Status of gymnosperms in the Indian Tertiary flora

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Gymnosperms, the most dominant group of plants during Mesozoic, were meagrely represented in the Indian Tertiary flora. The Tertiary gymnosperms occur in the form of petrified woods, cones and leaf-impressions, besides pollen, referable to the families Podocarpaceae, Araucariaceae and Cycadaceae. Until Late Cretaceous-Early Palaeocene the gymnosperms were widely distributed in the Indian peninsula. However, during Tertiary they declined to such an extent that towards the close of Pliocene Araucariaceae totally disappeared from the Indian subcontinent. The Podocarpaceae too, is now on the verge of extinction as it occurs in the restricted areas in northeast India and Nilgiri Hills in southern India. The causes of decline of these tropical gymnosperms and advent of the northern temperate members in the Indian subcontinent during Tertiary are discussed.

Key-words — Palaeobotany, Gymnosperms, Tertiary (India).

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साराँश

भारतीय तृतीयक युगीन वनस्पतिजात में अनावृतबीजीयों की स्थिति

राकेश चन्द्र मेहरोत्रा एवं नीलाम्बर अवस्थी

अनावृतबीजी पौधे, जो कि मध्यजीवी कल्प में सबसे अधिक प्रभावी पौधों का समूह था, भारतीय तृतीयक युगीन वनस्पतिजात में संख्या में बहुत कम थे। परागकणों के अतिरिक्त, तृतीयक कल्प में अनावृतबीजी पौधे अश्मीभूत काष्ठों, कोनों एवं पर्ण-छापों के रूप में मिलते हैं। ये सभी अश्मित अवयव पोडोकापेंसी, अराकेरिएसी एवं साइकेडेसी नामक कुलों से सम्बद्ध हैं। तथापि, तृतीयक कल्प में इनकी संख्या इतनी कम हो गई थी कि अतिनूतन कल्प की समाप्ति तक अराकेरिएसी कुल भारतीय महाद्वीप से पूर्णतः विलुप्त हो गया था। पोडोकापेंसी कुल भी अब लगभग विलुप्त ही होने वाला है क्योंकि इस कुल के प्रतिनिधि अब उत्तरी भारत के कुछ स्थानों तथा दक्षिणी भारत में नीलगिरि पहाड़ियों में ही पाये जाते हैं। इस शोध-पत्र में तृतीयक कल्प में भारतीय उपमहाद्वीप में उत्तरी शीतोष्ण सदस्यों के प्रादुर्भाव एवं उष्णकटिबन्धीय अनावृतबीजीयों के हास के कारणों की विवेचना की गई है।

GYMNOSPERMS were dominant during Palaeozoic and Mesozoic times. The Lower Gondwana period was dominated by *Glossopteris* and its allies. The Middle Gondwana was dominated by *Dicroidium* which was associated with some Lower Gondwana elements in the early part of Triassic. During its middle and upper parts it was associated with Ginkgoales, Bennettitales, Cycadales and Coniferales. The Upper Gondwana Period is said to be the best period for Indian gymnosperms, when the flora was dominated by diverse members of Ginkgoales, Pentoxylales, Cycadales, Bennettitales, Coniferales and Taxales and seemingly had covered extensive areas in the Peninsular India.

During the early part of the Post Gondwana,

probably during Middle to Late Cretaceous, the gymnosperms as a group suffered a drastic decline both numerically and geographically from which they never recovered to regain their former pristine position (Ramanujam, 1976). There are only a few reports of gymnospermous remains from the Late Cretaceous of Trichinopoly area of Tamil Nadu (Aiyengar & Jacob, 1952; Varma, 1955). The paper is mainly aimed to bring together all the unequivocal megafossil records of gymnosperms known from various Tertiary localities of India (see Map 1).

TERTIARY GYMNOSPERMS

Gymnosperms, occupying a subordinate posi-

Cycadales

There is a solitary record of fossil cycad. Paradkar (1976) described a petrified ovule as *Gymnovulites deccanii* from the Deccan Intertrappean beds (Early Tertiary) of Mohgaonkalan showing resemblance with the ovules of *Cycas*. The ovule is characterized by narrow curved neck, a flask-shaped lower part and two layered integuments.

Coniferales

The Coniferales were represented by the members of Podocarpaceae, Araucariaceae, Pinaceae and Cupressaceae.

