

INDIA: THE ORIGINAL HOMELAND OF *CERATOPTERIS* BRONGNIART (PARKERIAACEAE)

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ABSTRACT

The spores of *Ceratopteris* Brongniart (known as *Striatriletes* in fossil state) have been studied in detail and it has been found that this spore was recorded for the first time from the Middle-Upper Eocene in Kachchh, Meghalaya and Assam. In Venezuela, Caribbean islands, Nigeria and Malayasia, *Striatriletes* started its occurrence in the Lower Oligocene. It has also been presumed that (a) *Ceratopteris* evolved in India during Middle-Upper Eocene when it was near the equator and enjoying tropical climate; (b) the genus migrated from western coast of India towards equatorial Africa and then crossed the Atlantic Ocean to reach tropical Americas; (c) *Ceratopteris* migrated to Malayasia through north-east India and from there it reached to tropical Australia. Further, it has been suggested that the dominance of *Ceratopteris* spores in Oligocene-Miocene sediments of India, Venezuela, Caribbean islands, Nigeria and Malayasia is indicative of a big palaeogeographical province which may be called as *Ceratopteris* or *Striatriletes* province.

Key-words — *Ceratopteris*, Parkeriaceae, Pteridophytes, Palaeobiogeography (India).

सारांश

सिराटॉप्टेरिस ब्रोंगनिआ (पाकॅरिएसी) की उद्भवभूमि : भारत - रंजीत कुमार कर

आदिमक रूप में स्ट्रियाट्राइलिटोज के नाम से विदित सिराटॉप्टेरिस ब्रोंगनिआ के बीजाणुओं के विस्तृत अध्ययन से यह प्रेक्षित किया गया है कि मध्य-उपरि आदिनूतन काल में यह बीजाणु कच्छ, मेघालय एवं असम से सर्वप्रथम अभिलिखित किया गया था। वेनेजुएला, करीबीयन द्वीपसमूह, नाइजीरिया एवं मलेशिया में यह अधरि अल्पनूतन काल में मिलता है। यह भी अनुमान किया गया है कि (अ) मध्य-उपरि आदिनूतन युग में जब भारत भूमध्य रेखा के समीप था तथा यहाँ उष्णकटिबंधीय जलवायु विद्यमान थी, सिराटॉप्टेरिस का विकास हुआ था; (आ) भारत के पश्चिमी तट से भूमध्यरेखीय अफ्रीका की ओर इस वंश का अभिगमन हुआ, तत्पश्चात् उष्णकटिबंधीय अमेरिका तक पहुँचने के लिए यह अटलांटिक महासागर को पार कर गया; (इ) सिराटॉप्टेरिस का उत्तर-पूर्व भारत से अभिगमन हुआ जहाँ से यह उष्णकटिबंधीय ऑस्ट्रेलिया पहुँच गया। इसके अतिरिक्त यह भी प्रस्तावित किया गया है कि भारत, वेनेजुएला, करीबीयन द्वीपसमूह, नाइजीरिया एवं मलेशिया के अल्पनूतन-मध्यनूतन काल में सिराटॉप्टेरिस के बीजाणुओं की बाहुल्यता से एक बृहत् पुराभौगोलिक प्रदेश की उपस्थिति व्यक्त होती है जिसे कि सिराटॉप्टेरिस अथवा स्ट्रियाट्राइलिटोज प्रदेश की संज्ञा दी जा सकती है।

INDIA has been called by Whitmore (1981) as 'Noah's Ark' drifting northwards and covering a distance of roughly 5,000 km. The rate of drifting was, however, not uniform though it is generally assumed that at times it was more rapid than any other continent so far known. Johnson, Powell and Veevers (1976) calculated that to cover such a long distance India might have travelled at the rate of 35-175 mm per year.

