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# Some aspects of Palaeozoic pteridophytes of India: A critical reappraisal

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## ABSTRACT

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The present paper deals with spatial and temporal distribution of pteridophytic megafossils within Palaeozoic plant bearing horizons of India. An attempt has been made to describe the pteridophytic assemblages in various strata of different ages, dynamism of the relative dominance pattern of various types of pteridophytes within each assemblage vis-à-vis the environment they lived in. Critical discussion has been done regarding increasing diversity of Palaeozoic pteridophytic taxa, taxonomic riddles, plant architecture, ecological analysis and phylogenetic implications. Special attention has been given to the floristic regionalism of Lower Carboniferous flora of India in reference to the world palaeophytogeography and occurrence of admixture of Cathaysian, Euramerian and Gondwana pteridophytic elements in palaeoecotone zone near the northwestern boundary of Indian Gondwana Plate.

**Key-words**—Lycopods, Sphenopsids, Pteridophylls, Extra-Peninsular and Peninsular, Pre-Gondwana, Lower Gondwana.

## भारत के पुराजीवी टेरिडोफायटों के कुछ पहलू : एक आलोचनात्मक पुनर्मूल्यांकन

प्रदीप चंद्र श्रीवास्तव

## सारांश

वर्तमान शोध–पत्र भारत की पुराजीवी वनस्पति दिक्मान संस्तर–स्थिति में टेरिडोफायटिक गुरुपादपाश्म का स्थानिक एवं कालगत वितरण प्रस्तुत करता है। टेरिडोफायटों के सापेक्षिक प्रमुखता प्रारुप के गतिवाद प्रत्येक समुच्चय की तुलना में जिस पर्यावरण में वे विद्यमान थे, विभिन्न कालों के विभिन्न स्तरी में टेरिडोफायटी समुच्चयों को वर्णित करने का प्रयास किया है। पुराजीवी टेरिडोफायटी वर्गक, वर्गिकी प्रचालनी, वनस्पति स्थापत्यकला, पारिस्थितिक विश्लेषण और जातिवृत्तीय युगपत अंतर्वृद्धियों की बढ़ती विविधता के संबंध में आलोचनात्मक विवेचन किया गया है। भारत की निम्न कार्बोनीफेरस वनस्पतिजात की वनस्पति प्रादेशिकता का विशेष ध्यान रखते हुए विश्व पुरापादपभूगोल तथा कैथेसियन, यूरेमीरियन तथा भारतीय गोंडवाना पट्टिका को उत्तरपश्चिमी परिसीमा के समीप यूरेसंक्रमिका प्रदेश में गोंडवाना टेरिडोफायटी तत्वों के अधिमिश्रण की प्राप्ति को समझने का प्रयास है।

**संकेत–शब्द**—लायकोपॉड्स, स्फेनोप्सिड्स, पर्णाग पत्र, अतिरिक्त–प्रायद्वीपीय तथा प्रायद्वीपीय, गोंडवाना–पूर्व, निम्न गोंडवाना।

## INTRODUCTION

THREE geographical and geological divisions of Indian subcontinent have been recognized viz.; extra-Peninsular Himalayan region, Peninsular region and the Indo-Gangetic Plain (see Krishnan, 1949; Pascoe, 1950; Wadia, 1975). In both Peninsular and extra-Peninsular parts of India the base of the Palaeozoic rocks is formed by the Cambrian rocks. The strata from Ordovician to Middle Carboniferous ages are absent in the Peninsular part while the full succession of fossiliferous strata from Cambrian to Quaternary ages are found in the extra-Peninsular Himalayan belt particularly in the northern zone which is sometimes called as the Tibetan flank. In the extra-Peninsular region Palaeozoic mega-plant fossils which have



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been attributed to plants are known from Silurian and younger strata whereas in the Peninsular region the earliest plant megafossils are of the Lower Gondwana age. In extra-Peninsular part, the Pre-Gondwana exposures (Silurian-Middle Carboniferous) are known only from Panjab-Kashmir Himalaya which is famous for its fossiliferous formations. Because of its favourable climate, easy accessibility and availability of complete stratigraphical record, this area attracted both geologists and palaeobotanists. The earliest pteridophytic remains in Indian subcontinent were reported from the Silurian and Devonian strata of this region. Rich assemblages of Lower Carboniferous fossils have also been explored from this region while Lower Gondwana pteridophytes are known from both extra-Peninsular and Peninsular parts of India.

## PRE-GONDWANA PTERIDOPHYTIC ASSEMBLAGES

### Silurian and Devonian Pteridophytes

A retrospection of Indian Palaeozoic pteridophytes reveals that Silurian and Devonian pteridophytes have been reported from the extra-Peninsular Himalayan region lying between the basins of Indus River in the west and the Sutlej River in the east. From the Silurian strata of Po Series of Spiti in Himachal Pradesh fragmentary impressions of *Psilophyton*-like and *Hostimella*-like axes assignable to Psilophytales were reported by Sahni (1953) on the basis of their spiny and smooth forms, respectively. Similarly two types of fragmentary axes are also reported from Devonian strata of Kotsu Hill and Diuth Spur of Aishmuqam Formation in Kashmir Himalaya, viz. ?*Taeniocrada* and *Protolepidodendron* by Singh *et al*. (1982).

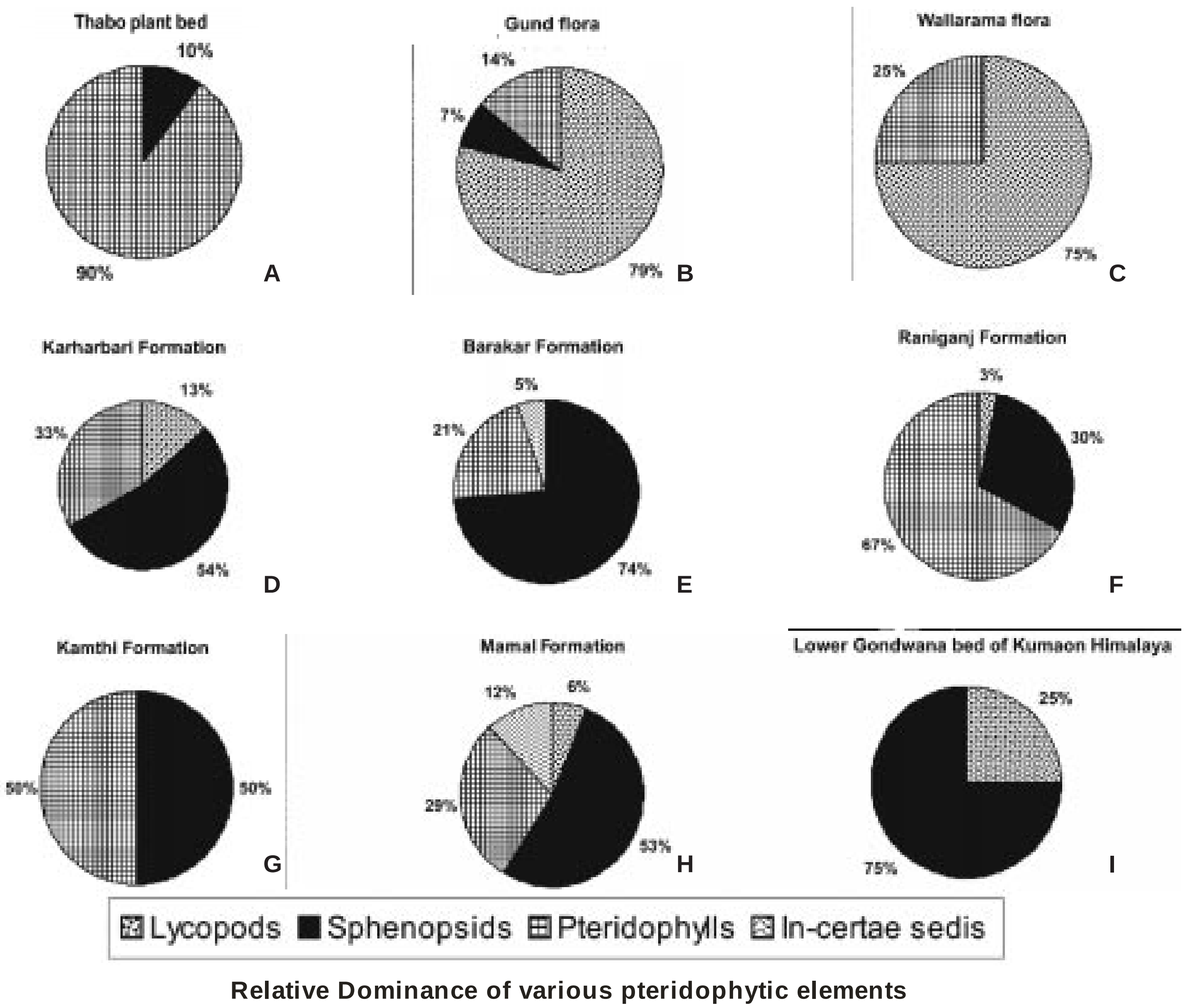


Fig. 1—A.-I. Pie graphs showing relative dominance of various pteridophytic elements in different Lower Carboniferous and Lower Gondwana Plant beds/floras and formations of India. A. Thabo plant bed, B. Gund flora, C. Wallarama flora, D. Karharbari Formation, E. Barakar Formation, F. Raniganj Formation, G. Kamthi Formation, H. Mamal Formation, I. Blaini Infrakrol Formation

However, no land plant characters like stomatiferous cuticles, vasculature (xylem) or cutinized spores have been obtained from the fossils of these localities. Harris (see Sahni, 1953) and Pant (1978) doubted the nature of so called vascular plant remains of Spiti fossils. Maithy *et al*. (1998) opined that these could be remains of sponge, *Protospongia concia* Rigby & Harris. The Ordovician age assigned to these strata by Mehrotra *et al*. (see in Maithy *et al*., 1998) itself casts doubts on vascular plant nature of these fossils.

**Early Carboniferous Pteridophytes**

Rich assemblages of Lower Carboniferous pteridophylls and lycopods have been reported from four formations and beds at three localities. (i) The Thabo Plant Bed of Po Series of Spiti, Himachal Pradesh (Gothan & Sahni, 1937; Høeg *et al*., 1955); (ii) Gund Formation in Pir Panjal Range (Pal, 1978; Pal & Chaloner, 1979; Singh *et al*., 1982), (iii) Syringothyris Formation (Kumar *et al*., 1987) and Fenestella Formation Stratum A (Pal, 1978) and Wallrama bed Stratum C of Liddar Valley in Kashmir Himalayas (Singh *et al*., 1982; Pant & Srivastava, 1995).

(i) *Thabo Plant Bed of Po Series, Spiti, Himachal Pradesh*—From Thabo plant bed of Himachal Pradesh pteridophylls like *Sphenopteridium*? *furcillatum*, *Sphenopteris* sp. and *Rhacopteris ovata* were reported by Gothan and Sahni, 1937. Later, Høeg *et al*. (1955) described sphenopsid like *Asterophyllites* sp. and sterile pteridophylls like ?*Rhodea* sp., *Rhacopteris ovata*, *R. inequilatera*, *Rhacopteris* sp. a and *Rhacopteris* sp. b., ?*Adiantites* sp. a and ?*Adiantites* sp. b. from the same locality. On the basis of taxonomic species diversity there are 90% pteridophylls and only 10% sphenopsids (Fig. 1A).