Podocarpaceae

The fossils of Podocarpaceae comprise leaf, ovule and woods. There is only one record of fossil

leaf of *Podocarpus* — *P. oligocenicus* described by Awasthi *et al.* (1992) from the Oligocene of Makum Coalfield near Ledo, Assam. Among modern species of *Podocarpus* the fossil leaf is very similar to that of *Podocarpus neriifolius* D. Don.

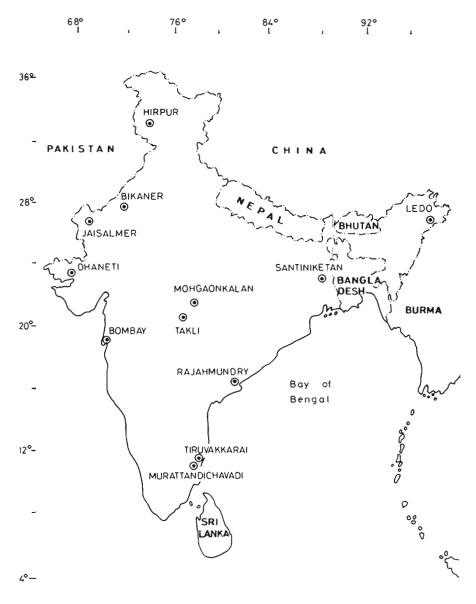
The only fossil ovule, Podocarpoovulites chitaleyi Sheikh & Kolhe 1982 of the family Podocarpaceae was described from the Deccan Intertrappean beds of Nagpur. The woods of this family commonly occur in the Indian Tertiary sediments. They have been described under the genus Podocarpoxylon or Mesembrioxylon from the Deccan Intertrappean beds (Mahabale & Rao, 1973; Lakhanpal et al., 1975; Bande & Prakash, 1984; Trivedi & Srivastava, 1989), Mio-Pliocene of Cuddalore Sandstones (Kräusel, 1949; Ramanujam, 1953, 1954; Agashe, 1969; Trivedi & Srivastava, 1989), ? Oligo-Miocene of Rajahmundry area (Mahabale & Satyanarayana, 1978) and Neogene of Kachchh (Lakhanpal et al., 1975) and Rajasthan (Guleria, 1986). Gothan (1905) instituted the genus Podocarpoxylon for the fossil woods of Podocarpus and Dacrydium, while Seward (1919) instituted another genus Mesembrioxylon saying that the use of

Table 1-List of gymnosperm megafossils from the Tertiary of India

Taxa	Modern comparable form	Formation, Locality & Age	Reference
Cycadales			
Gymnovulites deccarrii Paradkar	Cycadaceae	Deccan Intertrappean beds of Mohgaon Kalan; Early Tertiary	Paradkar, 1976
Coniferales			
Taxodioxylon cuddalorense Ramanujam	?Taxodiaceae	Cuddalore Series of Tiruvakkarai; Mio- Pliocene	Ramanujam, 1960, 1976
Cupressus sp. cf. C. torulosa	Cupressaceae	Lower Karewa beds of Hirpur; Mio-Upper Pliocene	Awasthi & Guleria, 1982
Mesembrioxylon fusiforme Sahni	Podocarpaceae	Deccan Intertrappeans of Rajahmundry; Early Tertiary	Mahabale & Rao, 1973
<i>M. dudukurense</i> Mahabale & Rao	Podocarpaceae	Deccan Intertrappeans of Rajahmundry; Early Tertiary	Mahabale & Rao, 1973
<i>M_rajmahalense</i> Jain	Podocarpaceae	Rajahmundry area; ?Oligo-Miocene	Mahabale & Satyanarayana, 1978
<i>Mesembrioxylon</i> sp. cf. <i>M. dudukurense</i> Mahabale & Rao	Podocarpaceae	Rajahmundry area; ?Oligo-Miocene	Mahabale & Satyanarayana, 1978
Podocarpoxylon vikramii Bande & Prakash	Podocarpaceae	Deccan Intertrappeans of Bombay; Early Tertiary	Bande & Prakash, 1984
<i>P_deccanensis</i> Trivedi & Srivastava	Podocarpaceae	Deccan Intertrappean beds of Mohgaon Kalan; Early Tertiary	Trivedi & Srivastava, 1989
P. kutchensis Lakhanpal et al.	Podocarpaceae	Kankawati Series of Dhaneti (Kutch); Pliocene	Lakhanpal <i>et al.</i> , 1975 <i>Contd</i> .