The scientists of the deep sea drifting expedition thought that the clue of relative and changing position of India and Australia might lie in the ocean floor between them comprising Bengal fan, central Indian basin, Ninety east ridge, and Wharton basin. McKenzie and Sclater (1971) detected prominent east-west magnetic anomalies in the Bengal fan and central Indian basin which constrain the position of India relative to Antarctica. The Ninety east ridge,

in the opinion of McKenzie and Selater (1971), marks a transform fault along which India migrated northward during the late Cretaceous and early Tertiary.

The wandering nature of India was no doubt deadly on some species but it also provided the unique opportunity to others to evolve and flourish. On its way, India might have also populated by other plants which were not indigenous to the soil. Of course, it would be very difficult to detect which plants were original and which were induced. Longwell (1963) observed that Nature's methods of distributing animals and plants are devious, some of them almost incredible. We may reckon as "vanishingly small" the probability that certain living forms can be transplanted between widely separated lands but by giving a million years or more a tiny probability may suffice. Otherwise it would be difficult to explain the presence of many tiny forms found indigenous or isolated in Pacific islands, thousands of miles away from their closest relatives or continents.

The water fern genus *Ceratopteris* Brongniart of the family Parkeriaceae may be considered here in this context. *Ceratopteris* is only genus of the family and one of the very few annual and aquatic ferns with exceptionally unstable sporangium wall. This genus is characterized by aquatic or subaquatic annuals with short, erect, rhizome bearing a few scattered small scales; stipes are green, fleshy with numerous vascular bundles. Fronds are moderate sized, pinnately decomposed, broad, glabrous, soft, herbaceous and dimorphic. Sterile fronds are with broad lobes, ovate or triangular, pinnate or bipinnatifid and often viviparous. Fertile fronds are larger, finely dissected with longer and narrower pinnules than the sterile. Venation of the fronds are reticulate. Sporangia are sessile or subsessile, seriate along the veins, large and occupying the entire surface, protected by continuous inflexed leaf margins. Annulus comprises 30-70 broad, thickened cells.

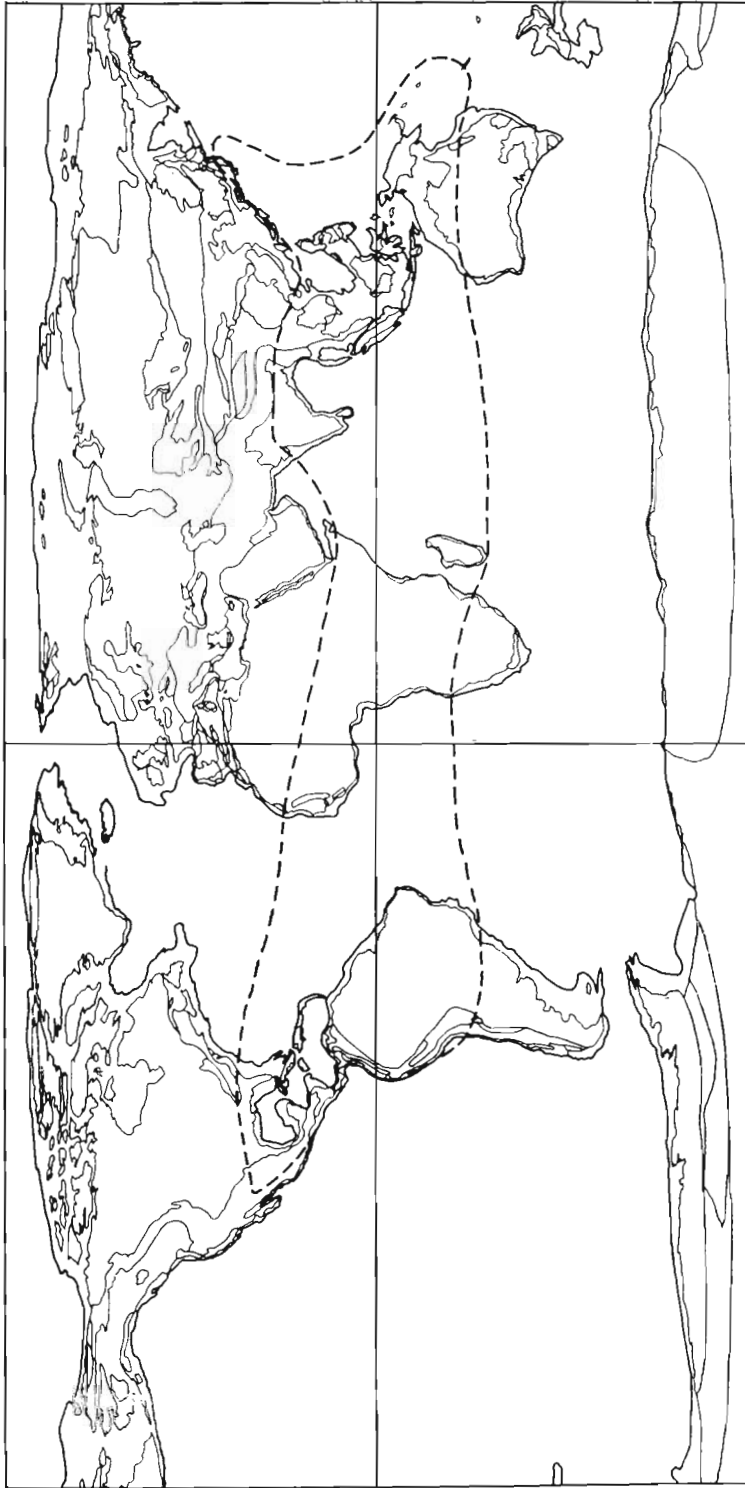
Ceratopteris pteridoides according to Copeland (1974) is a typical floating fern with inflated stipes which supply necessary buoyancy, able to root or grow on mud and can not exist elsewhere. The roots are freely produced from the lower surface of stipes to absorb the nutrients and