In view of the identification of *Rhacopteris ovata* (McCoy) Walkom, among the fossils of basal stage (Thabo) of Po Series, Pascoe (1959) regarded it to be homotaxial with the uppermost stage of Kuttung Series of Australia. The age of this basal stage of Po Series was estimated to be older than Middle Carboniferous since Sussmilch, 1935 regarded the Kuttung series to be of Middle Carboniferous age (see Pascoe, 1959, p. 740). On the contrary David, 1832 pointed out that even though the Kuttung bed belonged to Middle

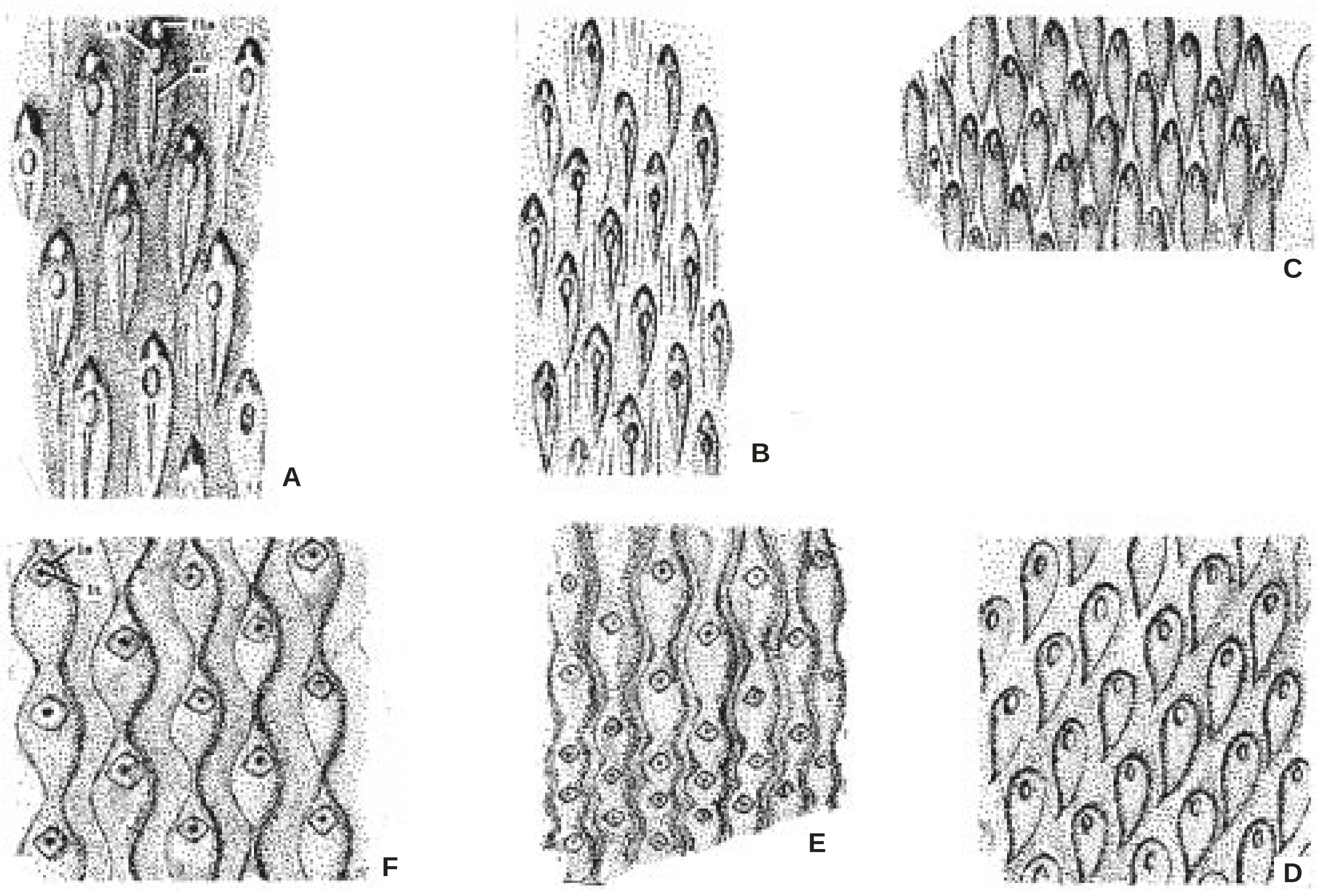


Fig. 2—A., B. *Pseudobumbudendron chaloneri* Pant & Srivastava showing false leaf scar(fls), infrafoliar bladder (ib) and median ridge (mr) in each leaf cushion. C., D. *Pseudobumbudendron meyenii* Pant & Srivastava showing false leaf scar and infrafoliar bladder in each leaf cushion. E., F. *Spondylodendron wallaramensis* Pant & Srivastava showing vertically fused leaf cushions, true leaf scar with leaf trace in each leaf cushion and alternating zones of large and small leaf cushions reflecting seasonal fluctuation in Fig. E. All x 2 (A.-F. After Pant & Srivastava, 1995).

Carboniferous its Rhacopteris flora has been referred to Dinantian by Seward *et al.* (see in Gregory & Barrett, 1931, p.125). Later a Naumurian to Westphalian age was assigned by Pal (1978) to the Thabo plant bed on the basis of its reported floral assemblage which commonly showed leaves of *Rhacopteris* especially *R. ovata* and the complete absence of lepidophytes. However, Khanna and Tewari (1983) made a palynological study of a stratum lying about more than 303 m above the plant bearing horizon (Thabo member) and identified twentyone genera of miospores. On the basis of this miofloral assemblage the above authors assigned a Lower Carboniferous age to the upper stratigraphic levels of the Po Formation.

(ii) *Gund Formation in Pir Panjal Range*—Pal (1978) reported some plant fossils from the so called unfossiliferous "Passage bed" of Middlemiss, sandwiched between marine deposits and regarded them as a distinct lithostratigraphical unit accumulated in fresh water and therefore, called this sequence as Gund Formation. This Formation is underlain by Syringothyris Limestone and is overlain by Fenestella shale. This Formation is best developed in Charil-Nawagaon Section, north of Banihal in Pir Panjal Range and its homotaxial beds are also known from Liwar-Kotsu Section of Liddar Valley area of Kashmir. On the basis of taxonomic species diversity there are 79% lycopods, 14% pteridophylls and 7% sphenopsids (Fig.1B). Following plants were described from the localities in the Pir Panjal Range-

Lycopods

- *Archaeosigillaria* sp.
- *Lepidosigillaria quadrata* Danze Corsin
- *Lepidodendropsis fenestrata* Jong. & Koop.
- *L. sigillarioides* Jongmans *et al.*
- *L. pranabii* Pal
- *L. gundensis* Pal
- *Cyclostigma indica* Pal

Sphenopsids

- *Archaeocalamites radiatus* (Brong.) Stur

Pteridophylls

- *Rhacopteris* cf. *circularis* Walton
- *Rhodea tenuis* Gothan

Pal (1978) described only two plants, viz. *Archaeocalamites radiatus* (Brong.) Stur and *Cyclostigma ungeri* Jongmans *et al.* from the homotaxial bed in Liddar Valley. Pal (1978) and Pal and Chaloner (1979) pointed out the similarities of the floristic assemblage found at Gund Formation with the Early Carboniferous Lepidodendropsis flora from Europe, Pocono Formation in U.S.A, Peru, Ghana, Morocco, eastern Sahara, Egypt, Syria, China, western Malaysia and North America. They discussed the significance of palaeogeography of the Himalayan area in relation to the floral migration or connection and also stressed the peculiarity of lithostratigraphic position of Gund Formation in relation to its precise age as Visean to Tournaisian. Pal (1978) believed the Gund flora to be older than the Thabo flora. The occurrence of *Lepidosigillaria quadrata* in the Gund Formation, was confirmed by Singh *et al*. (1982). They also reported *Archaeosigillaria minuta, Lepidodendropsis peruviana*, *Cyclostigma* cf. *pacifica* with some branched axes and assigned *Rhacopteris circularis* of Pal and Chaloner to *R. ovata*.

(iii) *Syringothyris & Fenestella formations in Liddar Valley of Kashmir Himalaya*—The strata of Syringothyris limestone and Fenestella shale are well developed in Liddar Valley area where Middlemiss (1910) reported a third intervening "passage bed" between the two. On the contrary Kumar *et al*. (1980, 1987) and Singh *et al*. (1982) recognized only two kinds of strata and regarded them as formations. They thought Syringothyris Limestone as consisting of stages A, B & C which are conformably overlain by four stages A, B, C & D of the Fenestella Shale. These authors regarded the A stage of Fenestella Shale as representing the Passage bed of Middlemiss and Gund Formation of Pal (1978) and Pal and Chaloner (1979).

The C stage of Syringothyris Formation, which is exposed at Kotsu Hill is regarded to be of Visean age and in its lower part Kumar *et al*. (1980, 1987) reported the occurrence of *Sublepidodendron* (Nathorst) Hirmer (without any figure and photograph) while Singh *et al.* (1982) described and figured *Palmatopteris* cf. *furcata* Potonie from the upper part. In the four stages of Fenestella Formation, stages A & C are believed to be of Middle Visean to Bashkirian age and these contain plant fossils. The fossiliferous exposures of "A" stage have been reported at road section near Kotsu, Gaos & Manigam while a single fossiliferous exposure of "C" stage at Wallarama

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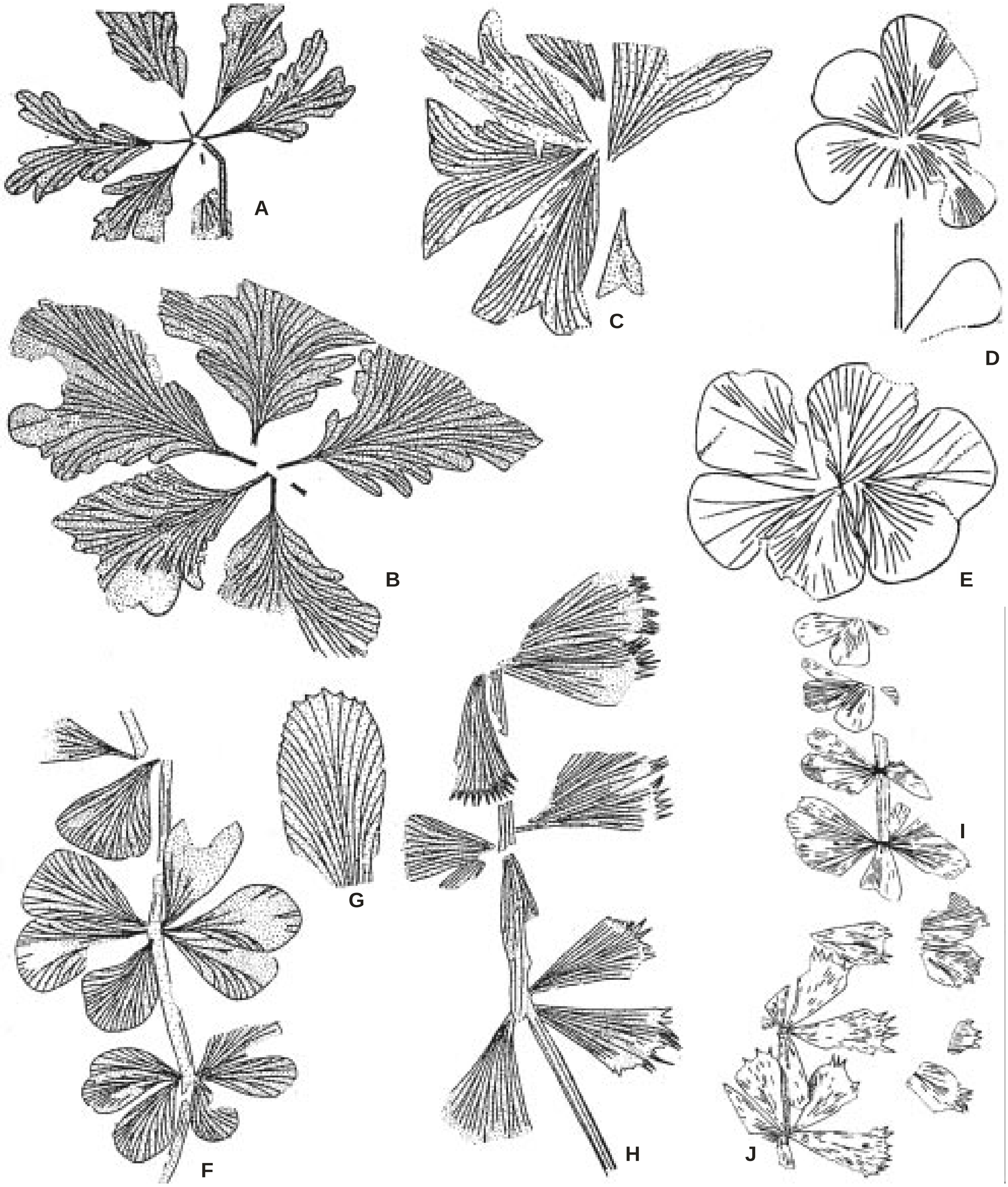
Fig. 3—A., B. *Sphenophyllum lobifolium* Pant & Srivastava; C. *Sphenophyllum utkalensis* Pant *et al.*; D., E. *Sphenophyllum churulianum* Srivastava & Rigby; F. *Sphenophyllum thonii* var. *minor* Sterzel; G. *Sphenophyllum thonii* var. *waltonii* Pant *et al.*; H. *Sphenophyllum thonii* var. *archangelskyii* Pant *et al.*; I *Sphenophyllum gondwanensis* Singh *et al.* A.-B. Symmetrical whorl with petiolate leaves having lobed margins and apical notch. A. x 1, B. Specimen No. 14283b of the D.D. Pant Collection x 1. C. An incomplete symmetrical whorl of leaves with smooth margins and apical notch. x 1.5. D, A symmetrical whorl of smooth margined large leaves, fragmentary axis and leaf indicating position of second whorl. Specimen No. 14447 of the D.D. Pant Collection, A.U. x 1. E. A symmetrical whorl of smooth margined large leaves. Specimen No. 14459 of the D.D. Pant Collection, A.U. x 1. F. A twig showing three symmetrical whorls of smooth margined small leaves. x 1. G. A single leaf with crenulations on distal leaf margin. x 3.7. H. A shoot showing three symmetrical whorls of cuneate leaves with deeply dentate distal margins. x 1. I A fragmentary axis showing six whorls of leaves with smooth margins in upper whorls and dentate distal margins in lower whorls. x 2. J. A fragmentary shoot with symmetrical whorl of leaves with dentate distal margins. x 2 (A. After Pant & Srivastava, 1995; C. After Pant *et al.*, 1985. F.-G. After Pant *et al.* 1984; I, J. After Singh *et al.*, 1987).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spur was first recorded by Sharma and Sehgal (1976). Singh *et al.* (1982) described the following plants from various localities of A and C stages-