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Podocarpus	Podocarpaceae	Shumar Formation of Jaisalmer, Rajasthan; Miocene	Guleria, 1986
Podocarpoxylon schmidianum (Sahni) Kräusel Syn. M. schmidianum Sahni	Podocarpaceae	Cuddalore Series of Tiruvakkarai; Mio- Pliocene	Kräusel, 1949
<i>P. tiruvakkarainum</i> (Ramanujam) Trivedi & Srivastava Syn. <i>M. tiruvakkarainum</i> Ramanujam	Podocarpaceae	Cuddalore Series of Tiruvakkarai; Mio- Pliocene	Trivedi & Srivastava, 1989
<i>P. sahnii</i> (Ramanujam) Trivedi & Srivastava Syn. <i>M. Sahnii</i> Ramanujam	Podocarpaceae	Cuddalore Series of Tiruvakkarai; Mio- Pliocene	Trivedi & Srivastava, 1989
<i>P. speciosum</i> (Ramanujam) Trivedi & Srivastava Syn. <i>M. speciosum</i> Ramanujam	Podocarpaceae	Cuddalore Series of Murattandichavadi; Mio-Pliocene	Trivedi & Srivastava, 1989
<i>P. mahahalei</i> (Agashe) Trivedi & Srivastava Syn. <i>M. mahahalei</i> Agashe	Podocarpaceae	Cuddalore Series of Tiruvakkarai: Mio- Pliocene	Trivedi & Srivastava, 1989
Podocarpoovulites chitaleyi Sheikh & Kolhe	Podocarpaceae	Deccan Intertrappean beds of Nagpur; Early Tertiary	Sheikh & Kolhe, 1982
Podocarpus oligocenicus Awasthi et al.	Podocarpus	Makum Coalfield near Ledo Assam; Oligocene	Awasthi <i>et al.</i> 1992
<i>Araucarioxylon deccani</i> (Shukla) Trivedi & Srivastava Syn. <i>Dadoxylon deccani</i> Shukla	Araucaria-Agathis	Deccan Intertrappeans; Early Tertiary	Trivedi & Srivastava, 1989
<i>A. resinosum</i> (Shukla) Trivedi & Srivastava Syn. <i>D.</i> <i>resinosum</i> Shukla	Araucaria-Agathis	Deccan Intertrappeans; Early Tertiary	Trivedi & Srivastava, 1989
A. eocenum (Chitaley) Trivedi & Srivastava Syrt. D. eocenum Chitaley	Araucaria-Agathis	Deccan Intertrappeans of Mohgaonkalan; Early Tertiary	Trivedi & Srivastava, 1989
<i>A. Chhindwarensis</i> (Billimoria) Trivedi & Srivastava Syn. <i>D. chhindwarensis</i> Billimoria	Araucaria-Agathis	Deccan Intertrappeans of Mohgaonkalan; Early Tertiary	Trivedi & Srivastava, 1989
<i>A. shuklae</i> (Singhai) Trivedi & Srivastava Syn. <i>D. shuklae</i> Singhai	Araucaria-Agathis	Deccan Intertrappeans of Mohgaonkalan; Early Tertiary	Trivedi & Srivastava, 1989
A. keriense Trivedi & Srivastava	Araucaria- Agathis	Deccan Intertrappean beds of Keria: Early Tertiary	Trivedi & Srivastava, 1989
A, mobgaoensis Lakhanpal et al.	Araucaria- Agathis	Deccan Intertrappean beds of Mohgaonkalan; Early Tertiary	Lakhanpal <i>et al.</i> , 1977
A. hikanerense Harsh & Sharma	Araucaria-Agathis	Mar Formation of Bikaner, Rajasthan; Pliocene	Harsh & Sharma, 1988
<i>Araucarioxylon</i> sp. Srivastava & Prakash	Araucaria- Agathis	Shantiniketan near Bolpur, West Bengal; Miocene	Srivastava & Prakash, 1984
Araucaria - Agathis	Araucaria-Agathis	Shumar Formation of Jaisalmer, Rajasthan; Pliocene	Guleria, 1986
<i>Dadoxylon</i> sp. cf. <i>D. harakarense</i> Surange & Saxena	Araucaria-Agathis	Rajahmundry area; ? Oligo-Miocene	Mahabale & Satyanarayana, 1978
Dadoxylon sp. cf. D. jamudhiense Maheshwari	Araucaria-Agathis	Rajahmundry area; ? Oligo-Miocene	Mahabale & Satyanarayana, 1978
<i>Mohgaostrohus sahnii</i> Prakash	Araucariaceae	Deccan Intertrappeans of Mohgaonkalan; Early Tertiary	Prakash, 1957 1962
Indostrobus bifidolepis Salıni	Araucariaceae	Deccan Intertrappean beds; Early Tertiary	Sahni, 1931
Takliostrobus alatus Sahni	Araucariaceae	Deccan Intertrappean beds of Takli; Early Tertiary	Sahni, 1931
Pityostrohus crassitesta Sahni	Araucariaceae	Deccan Intertrappean beds of Takli; Early Tertiary	Sahni, 1931
Harrisostrohus intertrappea Chitaley & Sheikh	Araucariaceae	Deccan Intertrappeans of Mohgaonkalan; Early Tertiary	Chitaley & Sheikh, 1973
Pinus wallichiana	Pinus	Lower Karewa beds of Hirpur; Mid- Upper Pliocene	Awasthi & Guleria, 1982
Abies sp. cf. A. pindrow	Abies	Lower Karewa beds of Hirpur; Mid- Upper Pliocene	Awasthi & Guleria, 1982