to provide additional buoyancy. It is the only fern, so far known, ever grown as a food crop by the natives.

Hooker and Baker (1868) noted the occurrence of *Ceratopteris* throughout the tropics in quiet water from Mexico and West Indies southward in Brazil and up to Florida in North America and in Asia from Punjab southwards up to tropical Australia, in Madagascar, Angola, west tropical Africa and particularly in Nigeria. It also occurs in Japan (Text-fig. 1).

In India, this genus (Chowdhury, 1973), is found in Dehradun and Haldwani in Uttar Pradesh, Gujarat except Kachchh, Maharashtra, Goa, Kerala, Tamil Nadu, Orissa, Bihar, West Bengal and Assam. He is of the opinion that there are about seven species of this genus of which two are found in the orient, one in Africa and three in tropical America. Lloyd (1972), on the other hand, after examining the extensive herbarium material opines that the genus *Ceratopteris* can be divided into four species based solely on morphological characters. These include *C. richardii*, found in Africa and tropical region of America, *C. pteridoides* of South and North America, *C. cornuta* distributed from Africa to northern Australia and *C. thalictroides*, a highly polymorphic species of circum-tropical distribution. According to him the important diagnostic characters include spore number per sporangium, annulus cell number, spore size, floating or rooting habit, stipe width, shape and dissection of sterile fronds, and frequency of vegetative budding. Out of them *C. richardii* is the most distinct and uniform species and has only 16 spores per sporangium and they may be up to 150 μ m in size. The remaining three species have 32 spores per sporangium. Lloyd (1972) thinks that *C. thalictroides* is the most diverse morphologically and probably polytypic. Distinct populations of this species occur in Japan, Surinam and Central America.

