 2002; Abbink *et al.* 2004; Schrank 2010). However, the majority of the Jurassic-Cretaceous ferns are considered to be elements of moist lush vegetation (Harris 1961) often occurring near river banks (Pelzer *et al.* 1992). The group is generally believed to attain high abundances under relatively humid conditions optimal for plant growth. This is highlighted by relations between lithologies indicative of moist environments with high spore abundances (Maheshwari & Jana 2004). The ferns in the Krishna-Godavari lithologically associated with claystone/mudstone and silty sandy stone. This facies association indicates overbank and backswampy depositional settings (Boggs 2006)

The pteridosperms such as *Pachypteris indica* (Oldham & Morris) Bose & Roy and *Thinnfeldia vemavaramensis* (Feistmantel) Chinnappa, Rajanikanth & Rao are associated with the sandstone and shale/mudstone facies respectively. The former is also known from the other basins like Kutch, Satpura, Rajmahal and Mahanadi (Rajanikanth & Chinnappa 2016), while the later is exclusive to the Krishna-Godavari Basin. *Pachypteris indica* is considered to produce large sized bushes that formed mangrove thickets along the river mouth inundated by tides (Banerji 2004). The frequent association of *Thinnfeldia vemavaramensis* with marine fossil fauna and leathery leaves suggest its coastal habitat.

Mesozoic cycadaleans are considered to occupy the low-lands and share the forest floor with ferns and favour fairly boggy conditions (Abbink *et al.* 2004). *Taeniopteris spatulata* McClelland is the only possible cycadalean taxa reported from the Krishna-

Godavari Basin. This taxon is considered to be grown on the river floodplain, distal to the river channel, but occupied fairly boggy conditions in clearings or near the forest margins (Chinnappa & Rajanikanth 2017). Where light was reduced from a closed canopy of conifers, cycadaleans colonized the forest floor in patches and together with fern thickets and presumably preferred areas of the canopy with less dense stands of trees.

The members of bennettitaleans were considered to grow in diverse niches, ranging from delta areas to coastal margins or in upland areas (Vakhrameev 1991; Abbink *et al.* 2004). However, it is generally assumed that most species favored humid environment (Pott *et al.* 2008) and preferred to grow at coastal margins (Vakhrameev 1991) and lowlands (Krassilov 1975). The spatial heterogeneity in the distribution pattern of various taxa in the fossil assemblages of the studied flora and their association with different sedimentary facies support the above views. The taxa like *Otozamites acutifolius* Feistmantel, *O. exhislopi* Bose, *O. imbricatus* Feistmantel, *O. gondwanensis* Bose, *D. hallei* Sahni & Rao, *D. ommevaramensis* Chinnappa, Rajanikanth & Rao, *Pterophyllum footeanum* Feistmantel, *P. incisum* Sahni & Rao and *Ptilophyllum heterophylla* Chinnappa, Rajanikanth & Rao are rich and exclusive to the near sea deposits and frequent association of the leaves with marine fauna suggests coastal habitat. Presence of recurved leaf margin, strongly cutinized guard cells and sunken stomata as observed in the species of *Otozamites* (Bose 1974; Bose & Banerji 1984) and characteristic leathery nature of the leaves is considered to be a strategy to minimize the water loss in the coastal zone (Vakhrameev 1991; Villar de Seoane 2001; Wright *et al.* 2005). The association of these leaves with shale is also in congruence with above interpretations (Boggs 2006). Similarly, the association of the other bennettitaleans such as *Dictyozamites indicus* Feistmantel, *Pterophyllum kingianum* Feistmantel, *Ptilophyllum deodikarii* Mahabale & Satyanarayana, *P. tenerrimum* (Feistmantel) Bose & Kasat, *Ptilophyllum* cf. *institacallum* Bose, *Ptilophyllum* cf. *amarjolense* Bose, *Ptilophyllum* cf. *gladiatum* Bose & Sukh-Dev, *Ptilophyllum* cf. *horridum* Roy and *Ptilophyllum* cf. *jabalpurense* Jacob & Jacob with cycadaleans and ferns indicates that, they are dwelling in the lowland areas. Their sedimentary association with claystone and clay sandstone also suggests flood deposits (Boggs 2006). The taxa like *Dictyozamites feistmantelii* Bose & Bano, *Ptilophyllum acutifolium* (Morris) Bose & Kasat, *P. cutchense* (Morris) Bose & Kasat have wide distribution and they are common in all type of lithologies and found in every fossil assemblage. This suggests that these taxa might favor the wide ecological niches.

