STUDIES ON THE SPORES OF *LYCOPODIUM* AND THEIR FOSSIL HISTORY WITH SPECIAL REFERENCE TO INDIA

R. K. KAR AND J. MANDAL

Birbal Sahni Institute of Palaeobotany, Lucknow-226 007

ABSTRACT

The spore morphology of 23 species of Indian *Lycopodium* and two species from outside has been investigated to know their fossil history particularly to the Indian subcontinent. Fossil spores comparable to *Lycopodium* are placed under many artificial genera. Various species of these fossil miospore genera from India have been critically reassessed and their affinity with the living forms discussed. It is postulated that *Lycopodium* grew luxuriantly in north eastern India from the beginning of Tertiary. The foveolate-fossulate type of spore-producing plant is very common at present while the reticulate type was dominant during the Tertiary. Evolutionary tendencies of the spores have also been discussed in the light of information gathered from fossil spores.

INTRODUCTION

Lycopodium plants are herbaceous, terrestrial or epiphytic. Vegetative leaves and sporophylls are either similar or dissimilar and sporangia are borne on the adaxial side of the sporophyll on the axil or on sporophyll and may aggregate to a strobilus or uniformly distributed. All the species are homosporous.

ROTHMALER (1944), SEN AND SEN (1978) and MANDAL AND SEN (1979) segregated *Lycopodium* into five different genera: *Huperzia* Bernhardi (1801), *Phlegmariurus* (Herter) Holub (1964), *Palhinhaea* Franco & Vasc. (1967), *Lycopodium* Linnaeus (1753) and *Diphasium* Presl *ex* Rothmaler (1944). They divided these genera on the basis of the habitat, nature of dichotomy of the stem and its stelar character, sporophylls, gametophyte, spore morphology and the basic chromosome numbers. The lycopodiaceous plants though exhibit luxuriant growth in some parts of India are confined to 27 taxa comprising all the five genera, viz. *Huperzia*, *Phlegmariurus*, *Palhinhaea*, *Lycopodium* and *Diphasium* (MANDAL & SEN, 1979; SEN & SEN, 1978). Most of the plants are commonly found in Himalayas, Jaintia and Khasi hills in Meghalaya, Parashnath and Chota Nagpur hills in Bihar, Nilgiri hills and Western Ghats. They are also frequently met with in Andaman and Nicobar Islands, hills of Assam and Tripura. They are rarely found in Sunderbans and plains of Bengal. Their distribution has been shown in Map 1 and is detailed below:

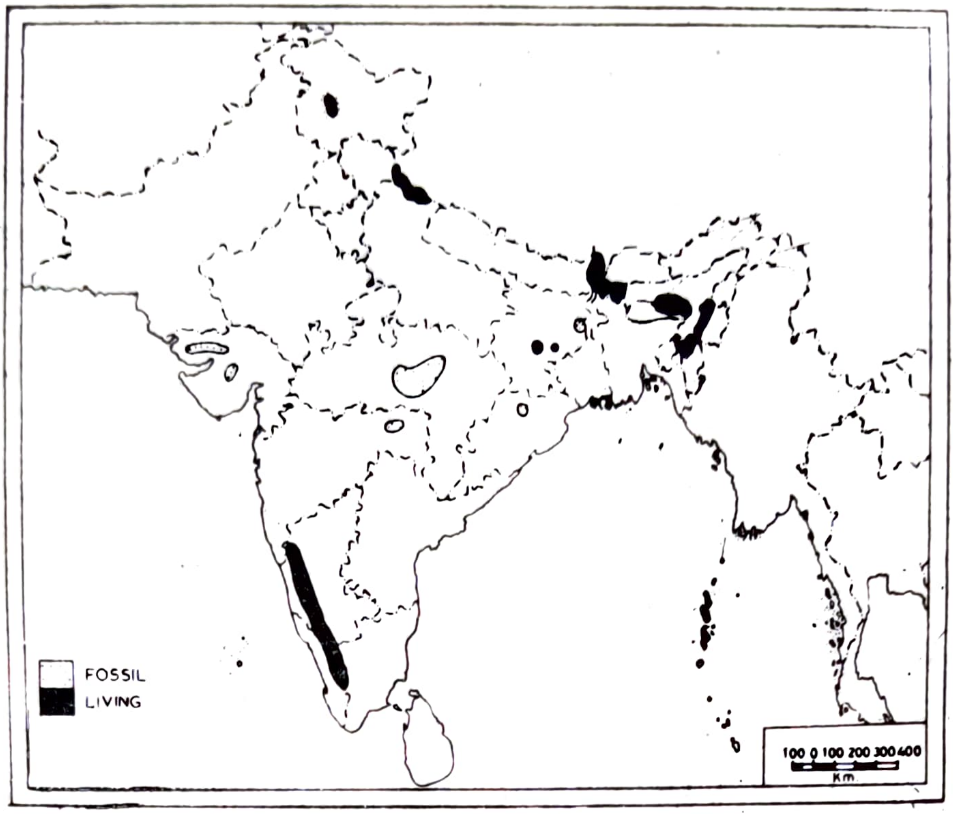
Alpine forest (above 3,900m)—*Lycopodium clavatum* L. (rare), *Huperzia selago* (L.) Bernh. ex Schrank & Mar. (rare), *H. herteriana* (Kümm.) Sen & Sen (rare), *Diphasium tristachyum* (Prush.) Rothm.