Lycopods

*Archaeosigillaria minuta* Lejal
*Lepidosigillaria* cf. *quadrata* Danzé Corsin
*Lepidodendropsis* cf. *peruviana* (Gothan) Jongmans
*L. fenestrata* Jongmans & Koopmans
*Cyclostigma* cf. *pacifica* (Steinmann) Jongmans

Pteridophylls

*Rhacopteris ovata* (McCoy) Walkom
*Triphyllopteris lescuriana* (Meek) Lesquereux
*Rhodea* cf. *subpetiolata* (Potonie) Gothan

Pant and Srivastava (1995) concentrated on Wallarama bed and described following taxa:

Lycopod

*Pseudobumbudendron chaloneri* Pant & Srivastava
*P. meyenii* Pant & Srivastava
*Spondylodendron wallaramensis* Pant & Srivastava
*Lepidodendropsis liddarensis* Pant & Srivastava
*Archaeosigillaria subcostata* Danzé Corsin
*Lepidosigillaria quadrata* Danzé Corsin
*Knorria* Sternburg
*Aspidiaria* Presl

Pteridophylls

*Nothorhacopteris argentinica* (Geinitz) Archangelsky
*Triphyllopteris lescuriana* (Meek) Lesquereux

On the basis of taxonomic species diversity Wallarama bed has 75% lycopods and 25% pteridophylls (Fig. 1C).

**Paradox of the Early Carboniferous flora (Uniformity vs. diversity)**

A retrospection of Lower Carboniferous phytogeography indicates that the authors dealing with this subject hold two almost paradoxical views. Seward (1933) and Jongmans (1952, 1954) opined that during Lower Carboniferous time a uniform Lepidodendropsis flora/Lepidodendropsis-Rhacopteris flora prevailed all over the world. The common elements of this flora were *Lepidodendropsis*, *Lepidosigillaria*, *Archaeosigillaria*, *Cyclostigma*, *Rhacopteris* and *Triphyllopteris*. On the contrary Rigby (1969; see in Pant & Srivastava, 1995), Vakharameev *et al.* (1970), Chaloner and Lacey (1973), Chaloner and Meyen (1973) and Archangelsky (1981, 1983) believe that the flora of that time was heterogeneous and characterized by differences between the floras of various regions particularly of Angara, Gondwana and the intervening parts. Chaloner and Lacey (1973) and also Chaloner and Meyen (1973) pointed out that the flora of Angaran region covering U.S.S.R., Tuva and Mongolia was distinct and included forms like *Lophiodendron*, *Tomiodendron*, *Lepidodendropsis*, *Sublepidodendron*, *Bothrodendron*, *Cardiopteris*, *Angaropteridium*, *Chacassopteris* and *Archaeocalamites*. Vakhrameev *et al.* recognized a distinct floristic province "Kazakhstan lying between Angara and Euramerian areas east of the Urals. It was characterized by the forms like *Archaeocalamites radiatus*, *Lepidodendron veltheimii*, *L. spitzbergensis*, *Lepidodendropsis*, *Caeonodendron*, *Cardioneura* and *Angaropteridium*. This flora is best developed in Karaganda Basin (Radczenko, 1961; see in Pant & Srivastava, 1995). Regarding the Godwana region, Archangelsky (1981, 1983) believed in wider or narrower endemicity of some floristic elements like, *Fedekurtzia* and *Nothorhacopteris*. Among these *Fedekurtzia* includes forms of *Rhacopteris argentinii* and *Triphyllopteris collumbiana* while *Nothorhacopteris* includes those forms of *Rhacopteris* spp. which show interstitial fibres. However, Pant (1996) regarded separation of *Rhacopteris* from Laurasian regions from *Nothorhacopteris* from Gondwana regions on the basis of finding of interstitial fibres in the latter, as untenable. He pointed out that in leaves of *Cordaites* fibres are seen on one face but not on the other (Pant & Verma, 1964). All the same in other plant groups, leaves with or without interstitial fibres are typically assigned to the same genus, e.g. *Glossopteris* (Pant, 1958), *Rhabdotaenia* (Pant & Verma, 1963) and *Noeggerathiopsis* (Pant & Verma, 1964).

The finding of *Tomiodendron varium* and *Ursodendron wijkianum* (the endemic genera of Angara) from the Lower Carboniferous of the Air Mountains of Nigeria, a place beyond the territory of the Angara and Kazakhstan provinces by Rouvre (1984) tends to support the view of uniformity. Further the occurrence of Angaran characteristic like infrafoliar bladder (known in Angaran genera *Tomiodendron* and *Lophiodendron*) in each leaf cushion of *Bumbudendron* in Argentina (Archangelsky *et al.*, 1981) and *Pseudobumbudendron* in India and Egypt (Pant & Srivastava, 1995) may also strengthen the view of uniformity of Lower Carboniferous flora. Though Archangelsky *et al.* (1981) have attributed occurrence of infrafoliar bladder in unrelated plants of two far flung areas to the homoplasy or parallel evolution but it is difficult to believe in view of absence of any marked physical barrier between

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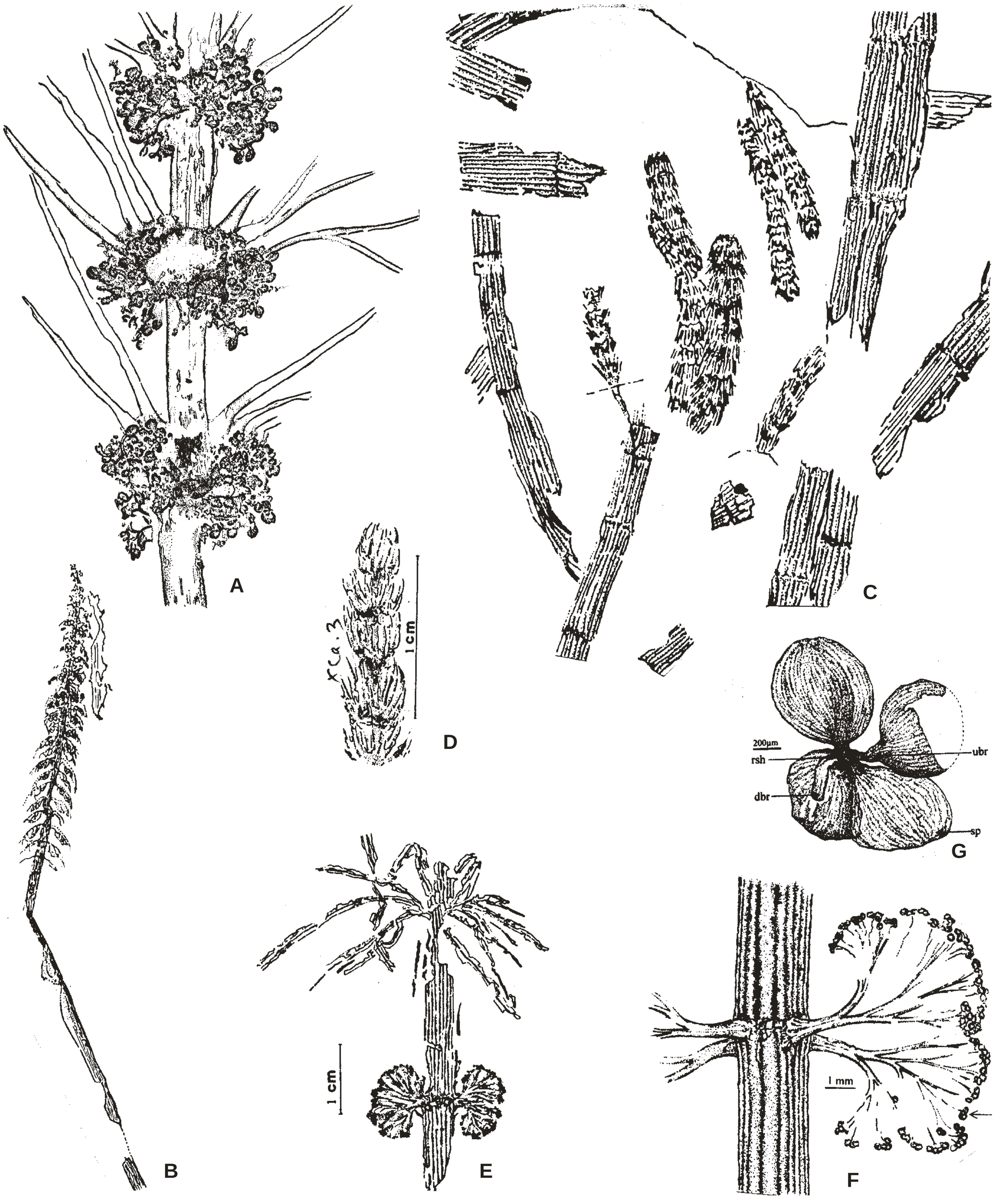
Fig. 4—A. *Giridia indica* Pant *et al.* B. *Sharmastachys pendulata* Banerjee & D'Rozario C., D. *Rajmahaliastachys elongata* Banerjee & D'Rozario. E.-G. *Tulsidabaria indica* Banerjee & D'Rozario A. twing showing whorls of bracts, forked sporangiophores and terminal sporangia. x 1.5. B. An elongated cone with whorls of sporangiophores with abaxial pendant sporangia. x 0.6. C., D. Detached and attached cones showing whorled bracts on nodes. C. x 1.5 ., D. x 2.8 E. Showing whorls of leaves and sporangiophores on successive nodes. x 1.2. F. Branching pattern of sporangiophores with ultimate branches bearing terminal sporangia. x 5. G. Distal branch of sporangiophore bearing 4 ultimate branches proximally fused to form shield and each distally terminating in single sporangium. x 25 (A. After Pant *et al.*, 1981; B.-D. After Banerjee & Rozario, 1999; E.-G. After Banerjee *et al.*, 2004).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these localities. Pant and Srivastava (1995) believed in the over all uniformity in the flora of Lower Carboniferous time along with the possibility of some local ecotypic differences in a flora which inhabited a vast worldwide territory.