Map — Showing distribution of gymnosperms in India during Tertiary.

Gothan's name implied affinities to recent genera for which there were no adequate reasons. Further, Bose and Maheshwari (1974) pointed out that since *Podocarpoxylon* of Gothan is a validly and legitimately published name, it is inadvisable to replace it by *Mesembrioxylon*. Therefore, recently Trivedi and Srivastava (1989) transferred the Indian species of *Mesembrioxylon* to *Podocarpoxylon* excepting a few which probably they forgot to do so. Podocarpaceous woods are generally characterized by growth rings, wood parenchyma mostly without resin contents, predominantly uniseriate xylem rays, number of cross-field pits 1-2 with apertures vertical or oblique, radial pits bordered and 1-2 seriate, opposite and rounded.

Araucariaceae

In the Indian Tertiary rocks the remains of Araucariaceae consist of woods and cones. The woods are described as *Araucarioxylon* Kraus or *Dadoxylon* Endlicher (Table 1) from the Deccan Intertrappeans (Lakhanpal et al., 1977; Trivedi & Srivastava, 1989), Neogene of Rajasthan (Guleria, 1986; Harsh & Sharma, 1988), West Bengal (Srivastava & Prakash, 1984) and Rajahmundry area (Mahabale & Satyanarayana, 1978). The important features of these woods are the presence of growth rings, 1-2 seriate xylem rays, absence of resin canals, bar of Sanio and xylem parenchyma, cross-field pits 1-10, radial pitting 1-3 or 4 seriate, bordered, alternate and hexagonal. For a long time all the fossil woods having such characters from Palaeozoic were assigned to Dadoxylon, while those from the younger formations were placed under Araucarioxylon, because the former were thought to belong to Cordaitales and the latter to Araucariaceae. According to Potonié (1902) and Gothan (1905) the name Dadoxylon should be used for the secondary wood with araucaroid type of tracheidal pitting irrespective of the age of fossil woods. Lepekhina (1972) has given a classification of fossil woods with araucaroid pitting. According to her there is no difference in the secondary wood of Araucarioxylon and Dadoxylon. Dadoxylon shows endarch primary xylem and rather large non-septate pith without secretory canals, while Araucarioxylon is based on secondary wood only. On this basis Trivedi and Srivastava (1989) transferred some of the species of Dadoxylon to Araucarioxylon.

The fossil comparable to that of *Araucaria* of Araucariaceae is represented by *Mobgaostrobus sabnii* Prakash 1957, 1962, described from the Deccan Intertrappean beds of Mohgaonkalan.

Pinaceae and Cupressaceae

There are no fossil record of Pinaceae and Cupressaceae from any Tertiary sediments of peninsular India. However, from extra-peninsular India Awasthi and Guleria (1982) have reported the woods of *Pinus, Cupressus* and *Abies* from the Lower Karewa beds (Upper Pliocene) of Kashmir.

Gymnosperms of uncertain affinities

Besides, there are cones of uncertain affinities described from the Deccan Intertrappean beds. These are *Indostrobus bifidolepis, Takliostrobus alatus, Pityostrobus crassitesta* (Sahni, 1931) and

Harrisostrobus intertrappea (Chitaley & Sheikh, 1973). Indostrobus is characterized by distinct bract and ovuliferous scale bearing a pair of inverted ovules at a distance from the cone axis. The locality from where it was collected is not known. Takliostrobus and Pityostrobus have been reported from Takli near Nagpur. In the former, the bract is fused with the expanded ovuliferous scale along the midline but laterally free and each ovuliferous scale has two ovules. The latter possesses double cone scales and cylindrical ovules with extremely thick integument, the greater part of which is sclerotesta. Harrisostrobus is another cone described from the Mohgaonkalan chert of the Deccan Intertrappean beds. The unique character of this cone is the presence of six ovuliferous scales per bract scale, one attached on bract scale and the rest on cone axis. The cone is compact, not woody and bears protecting scales and two ovules per ovuliferous scale. The affinities of all these cones with those of the extant conifers are not definitely known.