The spores of *Ceratopteris* are very characteristic and can be easily identified in the dispersed condition. They are generally subtriangular-subcircular in shape with rounded apices and straight to slightly convex interapical margin. The trilete rays are generally distinct, uniformly broad and extend half to three-fourth radius. Exine costate, costae appear as bands, running



TEXT-FIG. 1 — Showing the present day distribution of *Ceratopteris* Brong. (Parkeriaceae).

more or less parallel to each other in one inter-radial area and its corresponding distal side. Generally one set of costae is found in each inter-radial area on the proximal side; they may arise on proximal side parallel to the trilete rays or at the ray ends. Three corresponding sets of costae on the distal side may also be juxtaposed on the distal polar region leaving a triangular area in between them.

No other spores have similar features and this is also true in the spores of *Anemia* and *Mohria* which also have costate trilete spores. But the spores of *Anemia* and *Mohria* have two distinct sets of costae on proximal and distal surfaces (Kar, 1979).

The fossil spores of *Ceratopteris* are known as *Striatriletes* van der Hammen emend. Kar (1979). Germeraad, Hopping and Muller (1968) instituted *Magnastriatites* also to accommodate this type of spores. But according to Kar (1979) *Magnastriatites* is nothing but a junior synonym of *Striatriletes*. The genus *Cicatricosisporites* Potonié & Gelletich (1933) also resembles *Striatriletes* in the presence of costae. The costae in *Cicatricosisporites*, however, are restricted either to proximal or distal side and run parallel to each other.

The spores assignable to *Striatriletes* have been reported from India by Meyer (1958), Baksi (1962, 1965), Biswas (1962), Banerjee (1964), Banerjee, Misra and Koshal (1973), Ghosh, Jacob and Lukose (1964), Sah and Dutta (1968), Salujha, Kindra and Rehman (1972, 1974), Nandi (1975), Kar (1979), Kar and Saxena (1981), Kar and Jain (1981) and others.

Germeraad, Hopping and Muller (1968) had the unique opportunity to work out surface and subsurface material of Caribbean region, Venezuela, Nigeria and Malayasia for number of years. They reported the occurrence of fossil spores of *Ceratopteris* from the Lower Oligocene to Pliocene from Caribbean, Nigeria and Borneo. They observed that the source areas of this species are the alluvial plain and swamps near the coast. *Ceratopteris* grows in these regions as a small aquatic fern in shallow water, on the margin of lakes and river banks. This environment is liable to rapid local facies changes and is distinctly marked in the pronounced quantitative fluctuation in past coastal sediments. In marine sediments, Germeraad, Hopping and Muller

(1968) found the spores of *Ceratopteris* much rarer. They are, however, found in good quantities both in the shelf and geosynclinal facies of north-eastern India. Germeraad, Hopping and Muller (1968) remarked that the frequency of *Ceratopteris* spores in the Neogene of all the pantropical areas and their absence in the older Palaeogene and Cretaceous deposits indicate that the present day pantropical distribution of *Ceratopteris* may date only from the mid-Tertiary. They, however, observed that this is in contrast to the isolated systematic position and specialized morphology of the genus which is assumed to be of great antiquity. Its origin may have been local but as no ancestral forms are found this problem remains unsolved.

Copeland (1947) noted the extraordinary instability of the sporangium wall in *Ceratopteris* which has no parallel in other group of ferns. He remarked that the most probable affinity of *Ceratopteris* is to the Cheilanthes Group. If this supposition is true then the sporangium is to be regarded as degenerate, to the limit that in *C. pteridoides* it is rather a structureless sack holding the spores together. Copeland (1947) did not think *Ceratopteris* as primitive. The costate spores according to him recall those of *Orthiopteris*. He further observed that the degeneration of sporangial structure in *Ceratopteris* has taken it beyond easy inclusion in any family but there is no doubt that it has derived from some other families.

Whatever might be the origin of *Ceratopteris*, its subsequent development and dispersal in wide areas around tropical-subtropical countries throughout the world in a comparatively small span of time is very striking. According to Croizat (1952) ferns and fern allies can be divided into two elements: (a) that had associated with the angiosperms from the beginning, and (b) which had not associated so but later absorbed within the angiospermous floras. The former overtops the latter because the former travelled with angiosperms which were themselves Antarctic. He also observed that non-angiospermous dispersal ought to be studied in a special manner because so far the origin of these plants are concerned they are in the dimmest night of the ages.