## LOWER GONDWANA PTERIDOPHYTIC ASSEMBLAGES

The beds above the Lower Carboniferous rocks in Gondwanaland are characterized by a sudden large-scale extinction of plants due to wide spread glaciation. All the parts of the landmass retain undoubted evidence of the glaciation in the form of a basal striated boulder bed and overlying thick deposits of glacial conglomerate. On the Indian Plate the basal boulder beds are widely distributed, e.g. Kathwai in Salt Range of Pakistan, Hazra in Kashmir, Blaini in Shimla (Himachal Pradesh) Kumaon Himalaya, Bap in Rajasthan, Umaria in Madhya Pradesh and Talchir in Orissa. Only one pteridophyte, i.e. *Schizoneura* is reported by Sussmilch (1922) as interbedded with glacial tillites at Bacchus Marsh in Victoria, Australia but no such fossil is reported from the tillites in India. Gondwana glaciation is believed to have ranged from the Upper Carboniferous to the Upper Permian in different parts of the Gondwanaland. The ice age is thus estimated to have lasted for about 50 m.y. (Ahmad, 1987). In India, the glaciation is believed to have begun during the Late Carboniferous in Kashmir based on the occurrence of *Fenestella* in the marine and *Rhacopteris* in the terrestrial sediments underlying the tillite. Marine fossils found by Sinor in 1921 (see Sinor, 1923 near Umaria in central India indicate a similar or slightly younger age for the glaciation.

### Lower Gondwana pteridophytes from Peninsular India

In various stages of Lower Gondwana strata of Peninsular India extremely rich assemblage of pteridophytes has been reported as a result of the contribution of Royle (1833-1839) and Feistmantel (1876a, b; 1879; 1880; 1881), Surange (1966), Pant (1978, 1996), Pant and Mehra (1963), Pant and Nautiyal (1967), Pant and Kidwai (1968), Pant and Misra (1976, 1977); Pant *et al.* (1982), Pant and Srivastava (1989), Srivastava and Pant (2002), Srivastava (2004, also see Khare *et al.*, 2004), Pant *et al.* (1981, 1982), Maithy (1974a, b; 1978), Srivastava and

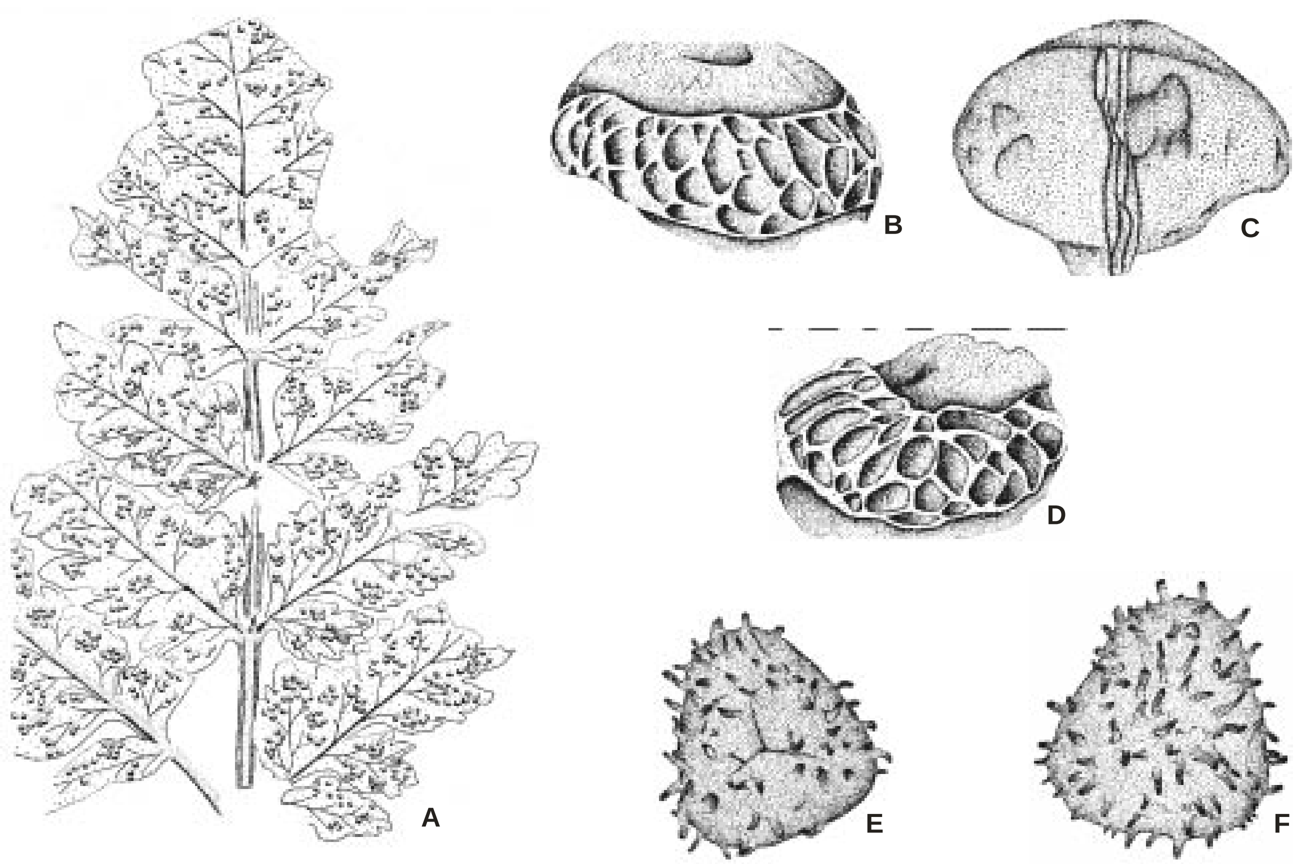


Fig. 5—A.-F. *Damudopteris polymorpha* Pant & Khare. A. Upper surface of fertile frond showing bipinnate nature with open forked veins and exinduciate groups of sporangia. x 1.5. B.–D. Sporangia showing multiseriate annulus on convex faces and reverse side. x 70. E., F. Proximal and distal faces of spores. x 700 (After Pant & Khare, 1974).

Rigby (1983), Singh *et al.* (1987), Maheshwari and Srivastava (1987), Singh and Chandra (1999), Banerjee and D'Rozario (1996a, b, 1999), Banerjee *et al.* (2004). These include various species of sphenopsids, like *Lelstotheca* (4 spp.), *Paracalamites* sp., *Phyllotheca* (7 spp.), *Raniganjia* (2 spp.) *Schizoneura* (3 spp.), *Sphenophyllum* (7 spp.), *Barakaria dichotoma*, *Giridia indica*, *Sharmastachys pendulata*, *Rajmahaliastachys elongata* and *Tulsidabaria indica*, lycopod like *Cyclodendron* (2 spp.) and fertile and sterile pteridophylls, viz. *Alethopteris* (2 spp.), *Botrychiopsis* (2 spp.), *Damudopteris* (2 spp.) *Damudosorus* (2 spp.), *Dichotomopteris* (6 spp.), *Leleopteris* (2 spp.), *Merianopteris major*, *Neomariopteris* (6 spp.), *Pantopteris gracilis*, *Pecopteris phegopteroides*, *Sphenopteris* (4 spp.), *Trithecopteris gondwanensis*, *Asansolia phegopteroides*, *Santhalia bansloensis*, *Palasthalia indica*, *Liknopetalon rajmahalensis*, etc. Lower Gondwana strata of extra-Peninsular India have yielded *Sphenophyllum* (2 spp.), *Lobatannularia* (3 spp.), *Pecopteris* (4 spp.), *Dizeugotheca*? *falcata*, etc. Stratigraphic succession of these pteridophytes is given here:

(i) *Talchir Formation*—The earliest post-glaciated fossiliferous strata of Upper Carboniferous/Lower Permian age in India are found in the Talchir Series. The time during which the Talchir sediments were being deposited is divided into a lower Talchir and an upper Karharbari Formation.

The rocks of Talchir Formation are found widely scattered in Damodar Valley West Bengal, Rajmahal Hills, Son Mahanadi Valley, Satpura Hills and Rajasthan in Peninsular India. Deposited immediately after glaciation, beds of this Stage do not contain any coal. The flora was depauperate and lived in an unfavourably cold climate. Pteridophytes are so far unrepresented in this stratum in India, though several megaspore taxa of lycopod affinity are known from the Talchir Formation sediments. Megafossil *Schizoneura* is found enterbedded in homotaxial tillites in Australia (Sussmilch, 1922) as stated earlier.

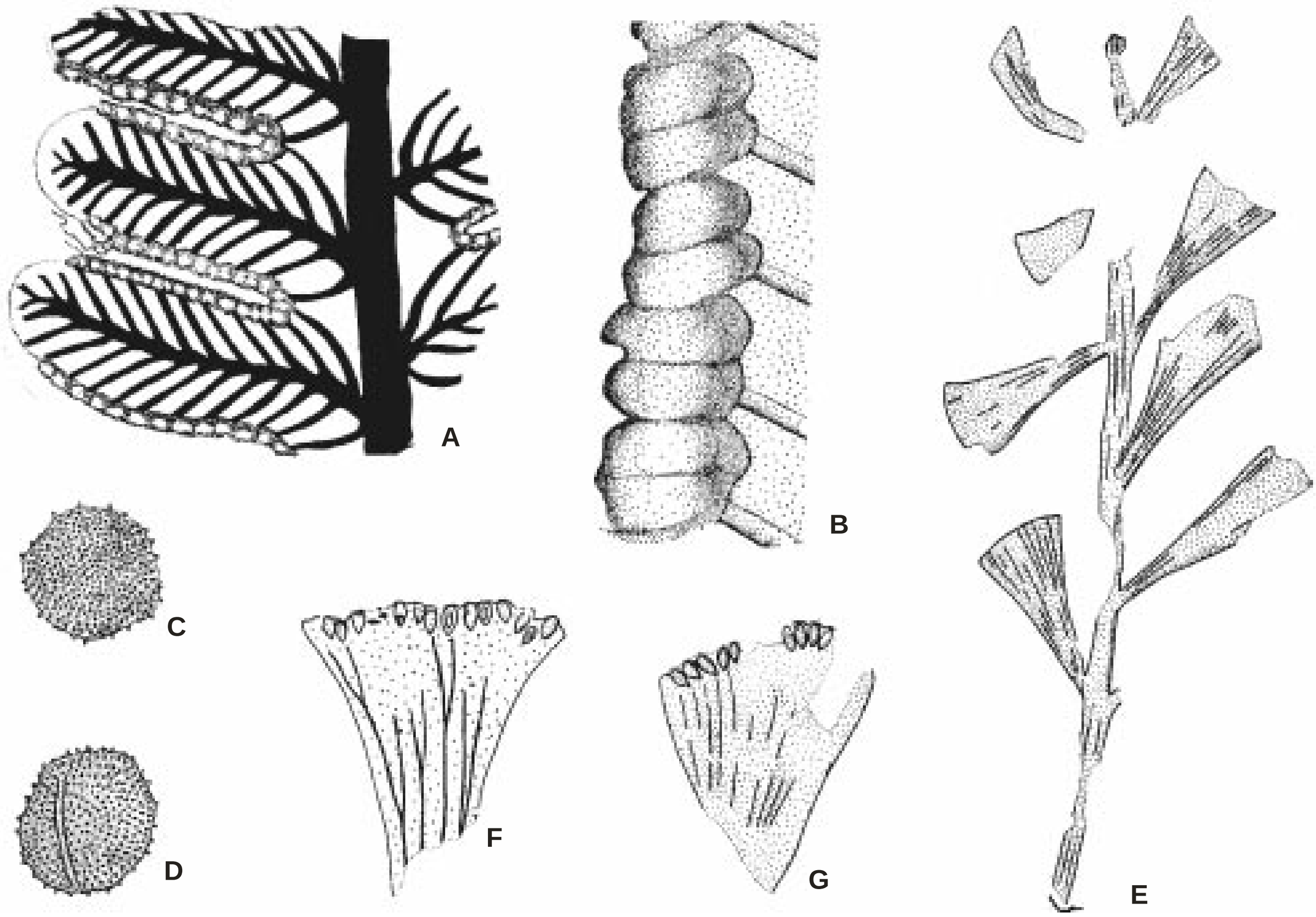


Fig. 6—A-D. *Asansolia phegopteroides* Pant & Misra E.-G. *Liknopetalon rajmahalensis* Srivastava & Pant. A. Pecopterid pinnules showing submarginal row of synangia. x 7. B. Row of tetrasporangiate contiguous synangia. x 35. C., D. Distal and Proximal views of spores. x 700. E. Axis bearing cuneate vegetative laminae in opposite and decussate arrangement. x 1. F., G. Fragments of fertile laminae with submarginal row of ovate to obovate sessile sporangia along the distal margin. F. x 2.8, G. x 1.4 (A.-D. After Pant & Misra, 1976; E.-G. After, Srivastava & Pant, 2002).