In addition, a wood of Taxodiaceae, *Taxodioxylon cuddalorense*, was described by Ramanujam (1960) from Cuddalore Sandstones. But the author (1976) later on was doubtful about its affinities with Taxodiaceae.

DISTRIBUTION OF MODERN GYMNOSPERMS IN INDIA

Gymnosperms occupy extensive tracts all along the subtropical and temperate areas of Himalaya and hilly areas of Kashmir, Assam and Arunachal Pradesh. They are represented by the members of Cycadales, Coniferales, Taxales and Gnetales. Ginkgoales do not occur in India. Among nine modern genera of Cycadaceae, only Cycas is found in India. The conifers are found predominantly in the Himalayas and are particularly rich in north-west Himalayas. The important genera are Abies, Cedrus, Larix, Picea, Cephalotaxus (Pinaceae), Pinus, Tsuga (Cephalotaxaceae), Cupressus, Juniperus (Cupressaceae) and Podocarpus (Podocarpaceae). Taxodiaceae is totally absent. The only conifer of Southern Hemisphere origin found in India is Podocarpus. The order Taxales is represented by Taxus and Amentotaxus, while Gnetales includes *Ephedra* and *Gnetum*. Most of these taxa are of Northern Hemisphere. The Southern Hemisphere forms mostly introduced are only *Araucaria* and *Agathis* (Sahni, 1990).

DISCUSSION

Even a cursory comparison of the Tertiary conifers of peninsular India with the modern conifers of the extra-peninsular Himalayan region would not fail to indicate a sharp difference between the two. The former were dominated by Podocarpaceae and Araucariaceae, while the latter by Pinaceae. The cumulative effect of the following factors could be ascertained for it:

- (a) Appearance of angiosperms
- (b) Northward movement of the Indian Plate and uplift of Himalayas.

The Indian landmass (Peninsular India) was the integral part of the then Southern Hemisphere Supercontinent "Gondwanaland" for the major part of the Mesozoic Era (Smith & Briden, 1979). However, during Late Cretaceous the Indian Plate got separated from the main landmass and started moving northward. This was the time when the angiosperm flora started appearing in India. During Palaeogene angiosperms became quite dominant as a result of their progressive diversification and expansion all over the peninsula thus reducing the gymnosperms to an extent that only Cycadaceae, Podocarpaceae and Araucariaceae could be observed. Towards the end of Palaeogene the Indian Plate collided with the Asian Plate resulting in the formation of mighty Himalayas which had adversely affected the gymnosperm population of peninsular India as they could not survive under changing conditions. As a result Araucariaceae suffered most and became totally extinct from India after Neogene (Ramanujam, 1978) while Podocarpaceae too is at the verge of its extinction (Rao, 1963) as it occurs in restricted areas only, especially in northeast India and Nilgiri Hills in southern India. However, establishment of land connections between India and neighbouring continents and the orogeny of Himalayas after Palaeogene also facilitated the entry of northern temperate conifers to the extra-Peninsular region. The palynological data from Siwaliks do suggest that the conifers, such as Pinus, Abies, Cedrus, Picea and Tsuga, etc. (Banerjee, 1968; Lukose, 1969; Nandi, 1972, 1975; Mathur, 1973; Saxena & Bhattacharyya, 1987; Singh & Saxena, 1980, 1981; Saxena and Singh, 1980, 1982a₅b; Singh & Sarkar, 1984; Saxena et al., 1982) had already reached the higher reaches of the newly emerged Himalayas from central and west Asian mainland by Miocene times (Ramanujam, 1976). There is also a report of pinaceous pollen in the Oligocene sediments of Himachal Pradesh (Mathur, 1984). However, absence of their megafossil record in the Siwalik sediments clearly indicates that they did not descend to the foot-hills zone. Thus it is evident that their pollen might have been transported from higher reaches in the north down into the Siwalik Basin. The occurrence of a northern temperate gymnosperm wood of Pinaceae from the Lower Karewa beds (Late Pliocene) of Kashmir (Awasthi & Guleria, 1982) suggests that by this time the Himalayas attained sufficient altitude to provide hospitable climate for rapid spread of this family.

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