But the case of *Ceratopteris* is entirely different; it is even younger than the angiosperms and within roughly 50 million years it has spread its tentacles all over the world in the tropics. It is a matter of great palaeogeographical importance to decipher its original home and subsequent dispersal in both old and new worlds. In trying to explain the distribution of vegetable species and the paths they have followed, a better result may be attained by studying the ways in which they spread at the present time than by setting up hypotheses of tremendous convulsion of nature which can neither be proved or disproved (vide Willie in Croizat, 1952). Croizat (1952) also thought that dispersal being older, it is dispersal phenomenon that gives a clue to the maps that are relevant in the case and not the other way round. He also remarked that faulty thinking in fundamentals is beyond doubt responsible for 90 per cent of the difficulties in modern biogeography. The literature conclusively shows that dispersal cannot be approached constructively in any other way but with a good understanding of its magnitude in time and space.

Thanks to the peculiar spore morphology of *Ceratopteris* and its association with potential oil bearing sedimentary rocks, the fossil history of this genus is quite precisely known. Germeraad, Hopping and Muller (1968) proposed several pantropical palynological zones of which *Proxapertites operculatus* Zone is the oldest and is probably Senonian in age. The next is the *Monoporites annulatus* Zone and the third in ascending order is *Verrucatosporites usmensis* Zone. In the latter zone there is sporadic occurrence of *Cicatricosisporites dorogensis* Potonié & Gelletich (1933) in the Caribbean area and in Paz del Rio section in Colombia.