Cold temperate—subalpine forest (2,700—3,900 m)

H. selago (L.) Berhn. ex Schrank & Mar., *H. herteriana* (Kümm.) Sen & Sen, *H. hamiltonii* (Spring ex Hook. *et* Grev.) Sen & Sen, *Palhinhaea cernua* (L.) Franco & Vasc. (rare), *P. cernua* var. *pendula* (Baker) Mandal & Sen, *Diphasium alpinum* (L.) Rothm., *D. tristachym* ((Prush) Rothm., *Lycopodium clavatum* L., *L. veitchii* Christ.

Warm temperate forest (1,500—2,700 m)

Huperzia selago (L.) Bernh. ex Schrank & Mar., *H. serrata* (Thumb.) Rothm., *H. herteriana* (Kümm.) Sen & Sen, *H. subulifolia* (Wall. ex Hook. & Grev.) Mandal & Sen, *H. obtusifolia* (Swartz) Rothm., *H. hamil-*



Map 1. Showing the past and present distribution of *Lycopodium* in India.

tonii (Spring ex Hook. & Grev.) Sen & Sen, *Phlegmariurus phlegmaria* (L.) Rauschert, *H. phyllanthus* (Hook. & Am.) Löve & Holub ex Holub, *Diphasium wightianum* (Wall. ex Grev. & Hook.) Pic. Ser., *D. casuarinoides* (Spring) Mandal & Sen, *D. complanatum* (L.) Rothm., *Palhinhaea cernua* (L.) Franco. & Vasc., *P. cernua* var. *mariana* (Baker) Mandal & Sen, *P. cernua* var. *pendula* (Baker) Mandal & Sen, *P. cernua* var. *curvata* (Baker) Mandal & Sen, *Lycopodium clavatum* L., *L. veitchii* Christ.

Tropical—subtropical forest (upto 1,500 m)

Huperzia selago (L.) Bernh. ex Schrank & Mar., *H. carinata* (Desv.) Rothm., *H. squarrosa* (Forst.) Rothm., *H. pulcherrima* (Wall. ex Hook. & Grev.) Pic. Ser., *H. subulifolia* (Wall. ex Hook. & Grev.) Mandal & Sen, *H. subulifolia* var. *assamica* Mandal & Sen, *H. gnidioides* (L. fil.) Rothm., *H. fordii* (Baker) Mandal & Sen, *H. laxa* (Presl) Sen & Sen, *Phlegmariurus phlegmarius* (L.) Rauschert, *P. phyllanthus* (Hook. & Am.) Löve & Holub ex Holub, *Palhinhaea cernua* var. *curvata* (Baker) Mandal & Sen and *Lycopodium clavatum* L.

The distributional pattern of different species in India indicates that the species belonging to the genera *Diphasium, Palhinhaea* and *Lycopodium* (*sensu stricto*) are retricted to the subalpine forest. On the other hand, most of the species of *Huperzia* and *Phlegmariurus* are confined to the tropical-subtropical forests. Some species, however, like *Lycopodium clavatum* and *Palhinhaea cernua,* show wide climatic tolerance and found from alpine to subtropical climatic zones.