Species of *Ginkgo* occur frequently in the flora; they represent mostly deciduous moist loving plants, growing alongside conifers. Although, the extant species is restricted to China, the ginkgoleans had wide distribution during the Mesozoic (Royer *et al.* 2003). Mesozoic ginkgoaleans seem to have been able to tolerate a wide range of climates from warm and wet temperate (or even cool) in coastal plain and lowland to inland riparian/swamp environments, respectively. In spite of their broad adaptability, however, it appears that the ginkgoaleans on the whole were more abundant and diverse in mesic, warm temperate to temperate climates and inhabited stable and ecologically saturated environments such as wetlands (Royer *et al.* 2003; Zhou 2009). The low diversity of the genus in the modern flora also suggests this ecologically restricted distribution (Alvin & Watson 1996). The *Ginkgo* leaves reported from the Krishna-Godavari Basin are associated with mudstone facies, which is indicative of floodplain deposits (Boggs 2006).

The coniferous taxa such as *Brachyphyllum regularis* Borkar & Chiplonkar, *B. sehoraensis* Bose & Maheshwari, *Pagiophyllum gollapallensis* Pandya & Sukh-Dev, and *Pagiophyllum* cf. *grantii* Bose & Banerji are found in an assemblage consists of ferns and cycadophytes, suggesting they share similar habitats such as lowlands. The presence of thin cuticle and amphistomatic condition in *Brachyphyllum sehoraensis* and *Pagiophyllum* cf. *grantii* (Bose & Maheshwari 1973; Bose & Banerji 1984; also indicate their growth at high water availability. Yet some species of *Brachyphyllum* such *B. feistmantelii* (Halle) Sahni, *B. rhombicum* Feistmantel, *Pagiophyllum* cf. *marwarensis* Bose & Sukh-Dev and *P. ommevaramensis* Chinnappa, Rajanikanth & Rao preferred to grow at coastal regions as indicated by their lithofacies association with shale and frequent mixing with marine fauna. The fertile parts reported here probably produced by *Brachyphyllum* and/or *Pagiophyllum*. Extant members of araucarians frequently grow near shores as they can withstand the influence of salt wind (Vakhrameev 1991). Their leathery leaves and thick cuticles are adaptations to such type harsh conditions. Evidence from the megafossil record indicates that araucarian trees usually grow in lowlands, probably coastal margins and preferred cooler environments (Venkatachala 1966; Ramanujam 1980; Vakhrameev 1991).

The members of podocarpaceae are numerically less represented in the megaflora when compared to any other members, but they are abundant in the microflora. In spite of their robust nature, the week representation of podocarps in the flora, in terms of their abundance suggest they probable growing away from the depositional site and find difficult to incorporate in the fossil assemblages (Spicer 1991). Being able to fly with wind the pollen might had reached the depositional site and preserved in good number. Today podocarps are particularly common in mountain areas of the tropics and subtropics. During the Mesozoic, the family inhabited relatively dry areas of upland forest (Vakhrameev 1991) or cool, wet upland forest (Doyle *et al.* 1982). High frequency of saccate pollen produced by Podocarpaceae is also indicative of its upland habitat (Abbink *et al.* 2004). The association of taxaceans with podocarps is indicative of their similar distribution.

The palaeoecology of the angiosperms in the present flora is not clear due to the limited megafossils evidance and lack of knowledge regarding their systematic affinities. The characteristic shapes of these leaves (ribbon shaped and dissected) suggest their aquatic nature (Chinnappa 2016). It has been believed that the early angiosperms were herbs/shrubs and mostly preferred to grow near water bodies (Feild *et al.* 2009). The angiosperms pollen reported here, possibly originated from the plants of the similar habitat.