(ii) *Karharbari Formation*—The Karharbari Formation follows the Talchir Formation. Climatic condition during the Karharbari Formation in peninsular India favoured the development of diverse floras and extensive thick peat accumulation. On the basis of floral evidence climatic conditions are interpreted to have been milder and warmer than during the Talchir Formation. Typical Karharbari floras are found in the Giridih Coalfield in Bihar but homotaxial beds occur above Talchir strata in West Bengal, Orissa and Madhya Pradesh extending southward to Andhra Pradesh and westward to Maharashtra and Rajasthan. The Gangamopteris bed of Kashmir Himalaya is also equated with the Karharbari Formation.

Compared to Talchir, there is a significant increase in the generic and specific diversity during Karharbari. The lycopods are represented only by two forms of a single genus *Cyclodendron*. Sphenopsids are dominant among the pteridophytic taxa and include three genera *Schizoneura* (2 spp.), *Phyllotheca* (6 spp.), and its unique fructification *Giridia*. Abundance of lycopod megaspore taxa indicates more diversity of lycopods.

The lycophytes and the species of *Gondwanidium-Botrychiopsis* complex are regarded as survivors form the preceding Early Carboniferous Lepidodendropsis-Rhacopteris flora. The leaves of *Rhacopteris* are morphologically similar to *Gondwanidium* and *Botrychiopsis*. Therefore, Retallack (1980) suggested that the bipinnate type specimen of *Rhacopteris ovata* (McCoy) Walkom should be referred to the genus *Botrychiopsis* Kurtz ex Archangelsky and Arrondo. Other pteridophylls present during the Karharbari Stage include the fern-like leaves of *Alethopteris whitbyense* and *Neomariapteris hughesii* and some forms of *Sphenopteris*. On the basis of species diversity there are 54% sphenopsids, 33% pteridophylls and 13% lycopods (Fig. 1D). The pteridophytic remains recorded from this Formation are as follows:

Lycopods

*Cyclodendron leslii* (Seward ) Krausel
*C.* sp. Maithy

Sphenopsids

*Phyllotheca ampla* Surange & Kulkarni
*P. australis* Brongniart
*P. crassa* Maithy
*P. indica* Bunbury
*P. sahnii* (Saxena ) Townrow
*Giridia indica* Pant & Misra
*Schizoneura gondwanensis* Feistmantel
*S. wardii* Zeiller

Sterile pteridophylls

*Alethopteris whitbyense* Feistmantel
*Botrychiopsis indicum* Maithy
(=*Gondwanidium indicum* Maithy)
*B. validum* (Gothan) Maithy
(=*Gondwanidium validum* Maithy)
*Neomariapteris hughesii* (Zeiller) Maithy
*Sphenopteris* sp. Maithy

(iii) *Barakar Formation*—The earliest bed of Damuda Series are assigned to the Barakar Formation. These are wide spread occurring in Rajmahal-Purnea, Galsi Basin, Damodar-Koel, eastern Son Mahanadi Basin, Rewa Basin, Mahanadi-Southeastern Son Valley Basin, Satpura Basin and the Wardha-Godavari Basin in peninsular India. The increasing richness of flora and the widespread peat accumulation suggest that the climate had moderated further during the Barakar Formation. The thickest Gondwana coal seam (134 m thick Jhingurdah coal bed) was deposited at this time. The finding of growth rings in petrified wood genera indicates that the climatic regime was markedly seasonal. Among the pteridophytes sphenopsids are represented by four species of *Lelstotheca*, four species of *Phyllotheca*, three species of *Sphenophyllum* and one species each of *Paracalamites*, *Barakaria* and *Schizoneura* along with fertile parts like *Sharmastachys*, *Rajmahaliastachys* and *Tulsidabaria* (Banerjee & D'Rozario, 1999; Banerjee *et al.*, 2004). Apart from these, a few sterile & fertile remains of *Liknopetalon rajmahalensis* a peculiar pteridophyte, were recorded from the Permian of Rajmahal Hills (Srivastava & Pant, 2002). It is peculiar in having axis with opposite decussate arrangement of cuneate vegetative leaves and similar fertile leaves with apparently sessile sporangia along the crenulate distal margin. On the basis of species diversity there are 74% sphenopsids, 21% pteridophylls and 5% lycopods (Fig. 1E). The pteridophytic remains recorded from this Formation are as follows:

Sphenopsids

*Lelstotheca robusta* (Feistmantel) Maheshwari
*L. striata* Maheshwari & Srivastava
*L. stricta* Maheshwari
*L. harikrishnae* Srivastava & Pant
*Barakaria dichotoma* Srivastava
*Paracalamites* sp. Maheshwari & Prakash
*Phyllotheca australis* Brongniart
*Phyllotheca griesbachii* Zeiller
*P. indica* Bunbury
*P. sahnii* (Saxena) Townrow
*Schizoneura gondwanensis* Feistmantel
*Sphenophyllum churulianum* Srivastava & Rigby
*S. gondwanensis* Singh *et al.*
*S. speciosum* (Royle) Zeiller
*Sharmastachys pendulata* Banerjee & D'Rozario
*Rajmahaliastachys elongata* Ban. & D'Roz.
*Tulsidabaria indica* Ban. & D'Roz.

Sterile and fertile pteridophylls

*Alethopteris lindleyii* (Royle) Schimper
*Cyathea* cf. *tschihatcheffii* Schmaulhausen
*Neomariapteris barakarensis* Srivastava
*Palasthalia indica* Srivastava
*Sphenopteris hughesii* (Feistmantel) Arber

In-certae-sedis

*Liknopetalon rajmahalensis* Srivastava & Pant

(iv) *Barren Measures*—Beds of the Barren Measures conformably lie over the strata deposited during the Barakar Formation. These beds have been identified in the Damodar

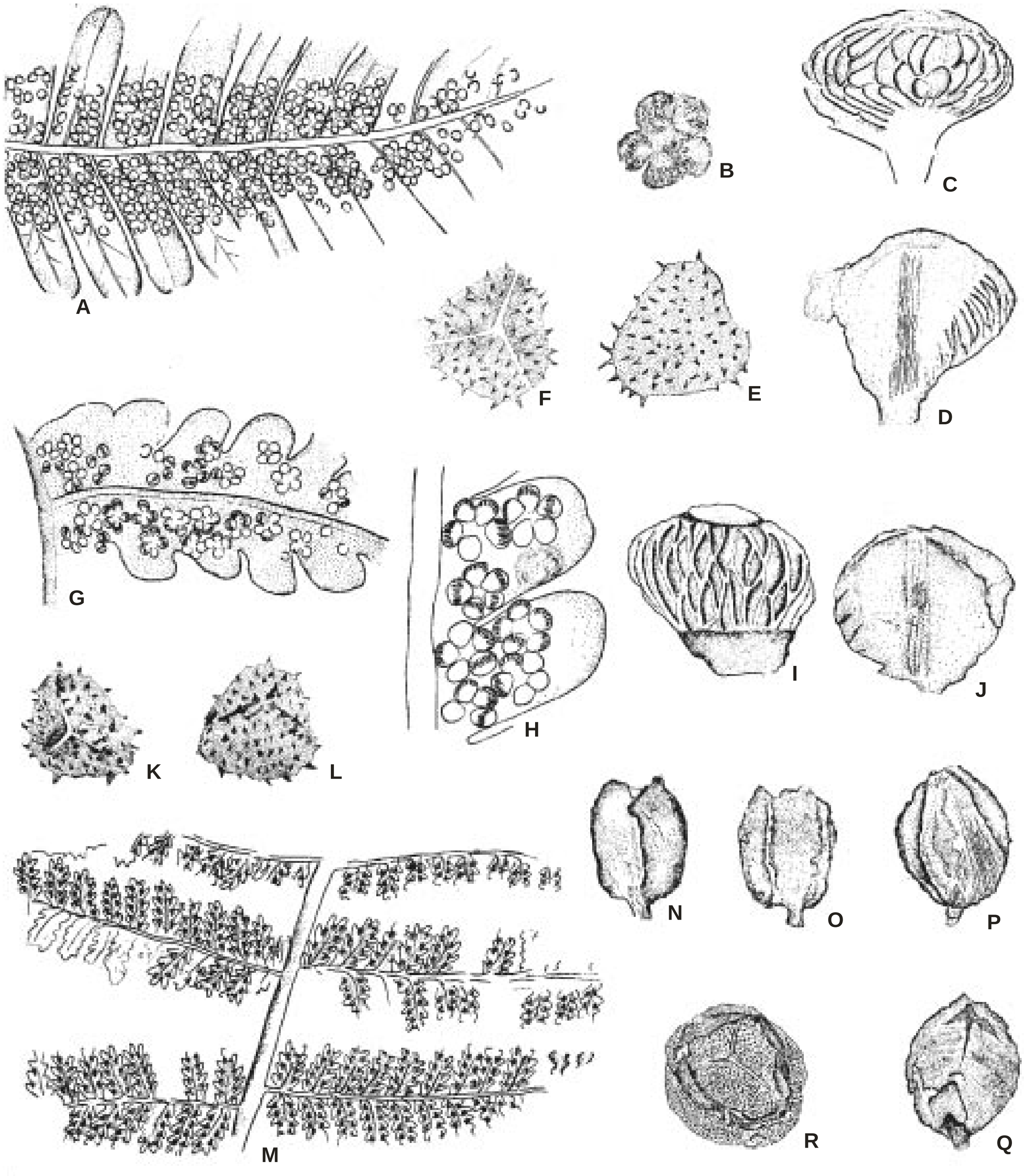


Fig. 7—A.-F. *Damudosorus searsolensis* Pant & Misra, G.-L. *Damudosorus raniganjensis* Pant & Misra, M.-Q. *Trithecopteris gondwanensis* Pant & Misra. A. Fertile pecopterid pinnules showing loosely organized sori x 4.2. B. Single sorus. x 525. C. Convex faces of sporangium. x 70. D. Flat face of sporangium. x 70. E. Distal face of spore. x 700. F. Proximal face of spore. x 700. G. Portion of a pinna showing short confluent pinnules with sori. x 4.2 H. Pinnules magnified to show the arrangement of sori. x 8.4. I. Convex face of sporangium. x 70. J. Flat face of sporangim. x 70. K. Proximal face of spore. x 700. L. Distal face of spore. x 700. M. Bipinnate fertile frond fragment. x 1. N.-Q. Different views of trisporangiate synangia. x 10.5. R. Proximal face of spore. x 420 (All after Pant & Misra, 1976).

Valley (where they are also called the Kulti beds or the Ironstone shales) and in Wardh Pranhita Godavari Basin, they are sometimes known as the Motur Stage. The decline in the fossil diversity in these beds especially in pteridophytic remains and the absence of coal beds suggests that the sediments accumulated during a period of increased warmth and aridity. The pteridophytic megafossils described from this Stage include a lycopod, *Cyclodendron leslii* and a pteridophyll *Neomariopteris hughesii.*

(v) *Raniganj Formation*—The strata deposited during the Raniganj Formation overlie those deposited during the Barakar Formation. The Raniganj strata are best developed in the eastern Son Valley. In central India correlative rocks are called the Kamthi Formation and homotaxial beds in the southeastern Son Valley are equivalent to Kamthi Formation. This Formation represents the zenith of Lower Gondwana Glossopteris flora, which attains its peak diversity and abundance during this time. The climatic conditions were favourable for the luxuriant growth of ferns and sphenopsids. On the basis of taxonomic species diversity there are 67% pteridophylls, 30% sphenopsids and 3% lycopods (Fig. 1F). It also contains extensive coal deposits.