FOSSIL LYCOPODS FROM INDIA

Fossil lycopods are rarely found in Palaeozoic and Mesozoic rocks of India. Surange (1966) and Kar (1968) described *Cyclodendron leslii* (Seward) Kräusel (1961) from the Barren Measures Succession (Middle Permian) of Jharia Coalfield, Bihar. Most of the specimens described by them are fragmentary but they show externally regular leaf scars arranged in quincuncial manner. The leaf scars are more or less spindle-shaped and depressed. Within each scar there is a raised part which is also depressed in the middle and having a small but sharp boss indicating perhaps the position of vascular supply to the leaf. Recently, CHANDRA AND RIGBY (1981) have recorded *C. leslii* from Handappa, Himgir Formation (Upper Permian), Orissa.

SRIVASTAVA AND KAPOOR (1967) reported *Lepidostrobus kashmirensis* from the Lower Gondwanas of Kashmir in association with *Gangamopteris*. The specimen is ill-preserved and exhibits only a cylindrical strobilus whose affinity is not properly known. KAPOOR (1969) also described *Lepidodendron* and an ill-preserved cone-like structure probably attached to a lycopod stem from the Lower Gondwanas of Zewan Spur, Kashmir. SURANGE (1971), however, doubted the identification of KAPOOR's *Lepidodendron*. In his opinion, the specimen does not show any ligule or parichnos scars and so it would be better not to place in *Lepidodendron*.

HØEG *et al.* (1956) investigated Carboniferous flora from the Thabo Stage of Spiti, western Himalayas. This flora is conspicuous by the absence of *Lepidodendropsis* or any other lycopods. PAL (1978) reported *Archaeosigillaria, Lepidosigillaria, Lepidodendropsis, Cyclostigma* and *Lepidodendron* from the Gund Formation (Lower Carboniferous) of Kashmir. Later, PAL AND CHALONER (1979) reinvestigated the assemblage and recorded the following lycopsids: *Archaeosigillaria* sp., *Lepidosigillaria* cf. *quadrata, Lepidodendropsis* sp., *Lepidodendropsis* cf. *sigillarioides, Lepidodendropsis* cf. *fenestrata* and *Cyclostigma ungeri*. According to them, this flora confirms the close comparability of the Lower Carboniferous flora of northern India with that of other areas both in Gondwana and the present northern hemisphere. SINGH *et al.* (1982) recorded rich lycopod assemblage from Upper Devonian and Lower Carboniferous of Kashmir Himalaya.

LELE (1962) noted the occurrence of *Lycopodites sahnii* from the Triassic bed of South Rewa Gondwana Basin, Madhya Pradesh. The species is characterized by a slender, unbranched stem with linear to elliptical scars of leaf base containing single leaf trace mark. Another species of *Lycopodites*, viz. *L. gracilis*, is also known from the Rajmahal Hills (Jurassic) of Bihar. BOSE *et al.* (1984) reported a new species of *Lycopodites*, viz. *L. ghoshii*, from Gardeshwar Formation (L. Cretaceous) of Gujarat. Specimens assignable to *Lycopodites* are also known from the Bhuj Formation (Lower Cretaceous) of Kachchh, Gujarat. The specimens recorded from the Rajmahal Hills are irregularly branched with spirally arranged tetrastichous leaves and in general more similar to *Selaginella* than *Lycopodium* though in *L. volubile* the above mentioned characters are also exhibited.

It may be mentioned here that the genus *Lycopodites* was instituted by BRONGNIART (1822) from the Tertiary. Various species have been attributed to this genus from Carboniferous to Tertiary and it seems more probable that some of them may not belong to *Lycopodium*. The leaf arrangement in some of *Lycopodium* and *Selaginella* are quite similar to each other and in the fossil condition where the ligules have remote chance of preservation the exomorphic features of both genera should be strikingly similar and would be very difficult to distinguish one from the other.