From the above discussion that the spore-producing bryophytes/pteridophytes are generally believed to prefer river banks and still some may have been underground cover under ben-

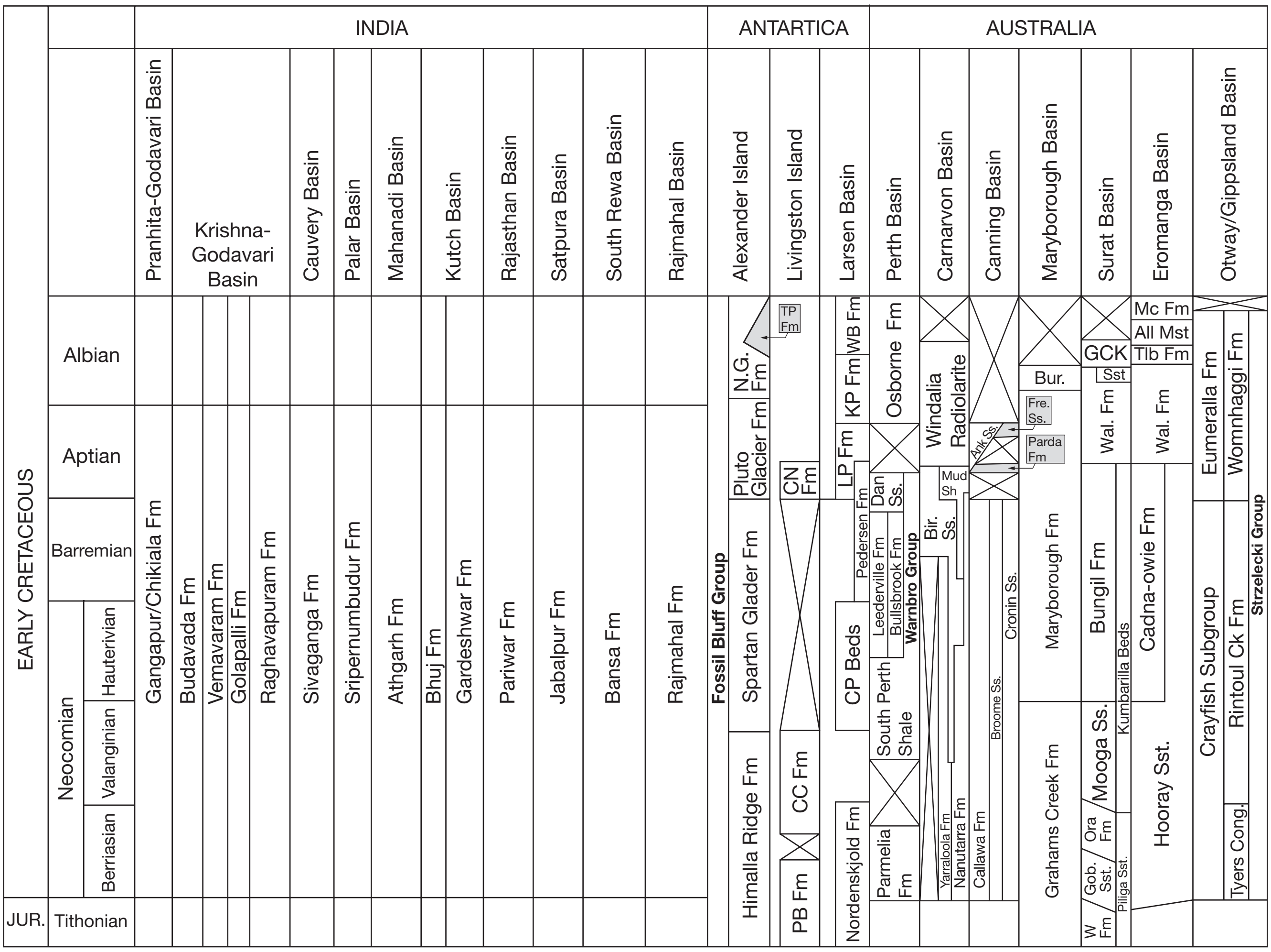

Fig. 10. — Correlation chart of the different Early Cretaceous basins from India, Antarctica and Australia, deducted from the information available in this article. Abbreviations: **All Mst**, Allaru Mudstone; **Ank Ss**, Anketell Sandstone; **Bir Ss**, Birdrong Sandstone; **Bur**, Burrum Coal Measures; **CC Fm**, Chester Cone Formation; **CN Fm**, Cerro Negro Formation; **Cong**, Conglomerate ; **CP Beds**, Crabeater Point Beds; **Dan Ss**, Dandaragan Sandstone; **Fre Ss**, Frezier Sandstone; **GCK**, Griman Ck Formation; **Gob. Sst**, Gobb Sandstone; **KP Fm**, Kotick Point Formation; **LP Fm**, Lagrelius Point Formation; **Mc Fm**, Mackunda Formation; **Mud Sh**, Muderong Shale; **N.G. Fm**, Neptune Glacier Formation; **Ora Fm**, Orallo Formation; **PB Fm**, President Beaches Formation; **Sst**, Surat Siltstone; **Tlb Fm**, Toolebuc Formation; **TP Fm**, Triton Point Formation; **Wal. Fm**, Wallumbilla Formation; **WB Fm**, Whisky Bay Formation; **W Fm**, West Formation.

nettitaleans and conifers. The cycadaleans probably grew on the river floodplain, distal to the river channel, but preferred fairly boggy conditions in clearings or on the outskirts of the forest. The bennettitaleans are considered to have inhabited lowlands to coastal regions. The ginkgoaleans are wetland lovers. The members of araucarian conifers are interpreted to dwell in lowlands yet some species may extend into coastal margins. The podocarps and taxaceans possibly occupied the upland regions. Palaeoecological reconstruction of the Early Cretaceous Krishna-Godavari Basin flora is illustrated in Figure 6.

PHYTOGEOGRAPHICAL CORRELATION

To a large extent type and distribution pattern of the land plants is constrained by its immediate physical environment (Spicer *et al.* 1994). This constraint has operated thorough out land plant evolution and has repeated morphologies under similar environmental conditions. During the Early Cretaceous, Indian subcontinent along with Australia and Antarctica constitute an east Gondwana (Fig. 9). The palaeoclimatic maps of the Scotese (2000) have shown that these land masses were under the influence of warm temperate conditions. Therefore, it is expected to be floral similarities among the Indian subcontinent, Australia and Antarctica. The palaeogeographic maps of the Jurassic and Cretaceous periods have shown that the east coast of India is closely associated with Western Australia and east Antarctica. Hence the comparison is here restricted to the floras of these regions.