The pteridophytic macrofossils include lycopod like *Cyclodendron leslii*, sphenopsids like, *Lelstotheca, Phyllotheca, Raniganjia, Schizoneura, Sphenophyllum* and a variety of sterile and fertile pteridophylls. Two families of ferns were recognized by Pant and Misra (1976) viz., Asterothecaceae for synangiate forms and Damudopteridaceae for free sporangiate forms. The pteridophytic remains recorded from this Formation are as follows:

Lycopod

*Cyclodendron leslii* (Seward) Krausel

Sphenopsids

*Lelstotheca robusta* (Feist.) Maheshwari
*Bengalia raniganjensis* Maheshwari *et al.*
*Phyllotheca australis* Brongniart
*P. griesbachii* Zeiller
*Raniganjia bengalensis* (Rigby) Pant & Nautiyal
*R. indica* (Srivastava) Rigby
*Schizoneura gondwanensis* Feistmantel
*S. raniganjensis* Banerjee
*Sphenophyllum lobifolium* Pant & Srivastava
*S. crenulatum* Srivastava & Rigby

Sterile and fertile pteridophylls

*Alethopteris lindleyii* (Royle) Schimper
*A.whitbyense* Feistmantel
*Asansolia phegopteroides* (Feistmantel) Pant & Misra
*Cyathea* cf. *tschihatcheffii* Schmaulhausen
*Cuticulatopteris polymorpha* Pant & Misra
*Damudopteris polymorpha* Pant & Khare
*D. raniganjensis* Pant & Khare
*Damudosorus raniganjensis* Pant & Misra
*D. searsolensis* Pant & Misra
*Dichotomopteris falcata* Maithy
*D. lindleyii* Maithy
*D. major* Maithy
*D. ovata* Maithy

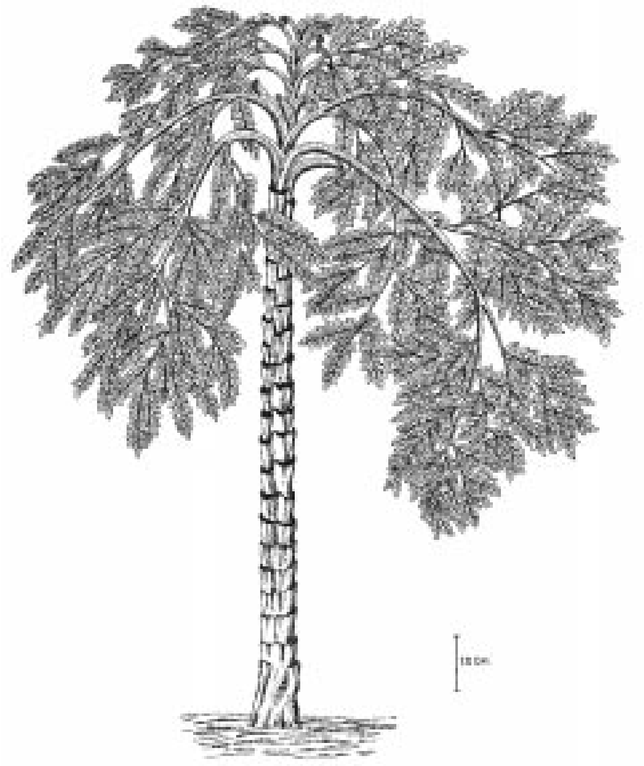

Fig. 8—*Neomariopteris hughesii* (Zeiller) Maithy Reconstruction of Plant. x 0.7 (After Singh & Chandra, 1999)

*Leleopteris raniganjensis* Srivastava & Chandra
*L. ovata* Srivastava & Chandra
*L. srivastavae* Srivastava & Chandra
*Neomarianopteris hughesii* (Zeiller) Maithy
*N. polymorpha* (Feistmantel) Maithy
*N. lobifolia* (Morris) Maithy
*Pecopteris phegopteroides* (Feistmantel) Arber
*Santhalia bansloensis* Maithy
*Sphenopteris hughesii* (Feistmantel) Arber
*Trithecopteris gondwanensis* Pant & Misra

(vi) *Kamthi Formation*—This stage may represent a phase of the Raniganj Formation which is locally developed in Kamthi and in Handappa, Orissa. It differs from Raniganj stage in having developed in relatively drier or upland areas characterized by seasonal climatic regimes as indicated by the wood genera (Prasad, 1986) with growth rings. The pteridophyic megafossils include three species of *Sphenophyllum* and three forms of sterile/fertile pteridophylls. On the basis of species diversity there are 50% pteridophylls and 50% sphenopsids (Fig. 1G). The pteridophytes recorded from this Formation are as follows:

Sphenopsids

*Sphenophyllum ?churulianum* Srivastava & Rigby
*Sphenophyllum speciosum* (Royle) Zeiller
*S. utkalensis* Pant *et al.*

Sterile and Fertile Pteridophylls

*Asansolia phegopteroides* Pant & Misra
*Neomariapteris khanii* Maithy
*Pantopteris gracilis* Chandra & Rigby

**Lower gondwana pteridophytes from extra-Peninsular India**

Survey of literature on Indian extra-Peninsular Lower Gondwana pteridophytes reveals that except the Kashmir Himalayas other parts have only stray occurrence of such remains. However, the study of these remains in Himalayan range is quite interesting since this part forms the northern boundary of Indian Gondwana and presents floristic admixture of exotic forms with the Gondwana forms.

(i) *Eastern and Kumaon Himalayas*—Except the Kashmir Himalaya the other Himalayan localities of India have yielded only meagre pteridophytic remains. From Tindharia area in Ranjit Valley in north of Darjeeling in Eastern Himalaya *Schizoneura* and *Phyllotheca* have been reported (see Pascoe, 1959). Similarly, Acharayya *et al*. (1975) have reported *Schizoneura* sp. from Arunachal Pradesh while Banerjee *et al*. (1979) reported *Schizoneura gondwanensis* from Singrimari area of Western Garo Hills.

From Nainital-Gethia-Bhowali section of Kumaon Tewari (1979) and Tewari and Singh (1979) described *Lepidodendron* sp., *Annularia* cf. *stellata*, *Phyllotheca* and *Calamites* from Blaini Infra Krol Formation. There are 75% sphenopsids and 25% lycopods (Fig. 1I).

(ii) *Kashmir Himalaya*—The earliest described fossil pteridophyte in Indian Palaeozoic strata is *Trizygia speciosa* which was recorded by Royle (1939) from Permian of Kashmir. Kapoor *et al*. (1992, 2004) envisaged only two Lower Gondwana Formations in Kashmir Himalaya, viz. Nishatbagh Formation below Panjal traps and Mamal Formation above Panjal Trap. The older Nishatbagh Formation has so far not yielded any pteridophytic remain. Among various horizons of Mamal Formation, Mamal Bed represents the youngest horizon with the richest pteridophytic assemblage. The type locality of this horizon is situated in a Nala section, near Mamal Village (Pahalgam) in Upper Liddar Valley area. The exposures in Aru area near Sheshramnag, Dunpathri and Wadwan Valley were considered to be floristically equivalent. The following pteridophytes have been reported from this bed by Srivastava and Kapoor (1969), Kapoor (1979), Singh *et al*. (1982), Pant *et al*. (1984), Pant and Srivastava (1991), Maheshwari *et al*. (1996) and Srivastava (2004) which include 53% sphenopsids, 29% pteridophylls, 12% incertae-sedis and 6% lycopods (Fig. 1H) listed here-

Lycopods

*Lepidostrobus kashmirensis* Srivastava & Kapoor

Sphenopsids

*Phyllotheca* Bunbury
*Schizoneura* Feistmantel
*Sphenophyllum speciosum* (Royle) Zeiller
*S. thonii* var. *minor* Sterzel
*S. thonii* var. *archangelskyii* Pant *et al.*
*S. thonii* var. *waltonii* Pant *et al.*
*Lobatannularia ensifolia* Halle
*L. lingulata* Halle
*L. sinensis* var. *curvifolia* Halle

Sterile and fertile pteridophylls

*Pecopteris mamalensis* (Singh *et al.)* Srivastava
*P. nautiyalii* Srivastava
*P. pahalgamensis* Srivastava
*P. arborescens* Schlotheim
*Dizeugotheca? falcata* Maheshwari *et al.*

Incertae-sedis

*Vinaykumaria indica* Pant & Srivastava
*Ahmadia biloba* Pant & Srivastava

After the works of Srivastava and Kapoor (1969), Singh *et al*. (1982), Pant *et al*. (1984), Maheshwari *et al*. (1994, 1996) and Pant and Srivastava (1991) on Mamal fossils, Srivastava (2004) has recently published results of his comprehensive reinvestigations of the flora of Mamal plant beds. Among the pteridophytes of this bed he added two species of pteridophylls, *Pecopteris nautiyalii* Srivastava and *P. pahalgamensis* Srivastava, one comb. nov. *P. mamalensis* (Singh *et al.*) Srivastava and for the first time reported *P. arborescens* Schletheim. Here again sphenopsids are dominant.

Srivastava (2004) suspected *Vinaykumaria indica* Pant and Srivastava known from the Mamal bed to be another species of *Liknopetalon* Anderson & Anderson recorded from South Africa and Permian of Rajmahal Hills, India. However, the fragmentary nature and Mamal taxon of doubtful vegetative status refrained him from merging *Vinaykumaria* in *Liknopetalon*. Another Mamal taxon of doubtful pteridophytic affinity is *Ahmadia biloba* Pant & Srivastava. It has detached sessile obcordate leaves showing an apically forked lamina and a concomitantly forked mid-vein. The lateral veins arising at an acute angle from mid vein or its forks show once or twice forked nature. One of the specimens shows one almost complete leaf and another one a basal fragment lying at right angle to each other with touching bases suggesting possibly a whorled phyllotaxis although no axis has been found preserved. The whorled nature may indicate the possible sphenopsid affinity. Among *Sphenophyllum* species, apically forked leaves are already known in *Sphenophyllum lobifolium* Pant & Srivastava and *S. utkalensis* Pant *et al.* Superficially it resembles *Benlightfootia* as well reported from Karroo flora of Wankie, South Rhodesia (now Zimbabwe).

It is noteworthy that among the pteridophytes the precise affinities of these taxa are uncertain. The report of *Lepidostrobus kashmirensis*, a cone of *Lepidodendron* from the Mamal bed by Srivastava and Kapoor (1969) appeared quite attractive at the first instance but neither the photograph of the specimen shows any sporangia or spore nor have the authors described their presence. The attempts of the present author to examine this fossil at GSI office at Kolkata turned futile. Since Srivastava (2004) has described the occurrence of glossopterid fructification *Scutum pantii* Srivastava from the Mamal bed which confirms the extension of territory of Glossopteris flora, the precise identification of the so called *Lepidostrobus kashmirensis* from the same bed may be rewarding for proving Angaran affinity of this bed.

### Floristic admixture in Mamal bed and Correlation of Permian beds of Kashmir Himalaya

A glance at Permian flora of Mamal bed shows an admixtue of Gondwanan, Cathaysian, Euramerian and Cathaysian-Euramerian elements. The typical Cathaysian forms are represented by *Lobatannularia ensifolia*, *L. lingulata*, *L. sinensis* var. *curvifolia*. Cathaysian-Euramerian element *Sphenophyllum thonii* var. *minor* is frequent. Eumarian affinity is reflected by diversity of pecopterids. The doubtful report of *Lepidostrobus kashmirensis* by Srivastava and Kapoor (1969) indicates Angaran affinity. *Sphenophyllum speciosum*, *S. thonii* var. *archangelskyii* (resembling *S. gondwanensis* from Barakar of Rajmahal) and *S. thonii* var. *waltonii* indicate Gondwanan affinity. The superficial resemblance of noble forms like *Vinaykumaria indica* with *Liknopetalon rajmahalensis* from the Permian of Rajmahal (Srivastava & Pant, 2002) and that of *Ahmadia biloba* with *Koraua bartoni* from the Irian Jaya of New Guinea (Rigby) and *Benlightfootia* form Wankie of S. Rhodesia, indicates Gondwana affinity. Among the various horizons of Mamal formations, Mamal is closest to Barakar Formation (Kapoor, 1979; Singh *et al*., 1982; Maheshwari *et al*., 1996; Srivastava, 2004). The common pteridophytic elements between Mamal Bed and Barakar Formation of Peninsular India are *Sphenophyllum speciosum*, deeply dentate form of *Sphenophyllum*, *S. thonii* var. *archangelskyii*, *Vinaykumaria indica* (resembling fan-shaped vegetative leaves of *Liknopetalon rajmahalensis*. Kaooor *et al*. (1992, 2004) lumped the so-called Vihi, Marahom, Munda and Mamal Bed in much thicker Mamal Formation. From Mamal Formation Maheshwari *et al*. (1996) isolated 12 genera of palynofossils. On basis of *Schizopollis* they correlated this Formation with lower most Barakar Formation of Peninsular India. Among these Vihi Bed shows characteristic occurrence of vertebrate (fresh water fishes and amphibians) and invertebrate fossils with the plant fossils having doubtful Lepidodendron-like axis. In these axes, leaf cushions may be fish scales as fresh water fishes have already been reported from the same bed by Kalapesi and Bana (1953). Marahom Bed (so called Gangamopteris Bed) shows the characteristic occurrence of *Gangamopteris* leaves along with pteridophytes like *Schizoneura gondwanensis*, *Sphenophyllum* sp. and *Sphenopteris polymorpha* and therefore this bed was correlated with Karharbari Formation of Peninsular India. Munda plant bed shows the presence of sterile pteridophylls like *Pecopteris*.