The anatomical characters of *Lycopodium* and *Selaginella* are, however, very distinct. SRIVASTAVA (1946) described *Lycoxylon indicum*-a petrified stem from the Rajmahal Hills. In transverse section, it shows plectostele in centre and thick-walled inner cortex outside the stele. These anatomical peculiarities are found in the genera *Lycopodium* and *Diphasium*. SHARMA (1971) described poorly preserved, fertile, heterophyllous lycopods as *Selaginellites* sp. A and *Selaginellites* sp. B, from the Rajmahal Hills which differs from known species of *Lycopodites* in the mode of branching.

Singh and Patil (1979) recorded a petrified strobilus of *Selaginella* from the Deccan Intertrappean beds of Mohgaonkalan, Madhya Pradesh. They suspected in one of the sporangium, 1-2 large spores-looking like megaspores. A distinct ligule-like outgrowth was also witnessed by them in between the sporangium and sporophyll.

SPORES OF LYCOPODIUM (*Sensu* LINNAEUS) FROM INDIA

Lycopodium plants are homosporous. They produce trilete, tetrahedral minute spores ranging from about 30-58 μm. The ornamentation pattern on the exine is mainly of three types; pitted, reticulate and rugulate. The shape and the size-range within the species is almost constant. All the terrestrial, procumbent forms under the genera *Lycopodium* (*s. s.*) and *Diphasium* produce reticulate exine with exception of *D. casurinoides* where exine is scabrate (Wilce, 1972). In the reticulate forms the polygons are irregular in shape and size distally, rarely muri are found to be incomplete (e.g. *L. volubile*). The muri extends over the equator on the proximal surface. Proximal polygons are unlike distal ones, form a few complete polygon and then the open ends of muri form loops or straight way ends near to laesurae. *L. veitchii* and *L. volubile* are two exceptions of the above mentioned forms, and proximal surface without any ornamentation. The spores of *L. volubile* are unique and can be separated easily from other reticulate forms. They possess a thin hyaline, narrow zona around the equator. As a whole, the reticulate forms are very static in nature. Wilce (1965) after studying about 300 taxa of the section *complanata*, commented that there is no quantitative character difference in spore sculpturing between the species. She observed that the most obvious difference between species was the variation in lacunar size and height of muri. All the epiphytic species and the only known three erect terrestrial species viz. *Huperzia selago, H. herteriana* and *H. serrata* have pitted exine. There are significant variations among the species in the shape of spore and the nature of pitting. *Huperzia selago, H. herteriana* and *H. serrata* are considered to be most primitive members of the family and are very peculiar in various characters. Spores of these plants are triangular with straight side walls, truncated corners, and are foveolate. The pits are large, oval, elongated with irregular face. Spores of rest of the species of *Huperzia* and *Phlegmariurus* are rounded-triangular in shape with convex sides and the pits on the surface are either free (i.e. foveolate, e.g. *H. gnidioides*) or fused (i.e. fossulate) forming irregular canals (e.g. *H. pulcherrima*) and still in some few pits only fuse (i.e. foveolate-fossulate e.g., *H. subulifolia*). These pitted type spore-producing forms are commonly inhabitant of tropical-subtropical climate. In all, 15 Indian species are known to possess this type of pitted exospore.

The members of the genus *Palhinhaea* have rugulate exospore on the distal surface and the trilete mark is situated in groove. A large number of spores within a functional sporangium are often abortive. Rugulate ornamentation occurs in small number of species.

The most interesting species among the extant *Lycopodium* (*s. l.*) is *L. densum* which possesses baculate spores (Wilce, 1972). Wilce (1972) made a preliminary survey of 161 spore samples using SEM and found that the spore form to be quite consistent within a sample and between samples of same taxon from widely separated localities. She recognised five broad classes of spore wall ornamentation. These are (i) foveolate-fossulate type (e.g. *L. selago, L. phlegmaria* etc.), (ii) rugulate type (e.g.

L. cernuum, L. carolinianum etc.), (iii) reticulate type (e.g. *L. veitchii. L. clavatum* etc.) (iv) baculate type (e.g. *L. densum* only) and (v) scabrate type (e.g. *L. casuarinoides* only). The work of Knox (1950), Wilce (1965, 1972), Sen and Sen (1978) and Mandal and Sen (1979) revealed that in certain species-groups there is very good correlation between gross morphology, habitat and the spore ornamentation types.