The poor dating of the Indian Mesozoic sediments is one of the significant constraints to compare the Indian Early Cretaceous flora with the other Gondwana floras. Unlike the Early Cretaceous successions of Australia and Antarctica, there are no precise age determinations for the Early Cretaceous successions of India (Fig. 10). The Indian Early Cretaceous successions were assigned age ranging from Neocomian to

Aptian almost covering the entire Early Cretaceous period. Palaeobotanical studies around the globe, however, indicated that except the appearance of angiosperms there are not many changes in compositions of flora during the intervals of the Early Cretaceous. This permits a broad scale comparison of the Indian Early Cretaceous flora with that of Australia and Antarctica.

The President Head flora, Antarctica, is distinctive, and appears to be characteristic of a high latitude flora (Cantrill 2000). Bryophytes and hepatophytes are abundant and diverse, a feature unique to the Cretaceous Antarctica (Drinnan & Chambers 1986; Cantrill 1997a, b). The President Head flora shares two species, *Dictyozamites falcatus* Medlicott & Banford and *Pachypteris indica* (Oldham & Morris) Bose & Roy and also eleven genera: *Lophosoria* Presl (= *Gleichenia*/*Gleichenites* Goeppert), *Sphenopteris*, *Pachypteris*, *Taeniopteris*, *Ptilophyllum*, *Dictyozamites*, *Cycadolepis*, *Araucarites*, *Pagiophyllum*, *Conites* and *Elatocladus*. However, at species level they differ from the Indian taxa. The most similar generic and possibly even specific comparison appears to be with the flora of the Western Australia. Similar to the Early Cretaceous KG flora, the Neocomian Western Australian flora is also dominated by bennettitaleans (McLoughlin 1996). Both these floras share several genera (*Gleichenites* [= *Microphyllapteris*], *Cladophlebis*, *Sphenopteris*, *Thinnfeldia*, *Taeniopteris*, *Ptilophyllum*, *Araucarites* [araucarian cone scale], *Pityospermum* [winged seed], *Elatocladus*) and some species like *Ptilophyllum acutifolium* and *P. cutchense* in common. The principle difference between the two floras is in the presence or absence of *Dictyozamites*. While it is absent from the Western Australian flora, it is more common in the Krishna-Godavari flora.