## DISCUSSION

### (1) Increasing diversity of pteridophytic assemblages

During last about thirty years there has been a sharp increase in pteridophytic macrofossils including the creation of new genera and species not only in Lower Gondwana assemblages but also in those of Lower Carboniferous age as well. The new taxa include lycopsids, sphenopsids and pteridophylls both vegetative and fertile. Studies of Pal (1978), Pal and Chaloner (1979), Singh *et al*. (1982) and Pant and Srivastava (1995) on Lower Carboniferous flora from Pir Panjal Range and Kashmir Valley have added several new taxa (Fig. 2A-F) to the knowledge of pteridophytes from extra-Peninsular India. Among lycopods the interesting new taxa have been *Pseudobumbudendron chaloneri*, *P. meyenii* and *Spondylodendron wallaramensis* (Fig. Pant & Srivastava, 1995). Similarly Pant *et al*. (1981, 1984), Pant and Srivastava (1991), Pant and Srivastava (1985), Srivastava (2004), Srivastava and Pant (2002), Banerjee and D'Rozario (1996a, b, 1999), have added new pteridophytic taxa to the list of pteridophytes from Lower Gondwana horizons from Peninsular as well as extra-Peninsular part of India. The newly added interesting sphenopsids are some new species and varieties of *Sphenophyllum* with symmetrical whorls of leaves, viz. *Sphenophyllum utkalensis, S. lobifolium, S. churulianum, S. gondwanensis*, *S. thonii* var. *archangelskii, S. thonii* var. *waltonii* (Fig. 3A-J). There is dire need to investigate new areas for better understanding of pteridophytic flora.

Variety of fertile remains of various sphenopsids have been described including *Giridia indica* Pant *et al.* (1981) from Karharbari Formation, *Sharmastachys pendulata* Banerjee & D'Rozario (1999), *Rajmahaliastachys elongata* Banerjee & D'Rozario (1996a, b) and *Tulsidabaria indica* Banerjee & D'Rozario (1996a, b) from Barakar Formation are quite encouraging (Fig. A-G). Similarly a number of fertile ferns with scattered sporangia, sori and synangia including *Damudopteris polymorpha* Pant & Khare (1974, Fig. 5A-F), *Damudosorus raniganjensis* Pant & Misra (1977), *D. searsolensis* Pant & Misra (1977), *Asansolia phegopteroides* (Feistmantel) Pant & Misra (1976), *Trithecopteris gondwanensis* Pant & Misra (1977) from Raniganj Formation (Figs 5, 6 & 7). A peculiar unclassifiable pteridophytic taxon, *Liknopetalon rajmahalensis* Srivastava & Pant (Fig. 6E-G) with opposite and decussate arrangement of cuneate vegetative laminae and submarginal, ovate and sessile sporangia along the distal margin of fertile laminae was described from Barakar of Rajmahal Hill (Srivastava & Pant, 2002).

### (2) Some taxonomic riddles

There are several cases of taxonomic riddles among Palaeozoic pteridophytes of India. Only two interesting cases have been discussed here.

(a) *Trizygia* vs *Sphenophyllum*—The transfer of *Trizygia speciosa* Royle (1939) to *Sphenophyllum speciosum* (Royle) Zeiller was accepted by most subsequent workers till authors like Maheshwari (1968) and Srivastava and Rigby (1983) started advocating the reinstatement of Royle's name *Trizygia speciosa* on the ground that it was a southern form having zygomorphic leaf whorls while northern *Sphenophyllum* has isophyllous leaves in whorls. Maheshwari (1974) pointed out that *Sphenophyllum* differs from *Trizygia* in having specialized subsidiary cells. However, our investigations showed that such cells around stomata are absent in *Sphenophyllum miravallis* (Hetterscheid & Batenburg, 1984, Pl . IX fig. 4; Pl. X , fig. 1) and in *S. emarginatum* (Batenburg, 1981 Pl. II fig. 3, Pl. IV figs 3, 4, 6, 7, 8; Pl. V; fig. 2). The only species which shows vaguely specialized subsidiaries in *S. majus* (see Abbott, 1958, Pl. 38, figs 44, 45) but even here all stomata do not seem to have equally specialized subsidiaries.

Lele (1976) pointed out the characteristic presence of hydathodes in leaves of northern *Sphenophyllum* and their absence in southern *Trizygia*. Pant and Srivastava (1989)

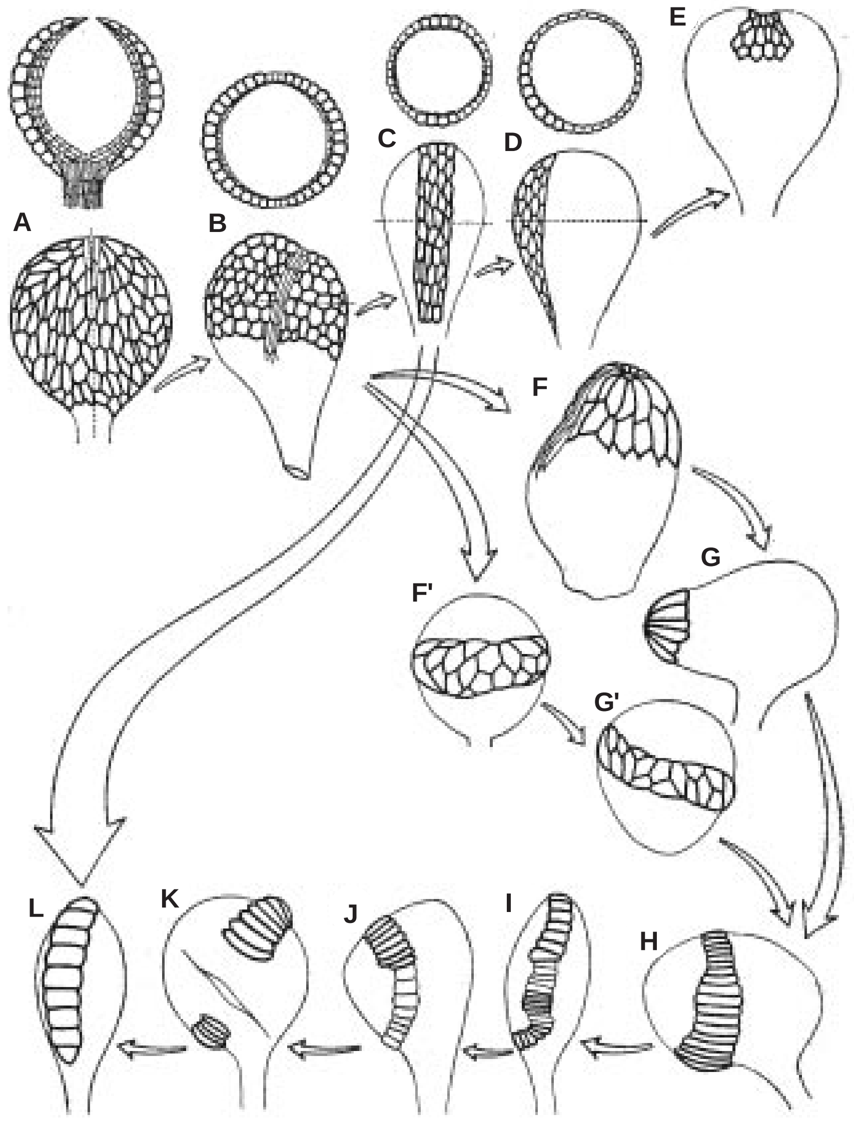


Fig. 9—A-L. Sporangia of various extinct and extant ferns sequenced to indicate phyletic slide of annulus. A. *Stauropteris oldhamia* with thick walled cells all over the wall and a distal stomium, top idealized V.S. of the same. B. *Botryopteris globosa* showing vertical stomium and annulus covering three fourth of the wall; top idealized T.S. of the same C. *Etapteris lacattei* showing multiseriate vertical annulus, top idealized T.S. of the same. D. *Botryopteris forensis* with unilateral multiseriate annulus, top idealized T.S. of the same. E. *Osmunda* showing terminal unilateral group of thick-walled cells. F. *Senftenbergia* with biseriate apical annulus. F'. *Damudopteris* with multiseriate transverse annulus. G. *Lygodium* with uniseriate apical annulus. G'. *Sermaya* with multiseriate oblique annulus. H. *Gleichenia* with uniseriate oblique annulus. I. *Plagiogyria* with uniseriate oblique annulus. J. *Loxsoma* with uniseriate obliaque annulus. K. *Hymenophyllum* with uniseriate oblique annulus. L. *Leptochilus* with uniseriate vertical annulus.

observed that the so-called hydathodes are found only in a few species of northern *Sphenophyllum* e.g., *S. emarginatum* (Abbott, 1958; Batenburg, 1981), *S. cuneifolium* (Radforth & Walton, 1960) and *S. orbicularis* (Remy, 1962). However, it can not be a generic characteristic since Storch (1980) and Batenburg (1982) have pointed out that hydathodes are sporadically present even in the leaves of the same species.

Asama (1970) created further complication with the creation of two para forms, viz. *Patatrizygia* and *Parasphenophyllum,* which included species from *Trizygia* and *Sphenophyllum* having ached veins. Except for Maithy (1978) and Singh *et al*. (1982) the vast majority of authors dealing with shoots of this kind have taken no notice of Asama's new genera. However, Srivastava and Rigby (1983) and Pant and Srivastava (1989) have criticized Asama's view since (i) In large wedge-shaped leaves with rounded shoulder it is not possible to determine where the apical margin ends and side margin begins (ii) In the same species, the smaller leaves have straight veins while larger leaves have arched veins. Pant (1978) and Pant and Srivastava (1989) have very clearly stated following points for rejection of name *Trizygia* and retention of name *Sphenophyllum*:

a. The anatomical features of radially symmetrical as well as asymmetrical whorled forms are same.

b. If *Trizygia* is separated on the ground of asymmetry from *Sphenophyllum* several northern forms with zygomorphic whorls like, *S. sinocoreanum*, *S. apicirratum* (Yao *et al.*, 2000) will also need to be referred to *Trizygia*.

c. In absence of reproductive parts generic separation of *Trizygia* from *Sphenophyllum* should be based at least on categorical multiple vegetative differences.

d. Geographical limitations cannot form a criterion for generic separation.

Finding of anisophyllous, isophyllous and intermediate (pseudotrizygoid) type of whorls of leaves in branches of different order of shoots of one and the same species of *Sphenophyllum miravallis* by Hetterschieid & Batenbrug (1984) has formed strong ground for rejecting symmetry of whorls as basis for separation of genera. However generic separation based on differences between fertile parts like those of *Lilpopia* Conert & Schaarschmidt (1970) from *S. emarginatum* made by Lilpop (1937) could form the only sound basis.