Huperzia subulifolia (Pl. 2, Fig. 24)—Rounded triangular, amb convex. Diameter 34.3 to 50 μm, average 43 μm, side walls nearly 1.5 μm thick. Laesurae simple, faint but prominent, 2/3 of the diameter, rarely arms wavy, angles between arms rarely unequal. Generally distally pitted, rarely a few on proximal surface. Few distal pits occasionally fused (i.e. fovoelate-fossulate), rarely typically foveolate. Pits circular, small.

H. serrata (Pl. 1, Figs. 3-4; Pl. 2, Fig. 40)—Nearly hexagonal due to truncated corners, amb straight to concave. Diameter 32 to 40.5 μm; average 35 μm. Laesurae thick, tapering and extends near to the margin. Side walls uniformly thick, 2.5 to 3.5 μm, often corrugated, angle between laesurae equal, rarely one arm curved. Pits on distal surface only, typically foveolate. Pits oval, elongated with irregular opening.

H. selago (Pl. 1, Figs. 1-2)—Elongated triangular, corners truncate, side walls straight to slightly concave, uniformly thick and occasionally corrugated due to pitting. Typically foveolate, rarely present proximally; pits oval, elongated with irregular opening, rarely a few fused. Laesurae stout, tapering, 1/2 to 2/3, rarely arm wavy. Wall 2.3 to 3.1 μm. Diameter 41.3 to 53 μm, average 45.2 μm.

H. herteriana (Pl. 1, Figs. 5-6)—Elongated triangular, slightly truncated corners. Diameter 39 to 54.6 μm, average 45.2 μm. Side wall straight, rarely concave, smooth, thick, nearly 2.5 μm. Laesurae stout, tapering, 3/4 to nearly touching margin. Distally pitted, strictly foveolate.

H. obtusifolia (Pl. 2, Fig. 21)—Rounded triangular with convex walls, side-walls uniformly thickened, 1.5 to 2.5 μm, often slightly corrugated. Laesurae prominent, tapering, straight, 2/3 of radius and rarely arms touches the margin. Distally pitted, more than 50% pits fuse i.e. fossulate. Diameter 49.1 to 57.7 μm, average 51.4 μm.

H. tetrastychya (Pl. 2, Fig. 22)—Triangular to rounded triangular, side walls uniformly thick, about 1.5 μm, smooth. Diameter 39 to 45.2 μm, average 44 μm. Laesurae stout, 1/2 to 2/3, rarely touching margin, straight. Pits on both the surfaces, very few proximally. Typically foveolate. Pits circular, large, occasionally absent at distal polar zone, nearly 80 on the distal surface.

H. gnidioides (Pl. 2, Fig. 23)—Rounded triangular, corners rounded, side walls convex, 1.5 to 3.1 μm thick, smooth, few pits on side walls. Laesurae straight, stout, 2/3, generally one arm near to the margin. Only distally pitted, typically foveolate, occasionally absent on polar zone. Diameter 54.6 to 67 μm, average 57.7 μm.

H. pulcherrima (Pl. 2, Fgs. 25-26, 39)—Rounded triangular to rarely spherical, corners rounded, less thickened than the side walls. Side walls 1.5 to 2.3 μm, corrugated. Laesurae simple, 1/2 to 2/3 rarely upto margin. Proximal surface devoid of pits. Distally fossulate, hardly single pit remains free. Generally preserve proximally. Single oval grain with triletoid mark. Diameter 42.1 to 48.3 μm, average 43.6 μm.

H. hamiltonii (Pl. 1, Figs. 13-14)—Rounded triangular to spherical, corners rounded, rarely one corner more angular, side walls nearly 1.5 μm thick, often corrugated. Laesurae faint, tapering, 2/3 to near margin. Proximal surface smooth. Distally foveolate-fossulate. Pits circular, smallest among the pitted species. Diameter 29.6 to 37.4 μm, average 34.3 μm.

H. subulifolia var. **assamica** (Pl. 1, Fig. 16)—Triangular, side walls smooth, uniformly thick, 2.3 to 3.1 μm. Laesurae very stout, nearly touching margin, tapering, occasionally curved. Only distally pitted, foveolate, a few pits fuse generally, occasionally polar region devoid of pits. Diameter-45.2 to 54.6 μm, average 50.7 μm.