The phytogeographical distribution and diversity of the Indian East Coast flora during the Early Cretaceous was influenced by drifting of the Indian subcontinent. During this period initiation and separation of East Coast from the East Antarctica and West Australia basins influenced deposition of plant relics (Sastri *et al.* 1981; Lal *et al.* 2009). The similar floral constituents from these regions support such an interpretation (Dettmann 1963; Dettmann & Playford 1969; Truswell *et al.* 1999; Sajjadi & Playford 2002a, b; Chinnappa 2016). Conversely, the Indian East Coast Early Cretaceous flora differs slightly from that of the Antarctica (Bose *et al.* 1991; Cantrill 2000) and Australia (Hill 1994; McLoughlin 1996; McLoughlin *et al.* 2002) floras in the prevalence of bennettitalean remains, although the general composition of conifers is similar.

The Early Cretaceous floras from India are also well known from the other basins such as Cauvery, Palar, Mahanadi, Pranhta-Godavari, Rajmahal, Kutch, Rajasthan Satpura and South Rewa (Fig. 1). The Krishna-Godavari Basin represent diverse plant groups, they are primarily dominated by the bennettitaleans. Thus the floras show close similarity with the floras from other pericratonic Early Cretaceous succession such as Cauvery, Palar and Mahanadi. The taxa common to these basins includes *Taeniopteris spatulata* McClelland, *Ptilophyllum acutifolium*, *P. cutchense* (Morris) Bose & Kasat, *Elatocladus plana* (Feistmantel) Seward and *Araucarites cutchense* Feistmantel. The fossil flora from adjoining intracratonic rift basins i.e., Pranhta-Godavari (PG) differs in the dominance of conifers. Except *Ptilophyllum* other bennettitalean genera like *Dictyozamites*, *Otozamites*, *Anomozamites*, and *Pterophyllum* are rare and *Ginkgo* is totally absent from the PG flora. Among the other Early Cretaceous floras of India, the KG flora is closely comparable with the flora of Rajmahal (Banerji 2000). Both these floras are predominated by bennettitalean foliages and share many taxa. The taxa common to both the floras are: *Dictyozamites falcatus*, *D. indicus* Feistmantel, *Otozamites imbricatus*, *Ptilophyllum distans* (Feistmantel) Bose & Kasat, *P. incisum*, *Ptilophyllum acutifolium*, *P. cutchense*, *P. rarinervis* (Feistmantel) Bose & Kasat, *P. tenerrimum*, *Williamsonia blandfordii* Feistmantel, *W. indica* Seward, *W. kakadbhitensis* Pandya & Sukh-Dev and *Cycadolepis indica* Gupta, *Brachyphyllum expansum* (Sternberg) Seward, *Pagiophyllum* cf. *marwarensis* Bose & Sukh-Dev, *Elatocladus confertus* Seward & Sahni, *E. plana*, *E. jabalpurensis* (Feistmantel) Sahni and *E. tenerrimus* (Feistmantel) Sahni. The major difference between these floras is in presence and/or absence of pentoxylaleans, which are common from the Rajmahal.

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APPENDIX 1. — List of the macroflora reported from the Krishana-Godavri Basin.