(b) *Asansolia* vs *Dizeugotheca*—Before Pant and Misra (1976) assigned leaves bearing submarginal contiguous tetrasporangiate synangia to *Asansolia* (Fig. 6A-D), Archangelsky and de la Sota (1960) had assigned similar Lower Gondwana leaves to a species of *Dizeugotheca* (*D. neuburgiae*). The type species of this genus, *D. waltonii*, also possessed tetrasporangiate synangia superficially attached on to the lower surface of the pinnules. Pant and Misra (1976) pointed out that in having confluent marginal synangia, *D. neuburgiae* seemed generically different from the type species, *D. waltonii* and they created another genus *Asansolia* for species of that kind on the basis of the criteria outlined by Bower (1923, 1926). They referred *D. neuburgiae* to *Asansolia*. However, a re-examination of the types of *Dizeugotheca waltonii* and *D. neuburgiae* has shown that both species were correctly assigned to the same genus in which elongate sporangia organized in tetrasporangiate synangia are arranged transversely covering the entire half width of pinnules. Lele *et al.* (1981) and Maithy (1975) studied some Indian fertile fronds bearing sporangia "arranged in two pairs lying laterally, the upper pair being larger than the lower" and they treated *Asansolia* as a synonym of *Dizeugotheca*.

According to Pant and Misra (1976) separation of two genera is based on the occurrence of submarginal contiguous synangia in *Asansolia* and superficial noncontiguous synangia in *Dizeugotheca*. The present author has found that in *Dizeugotheca* elongate sporangia organized in tetrasporangiate synangia are arranged transversely covering the entire half width of pinnule with the attachment of synangia near the margin of fertile pinnules with an unmodified limb while *Asansolia* has a shorter sporangia also attached near the pinnule margin, but not rigidly aligned across the half width of pinnules.

**(3) Anatomical studies**

The morphology of Indian Palaeozoic pteridophytes is based on impressions and compressions only. Unfortunately petrified remains of pteridophytes of this age have not been found so far. Therefore, it has not been possible to work out structural details like *Acitheca, Scaphidopteris, Sturiella* and *Lagenopteris* and *Grandeuryella renaultii* studied by Lesnikowaska and Galtier (1991, 1992) from France. We are not able to work out the foliar and cauline anatomy of pteridophytes as worked out by Galtier *et al.* (2001) in case of *Rastropteris pingquanensis*. Likewise it is unlikely to understand evolutionary trends in stellar morphology, xylem maturation pattern, trace formation, petiole anatomy and ontogeny of Indian Gondwana pteridophytes as described by Galtier & Phillips (1996) in case of some Palaeozoic ferns.

**(4) Understanding of plant architecture**

Among the Palaeozoic pteridophytes of India the maiden attempt of reconstructing a plant has been made by Singh & Chandra (1999) in case of *Neomariopteris hughesii* (Zeiller) Maithy on basis of 55 hand specimens from Ib River Coalfield, Sambalpur, Orissa (Fig. 8). While reconstructing *Neomariopteris hughesii* Singh & Chandra (1999) have not attempted for computer simulation. They have rather used their imagination in reconstruction of trunk of this plant. The trunk has been drawn to be almost similar to that of *Medullosa noei* reconstructed by Stewart and Delevoryas (1956) from Pennsylvanian of Ohio. The height of the trunk has been shown to be approximately 1.3 m. along with numerous left

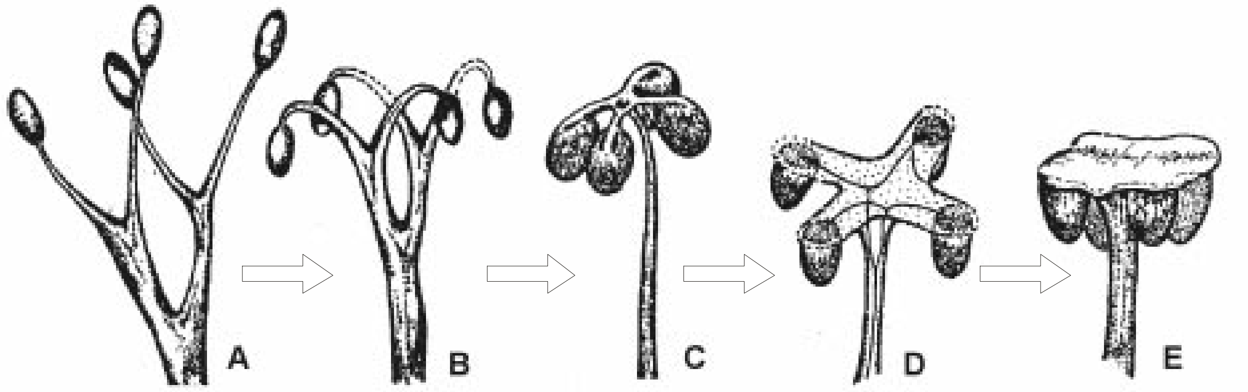


Fig. 10—A-E. Possible successive stages of evolution of *Equisetum* sporangiophore. A. *Protohyenia* Dichotomously branched fertile axis terminated by erect sporangia B. *Arctophyton*/ *Hyenia* Recurvation of sporangia bearing branches. C. *Tulsidabaria indica* Initial stage towards the formation of the shield and pendant position of sporangia, the possible missing step of Boureau (1964). D. *Gondwanostachys australis* Flattened shield showing dichotomy with four pendant sporangia. E. *Equisetum* Sporangiophore with peltate shield and pendant sporangia.

over leaf bases exactly like that of *Medullosa*. The longest fragment in their collection is only 12 cm long. This only fragment of trunk which has been used as a base for reconstructing leaf bases is shown in Pl. 1 fig. 4 (correlated with fragment F in Text fig. 2F). This specimen fails to show the leaf bases as reconstructed on the trunk. However, there has been gross lack of computer simulation for understanding architecture of pteridophytes on the basis of small fragments like Daviero *et al.* (2000) and Daviero and Lecoustre (2000). There is need to use of computer programs like L-System and AMAP approach (AMAP1-AMAPsim & AMAPpara) for computer modelling.

### (5) Ecological analysis

On basis of critical analysis of Lower Carboniferous flora of Kashmir Himalaya Pant & Srivastava (1995) and Pant (1996) had proposed the prevalence of regionalism in vast worldwide Lepidodendropsis flora existing in this period on the basis of appearance of characteristic infrafoliar bladder (in *Pseudobumbudendron* Pant & Srivastava) matching with those of contemporary lepidophytes known from Angara area. They had also suggested a rather dry or physiologically dry climate with seasonal fluctuations on the basis of interstitial fibers in leaves of *Nothorhacopteris* Archangelsky and *Triphyllopteris* Schimper along with alternating zones of large and small leaf cushion on the lepidophytic axes assigned to *Spondylodendron wallaramensis* Pant & Srivastava, *Lepidosigillaria quadrata* Kräusel & Weland and *Archaeosigillaria subcostata* Danzé-Corsin. They had further pointed out the existence of Wallarama flora in coastal clastic swamp. Recently Srivastava (2006) reoriented his idea about palaeophytogeography of Lower Carboniferous Period agreeing with the views of Guerra-Sommer *et al.* (2001) and Iannuzzi and Pfefferkorn (2002). Guerra-Sommer *et al.* (2001) inferred that arboescent cormophytic lycophyte communities were not only important landscape elements but also palaeoecological and palaeoclimatic markers of wet lowlands associated with coastal plains in Western Gondwana during Visean-Serpukhovian and Artinskian-Kungurian intervals on the basis of *Pseudobumbudendron* and *Bumbudendron-Brasilodendron*, respectively. On the basis of qualitative analysis of Lower Carboniferous floras of Gondwana areas Iannuzzi and Pfefferkorn (2002) proposed the existence of a pre-glacial, warm-temperate floral belt in Gondwana (Late Visean, Early Carboniferous) called Paracal floral realm which is justified.

Qualitative ecological analysis of pteridophytic macrofloristic elements of various horizons of Peninsular Lower Gondwana and admixture of floras on the basis of exotic looking pteridophytic elements in the extra-Peninsular Lower Gondwana flora, e.g. Flora of Mamal Bed in Kashmir Himalayas has been very thoroughly analyzed by a number of workers like Pant (1996), Srivastava and Kapoor (1969), Singh *et al.* (1982), Pant *et al.* (1984), Maheshwari *et al.* (1996) and Srivastava (2004). Gradual warming of younger Lower Gondwana horizons leading to greater diversity of sphenopsids and sterile and fertile pteridophylls. The peculiar co-occurrence of elements of Cathaysian, Euramerian, Angaran and Gondwanan phytochorias in Mamal Formation of Kashmir Himalaya suggests that this area may be regarded as a palaeoecotone between these phytogeographical provinces.

However, there is need of undertaking quantitative and autecological studies of Indian Palaeozoic pteridophytes like DiMichele and Phillips (2002) and Rößler (2000). Rößler (2000) who visualized the Late Palaeozoic tree fern *Psaronius* as an ecosystem in itself since *Psaronius* tree ferns showed several interactions like *Psaronius-Psaronius*, *Psaronius-Ankyropteris*, *Psaronius-Tubicaulis*, *Psaronius-Anachoropteris*, *Psaronius-?Grammtopteris*, *Psaronius-Dadoxylon*, *Psaronius–Callistophyton*, *Psaronius* and evidence of animal life. Due to limitation of available preservational types as impressions and compressions only in India, there are meagre chances of such work.

### (6) Phylogenetic implications

Some of the contributions on Indian pteridophytes have formed basis in solving phylogenetic problems. The study of sporangia of *Damudopteris polymorpha* by Pant and Khare (1974) has been helpful in explaining the phyletic slide of annulus in fern sporangia (Fig. 9). The sporangia of this interesting fern are rounded or oval, planoconvex with a minute multiseriate stalk (Fig. 5B-D). Further each sporangium is provided with a transverse, multiseriate and incomplete annulus on the convex side. The stomium is marked by narrow thin walled cells running vertically through gap in annulus on flat side of the sporangium. Bower (1923) proposed theory of phyletic slide of the annulus in leptosporangiate ferns. He derived vertical annulus of advanced Mixtae from *Senftenbergia* through other Schizeaceae-*Gleichenia*, *Plagiogyria*, *Loxsoma* and *Hymenophyllum*. Pant and Khare (1974) envisaged that annulus might be derived from sporangium like that of *Stauropteris oldhamia* Binney (Fig. 9). From this *Botryopteris globosa* Darrah type of sporangium evolved where only three fourth of apical portion of the wall is occupied by annulus like induated cells and between them a continuous stomium runs vertically on both sides. From this evolved *Damudopteris*-type of sporangium and this in turn gave rise to sporangium like that of *Sermaya* Eggert & Delevoryas with multiseraiate oblique annulus. Thereafter, vertical annulus followed the same line of evolution as suggested by Bower.

Similarly evolution of sporangiophore of *Equisetum* has been explained using the structure of *Tulsidabaria indica* Banerjee *et al.* (2004). The twice-forked nature of the ultimate branch tip and the occurrence of four sporangia at the terminal position of branches of *Tulsidabaria* are common with *Gondwanostachys* and *Kretrophyllites*. The critical morpho-anatomical study of the penultimate and ultimate sporangia bearing branches of *Tulsidabaria* have revealed some interesting features suggesting possible representation of the primitive stages in the evolution of the equistalean sporangiophores (Fig. 10). The formation of thick tissue in place of the penultimate branches above the distal branch and at the base of the ultimate branches simulate a rudimentary shield-like structure. It might be presumed to be an initial condition in the formation of the sporangia bearing peltate shield of equisetalean sporangiophore. Further coalescence of the penultimate branches with ultimate branches could have formed the sporangia bearing petlate shield. The adpressed sporangial cuticle to the ultimate branch suggests possible recurvation of sporangia towards the stage of pendant sporangia. Thus *Tulsidabaria* sporangiophore fits well as the missing "intermediate" between *Arctophyton-Hyenia* on one hand and *Gondwanostachys australis* on the other leading to the formation of *Equisetum*-type of sporangiophores in the sequence proposed by Boureau (1964), Page (1992) and Stewart and Rothwell (1993) supporting the concept of telomic branching system. There is dire need to use computer programs like PAUP for preparing cladograms as Bateman (1994) and Retallack (1997) have done in case of heterosporous lycopods.

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