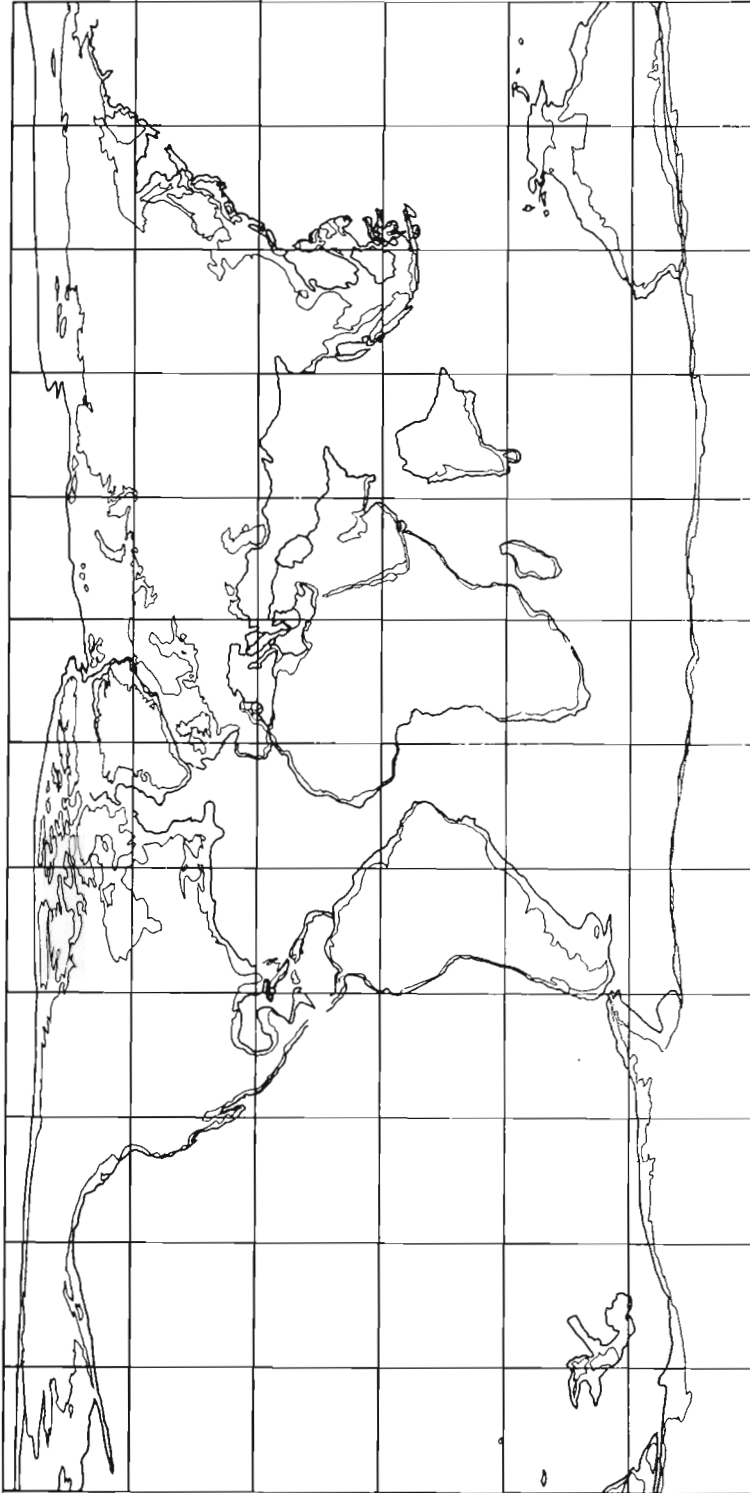
In the presence of smaller foraminifera: *Globigerina ampliapertura*, *G. ciproensis*, *Globorotalia opina opina* and *G. kugleri* in the Caribbean area the age of the overlying *Cicatricosisporites dorogensis* Zone may be assigned to Oligocene. In Nigeria, the same age is indicated by the presence of *Globigerina ciproensis*, *G. ciproensis angulituralis* and *Globorotalia kugleri*. It may be mentioned here that Trivedi, Ambwani and Kar (1981) has already pointed out that the specimen illustrated by Germeraad, Hopping and Muller (1968,

pl. 2, fig. 2) as *Cicatricosisporites dorogensis* Potonié & Gelletich (1933) may not belong to *Cicatricosisporites* but to *Malayaeaspora* Trivedi, Ambwani & Kar (1981).

The next overlying *Magnastriatites howardi* Zone is marked by the first appearance of *Magnastriatites howardii*. As has been stated earlier, Kar (1979) made *Magnastriatites* as a junior synonym of *Striatriletes* van der Hammen emend. Kar (1979). According to Germeraad, Hopping and Muller (1968), in Paz Del Rio Section, Colombia and Benin West-1, Nigeria, the boundary is sharply defined. The age of this zone starts from the Lower Oligocene in Caribbean, Nigeria and Borneo and continues up to Pliocene.

In India, the history of the fossil spores of *Ceratopteris*, viz., *Striatriletes* is, however, different. Kar and Saxena (1981) worked out a bore-core near Rataria, southern Kachchh, Gujarat where they recorded *Striatriletes susannae* van der Hammen emend. Kar (1979) and *Striatriletes multicostatus* Kar & Saxena (1981) from the bore-core along with *Cheilanthoidespora enigmata*, *C. monoleta*, *Couperipollis kutchensis*, *Tricolpites reticulatus*, *Lakia-pollis ovatus*, *Hystrichosphaeridium tubiferum*, *Oligosphaeridium complex*, *Cordosphaeridium gracilis* and *Hystrichokolpoma eisenacki*. On the basis of this palynological assemblage, Kar and Saxena (1981) assigned a Middle to Upper Eocene age. It may be pointed out here that there is no exposures of Upper Eocene rocks in Kachchh and thus a Middle Eocene age for the bore-core seems to be appropriate.