PTERIDOPHYTES
Cladophlebis medlicottiana (Oldham) Pascoe, 1959
C. polypodioides Brongniart, 1849
Cladophlebis cf. *longipennis* Seward, 1925
Cladophlebis sp.
Gleichenia bosahii (Bose) Pant & Srivastava, 1977
G. nordenskioeldii Heer, 1874
Marattiopsis macrocarpa (Oldham & Morris) Seward & Sahni, 1920
Onychiopsis cf. *psilotoides* (Stopes & Web) Ward, 1905
Todites indicus (Oldham & Morris) Bose & Sah, 1968
Sphenopteris specifica (Feistmantel) Roy, 1968
Sphenopteris sp.

GYMNOSPERMS

PTERIDOSPERMS
Thinnfeldia vemavaramensis (Feistmantel) Chinnappa, Rajanikanth & Rao, 2015
Pachypteris indica (Oldham & Morris) Bose & Roy, 1968

CYCADALEANS
Taeniopteris spatulata (McClelland) Bose & Banerji, 1981
Taeniopteris sp.

BENNETTITALEANS
Anomozamites sp.
Cycadolepis indica Gupta, 1954
Cycadolepis sp.
Dictyozamites falcatus Medlicott & Banford, 1879
D. feistmantelii Bose & Bano, 1978
D. hallei Sahni & Rao, 1933
D. indicus Feistmantel, 1876
D. ommevaramensis Chinnappa, Rajanikanth & Rao, 2014
D. sahnii Gupta & Sharma, 1968
Otozamites acutifolius Feistmantel, 1879
O. bengalensis Schimper, 1870
O. exhislopi Bose, 1974
O. gondwanensis Bose, 1974
O. imbricatus Feistmantel, 1879
O. vemavaramensis Bose & Jain, 1967
Otozamites sp.
Pterophyllum footeanum Feistmantel, 1879
P. incisum Sahni & Rao, 1933
P. kingianum Feistmantel, 1877
Pterophyllum sp.
Ptilophyllum acutifolium (Morris) Bose & Kasat, 1972
P. cutchense (Morris) Bose & Kasat, 1972
P. deodikarii Mahabale & Satyanarayana, 1979

BENNETTITALEANS (continuation)
Ptilophyllum heterophylla Chinnappa, Rajanikanth & Rao, 2014
P. rarinervis (Feistmantel) Bose & Kasat, 1972
P. tenerrimum (Feistmantel) Bose & Kasat, 1972
Ptilophyllum cf. *distans* (Feistmantel) Bose & Kasat, 1972
Ptilophyllum cf. *institacallum* Bose, 1959
Ptilophyllum cf. *amarjolense* Bose, 1953
Ptilophyllum cf. *gladiatum* Bose & Sukh-Dev, 1958
Ptilophyllum cf. *horridum* Roy, 1963
Ptilophyllum cf. *jabalpurense* Jacob & Jacob, 1954
Williamsonia blandfordii Feistmantel, 1876
W. indica Seward, 1917

GINKGOALEANS
Ginkgo crassipes (Feistmantel) Chinnappa, 2016
G. feistmantelii (Bose & Sukh-Dev) Chinnappa, 2016
Ginkgo sp. A
Ginkgo sp.

CONIFERALEANS
Araucarites cutchensis Feistmantel, 1877
A. fibrosa Sukh-Dev & Bose, 1972
A. macropteris Feistmantel, 1877
A. minutus Bose & Maheshwari, 1973
Brachyphyllum expansum (Sternberg) Seward, 1904
B. feistmantelii (Halle) Sahni, 1928
B. regularis Borkar & Chiplonkar, 1973
B. rhombicum Feistmantel, 1879
B. sehoraensis Bose & Maheshwari, 1973
Brachyphyllum sp.
Conites sessilis Sahni, 1928
Conites sp.
Elatocladus confertus Seward & Sahni, 1920
E. jabalpurensis (Feistmantel) Sahni, 1928
E. loyolii Chinnappa, Rajanikanth & Rao, 2014
E. plana (Feistmantel) Seward, 1919
E. tenerrimus (Feistmantel) Sahni, 1928
E. vemavaramensis Pandya Pandya, Srivastava & Sukh-Dev, 1990
Elatocladus sp.
Harrisiophyllum hacketioides Pant, Srivastava & Pant, 1983
Pagiophyllum feistmantelii Halle, 1913
P. gollapallensis Pandya & Sukh-Dev, 1990
Pagiophyllum cf. *grantii* Bose & Banerji, 1984
Pagiophyllum cf. *marwarensis* Bose & Sukh-Dev, 1972
P. ommevaramensis Chinnappa, Rajanikanth & Rao, 2014
Pagiophyllum sp.
Pityospermum godavarianum Chinnappa, Rajanikanth & Rao, 2015
Torreyites constricta (Feistmantel) Seward & Sahni, 1920

Appendix 2. — List of the microflora reported from the Krishana-Godavri Basin.

BRYOPHYTES
Foraminisporis dailyi Dettmann, 1963
F. wonthaggiensis Dettmann, 1963
Coronatispora sp.
Aequitriradites spinulosus Cookson & Dettmann, 1961
Coptospora cauveriana Venkatachala, 1973
Cooksonites variabilis Pocock, 1962
Staplinisporites caminus Pocock, 1962

PTERIDOPHYTES
Alsophyllidites grandis Sah & Jain, 1965
Appendicisporites sellingii Pocock, 1964
Baculatisporites comaumensis Potonié, 1953
B. baculatus Krutzsch, 1959
Biretisporites potoniae Delcourt & Sprumont, 1955
Ceratosporites equalis Cookson & Dettmann, 1958
Cicatricosisporites australiensis Potonié, 1956
C. hughesii Dettmann, 1963
C. lodbrokiae Dettmann, 1963
Cicatricosisporites sp.
Conbaculatisporites densibaculatus Sharma, Jain & Venkatachala, 1977
Concavissimisporites punctatus Pocock, 1964
C. variverrucatus Brenner, 1963
Concavissimisporites sp.
Contignisporites cooksoniae Dettmann, 1963
C. glebulentus Dettmann, 1963
C. multimuratus Dettmann, 1963
Contignisporites sp.
Crybelosporites punctatus Dettmann, 1963
C. striatus Dettmann, 1963
C. stylosus Dettmann, 1963
Crybelosporites sp.
Cyatheacidites tectifera Archangelsky & Gamerro, 1965
Cyathidites asper Dettmann, 1963
C. australis Couper, 1953
C. cutchensis Singh, Srivastava & Roy, 1964
C. jurassicus Kar & Sah, 1970
C. minor Couper, 1953
C. pseudopunctatus Singh, Srivastava & Roy, 1964
C. punctatus Delcourt, Dettmann & Hughes, 1963
C. rajmahalensis Sah & Jain, 1964
C. trilobatus Sah & Jain, 1964
Cyathidites sp.
Deltoidospora diaphana Wilson & Webster, 1946
D. juncta Singh, 1964
Densoisporites microregulatus Brenner, 1963
D. velatus Dettmann, 1963
Dictyophyllidites harrisii Couper, 1958
Gleichiniidites circinidites (Cookson) Dettmann, 1963
G. senonicus Dettmann, 1963
Impardecispora purverulenta (Verbitzkaya) Venkatachala, Kar & Raza, 1969
I. trireticulosa Venkatachala, Kar & Raza, 1969
I. tribotrys (Dettmann) Venkatachala, Kar & Raza, 1969

PTERIDOPHYTES (CONTINUATION)
Impardecispora sp.
Ischyosporites punctatus Cookson & Dettmann, 1958
Ischyosporites sp.
Klukisporites foveolatus Pocock, 1965
K. scaberis Dettmann, 1963
Laevigataletes sp.
Laevigatazonaletes sp.
Laevigatimonoletes sp.
Laevigatisporites sp.
Leptolepidites major Couper, 1953
L. verrucatus Couper, 1953
Leptolepidites sp.
Liratosporites sp.
Lycopodiumsporites crassimacerius Hedlund, 1966
L. eminulus Dettmann, 1963
L. regulatus Semenova, 1970
L. reticulum Venkatachala & Kar, 1968
L. reticulumsporites Dettmann, 1963
Lycopodiumsporites sp.
Matonisporites sp.
Murospora florida Pocock, 1961
Neoraistrickia truncatus Potonié, 1956
Ornamentifera granulosa Sharma, Jain & Venkatachala, 1977
Ornamentifera sp.
Osmundacidites wellmanii Couper, 1953
Plicifera senonicus (Ross) Bolkhovitina, 1966
Polycingulatisporites reduncus Playford & Dettmann, 1965
Reticulatazonalesporites sp.
Reticulatisporites sp.
Retitriletes austroclavatidites (Cookson) Krutzsch, 1963
R. circolumenus Backhouse, 1978
R. eminulus Srivastava, 1975
Sestrosporites pseudoalveolatus Dettmann, 1963
Striatella balmei Filatoff & Price, 1988
Taurocusporites segmentatus Stover, 1962
Thymospora sp.
Todisporites minor Couper, 1953
Triletes verrucosus Faddeeva, 1965
Triletes sp.