The palynological investigation of the Tertiary sediments in north-eastern India worked out by Baksi (1962, 1965, 1973), Biswas (1962), Sah and Dutta (1966, 1968), Dutta and Sah (1970), Banerjee and Misra (1972), Salujha, Kindra and Rehman (1972, 1974), Sein and Sah (1974), and others revealed that *Ceratopteris* spores occur for the first time in the Kopili Formation (Upper Eocene). On the basis of this spore, Sein and Sah (1975) demarcated the Middle Eocene (Sylhet Limestone) from the Upper Eocene. The percentage of this spore is further increased in Oligocene represented by the Barail Group in both shelf and geosynclinal sediments. In Miocene, this spore is equally abundant but gradually declines in Pliocene.



TEXT-FIG. 2 — Cylindrical equidistant map of the world (after Smith, Hurley & Briden, 1981) during Palaeocene. Note the position of India and its nearness to the east coast of Africa.

From the above information, it becomes apparent that the oldest fossil record of *Ceratopteris* spore is from the Middle-Upper Eocene in India while in Malayasia, Venezuela, Nigeria and Carribean it starts from the Oligocene. In this context, the relative position of India during Eocene with reference to Africa, Malayasia and Australia may provide a new vista of knowledge hitherto unconsidered.

Smith and Briden (1977) and Smith, Hurley and Briden (1981) published a series of maps showing the wandering continents and their relative position from one another. They did not profess these maps without errors but certainly provide the basic position of the continents to formulate some hypotheses. They have also not shown the microcontinental islands in the oceans.

About 60 million years ago during Palaeocene they have placed India in the cylindrical equidistant map projection below the equator. The western coast of India was almost running parallel to the eastern coast of Africa and Madagascar was comparatively closely placed. India in this position was ideally placed for the propagation of *Ceratopteris* because it was almost in the realm of tropical zone. The modern distribution of *Ceratopteris* bespeaks with eloquence its love for the tropical subtropical climate. At that time Kachchh was nearer to equator than Assam and was also nearest to the eastern coast of Africa (Text-fig. 2).

Approximately about 40 million years ago during the Upper Eocene as shown in the cylindrical equidistant map by Smith, Hurley and Briden (1981), major part of India had already crossed the equator. The north-eastern India was almost in touch with Malayasia though north India was still quite away from the mainland of Laurasia.

During Lower Miocene about 20 million years ago, as depicted by Smith, Hurley and Briden (1981), the southern most tip of India has already passed equator and

land connection between India and Laurasia firmly established.

Considering the wandering nature of India and its relative position in relation to other continents during Tertiary, it may be envisaged that during Middle-Upper Eocene *Ceratopteris* evolved in India. From the western coast of India, the genus migrated towards equatorial Africa and from there to tropical region of North and South America by crossing the Atlantic Ocean. The north-east India, particularly Assam also played an important role to disperse *Ceratopteris* in Malayasia and tropical Australia. Madagascar was perhaps populated through Africa and Japan through Malayasia.

As is well known that *Ceratopteris* is a herbaceous water fern which can survive only in fresh water, of warm climates. How could such a small plant disperse so quickly and how it could cross the Atlantic and other oceans are matters of speculation. Even if it is admitted that the Atlantic Ocean was not so wide during the Upper Eocene, it has to be assumed that the plant must have possessed a very effective means of dispersal. The credit perhaps goes to the robustly built costate spores for this. The spores might have travelled long distances with the help of favourable winds and water currents. Besides, some water fowls might have been instrumental in dispersing the adhering sticky spores into far off places. It would be no wonder if some birds also swallowed the spores along with mud and the undigested spores later came out to germinate in new places.

The overwhelming dominance of *Ceratopteris* spores in Oligocene and Miocene sediments of India and also its regular occurrence in similar sediments of Caribbear, Nigeria and Malayasia makes it a big palaeogeographical province which may be called as *Ceratopteris* or *Striatriletes* province.

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