APPENDIX 2 (continuation). — List of the microflora reported from the Krishana-Godavri Basin.

GYMNOSPERMS
Abietineaepollenites ellipticus Kar & Sah, 1970
A. robustus Kar & Sah, 1970
Alisporites grandis Dettmann, 1963
Alisporites sp.
Araucariacites australis (Cookson, 1947) Cooper, 1953
A. indicus Sukh-Dev, 1961
Callialasporites dampieri Sukh Dev, 1961
C. monoalasporus Sukh Dev, 1961
C. segmentatus Srivastava, 1963
C. triletus Singh, Srivastava et Roy, 1964
C. trilobatus Sukh Dev, 1961
Callialasporites sp.
Cedripites cretaceus Pocock, 1962
C. nudis Kar & Sah, 1970
Classopollis classoides Fensome, 1983
C. torosus Burger, 1965
Entylissa sp.
Florinites sp.
Ginkgocycadophytus srivastavae Kar & Sah, 1970
G. nitidus Venkatachala, 1969
Granuloperculatipollis flavatus Kar, 1970
G. subcircularis Kar & Sah, 1970
G. triletus Kar & Sah, 1970
Indusiisporites microsaccatus Kar & Sah, 1970
Laricoidites indicus Singh, Srivastava & Roy, 1964
Microcachrydites antarcticus Couper, 1953
Pityosporites sp.
Platysaccus sp.
Podocarpidites alareticulosus Sah & Jain, 1965
P. cristiexinus Sah & Jain, 1965
P. ellipticus Cookson, 1947
P. grandis Sah, 1965
P. multisimus (Bolkhovitina) Pocock. Venkatachala, Kar & Raza, 1969
P. rarus Singh, Srivastava & Roy, 1964
P. typicus Sah, 1965
Podocarpidites sp.
Podosporites raoi Singh, Srivastava & Roy, 1964
P. tripakshii Rao, 1943
Podosporites sp.

ANGIOSPERMS
Asteropollis asteroides Hedlund & Norris, 1968
Clavatipollenites hughesii Couper, 1958
Clavatricolporites leticiae Leidelmeyer, 1966
Liliacidites reticulatus Doyle, 1975
Polybrevicolpites sp.
Polycolpites sp.
Racemonocolpites facilis González-Guzmán. 1967
R. ramonus González-Guzmán. 1967
Rousea georgensis Dettmann, 1973
Spinizonocolpites echinatus Muller, 1968
Tricolpites georgensis (Brenner) Dettmann, 1973
Tubulifloridites lilleie (Couper) Farabee & Canright, 1986
Turonipollis helmegii Van Ameron, 1975

INCERTAE SEDIS
Apiculatasporites sp.
Apiculatimonoletes sp.
Apicultaletes sp.
Bhujiasporites sp.
Complexiopollis complicatus Góczán, 1964
Coniatisporites telata Singh, 1972
Dictyotosporites complex Cookson & Dettmann, 1958
Dictyotosporites speciosus Cookson & Dettmann 1958
Erdtmannipollis sp.
Odontochitina operculata Deflandre & Cookson, 1955
Periplecosporites sp.
Ramanujamiaspora reticulata Ramanujam, 1957
Regulatisporites sp.
Setosisporites sp.
Singhipollis rudis Kar & Sah, 1970
Singhipollis triletus Singh, Srivastava & Roy, 1964
Striatotuberculatisporites sp.