H. squarrosa (Pl. 1, Fig. 12)—Subtriangular, corners round, side wall convex, 1.3 to 2.3 μm, smooth. Diameter 40.5 to 4.7 μm. Laesurae faint, tapering, extends upto margin. Pitted on both the surfaces, few proximally. Foveolate, some may fuse, sparse towards centre.

H. carinata (Pl. 1, Fig. 7)—Rounded triangular, corners rounded, side walls convex, 1.3 to 2.3 μm, smooth, laesurae stout, tapering nearly extends to the margin. Pits circular, large, foveolate, on the distal surface only. Spores are about 30 μm in average diameter.

H. fordii (Pl. 1, Fig. 15)—Trilete, nearly spherical, exine about 1 μm thick. Laesurae faint, 2/3 of spore radius. Distally pitted, proximally laevigate, 3.5 to 39 μm in diameter (36.5 μm average).

H. laxa (Pl. 1, Fig. 8)—Rounded triangular, corners rounded, side wall 1.3 to 2.3 μm, smooth. Laesurae stout, tapering near to the margin. Pitted on both the surfaces, few on proximal surfaces. Distal pits crowded, foveolate. Diameter 29.5 to 38.2 μm, average 32.5 μm.

Phlegmariurus phlegmarius (Pl. 1, Figs. 9-10)—Broadly triangular, corners broad, often one corner angular. Side walls smooth 1.3 to 3.1 μm, convex. Laesurae strong but faint, often curved nearly touching margin. Distally pitted, pits small, crowded, typically foveolate, occasionally devoid at polar zone. Generally preserve distally. Diameter-37.4 to 46 μm, average 40.5 μm.

P. phyllanthus (Pl. 1, Fig. 11; Pl. 2, Fig. 27)—Rounded triangular to spherical, corners broadly rounded. Side walls slightly convex, 2.3 to 3.1 μm. Laesurae stout, tapering 2/3 to nearly margin, smooth, rarely bent. Corners less thickened than the side walls. Proximally without any ornamentation. Distally pits crowded, a few occasionally fused (foveolate-fossulate). Diameter-34.3 to 50.7 μm, average 46.8 μm.

Palhinhaea cernua (Pl. 2, Figs. 33-34)—Triangular, corners rounded, thinner than side walls. Side wall convex, smooth, 3.1 to 4.7 μm; laesurae 1/2 to 2/3, situated within a groove, thick at the joint. Distal ornamentation rugulate. Diameter-35.8 to 45.2 μm, average 37.4 μm.

Diphasium wightianum (Pl. 2, Figs. 31-32)—Rounded triangular, laesurae 3/4 of radius, occasionally wavy, reticulation on proximal surface forms loop, ends openly near to the mark. Distal reticulation regular. Diameter-56.1 to 65.5 μm, average 60 μm.

D. alpinum (Pl. 2, Fig. 38)—Rounded triangular to circular, laesurae 1/2 to 2/3, often curved. Distal muri often incomplete. Proximally complete polygons elongated. Diameter-39 to 48.3 μm, average 45.2 μm.

D. complanatum (Pl. 1, Figs. 19-20)—as in *D. alpinum* average diameter about 35 μm.

D. tristachyum—as in *D. wightianum*, average diameter about 44.5 μm.

Lycopodium clavatum (Pl. 1, Figs. 17-18)—Rounded triangular, laesurae tapering 3/4 to near to the margin, reticulate. Proximally redges end abruptly around the laesurae leaving open muri. Diameter-35.8 to 50 μm, average 41.3 μm.

L. veitchii (Pl. 3, Figs. 28-29, 37)—Rounded triangular, laesurae 1/2 to 3/4 reticulate, muri occasionally incomplete distally, proximal surface laevigate. Diameter 35.1 to 46.8 μm, average 43 μm.

L. volubile (Pl. 2, Figs. 30, 35-36)—Triangular, laesurae near to the margin. Distal polygons commonly incomplete. Proximal surface smooth. A narrow, thin, hyaline membrane around equator as wing. Spore diameter 41.2 to 48.3 μm, average 46 μm.

FOSSIL SPORES COMPARABLE TO LIVING *LYCOPODIUM* (*SENSU* LINNAEUS) SPORES

In dealing with the fossil spores, *Lycopodium (sensu* Linnaeus) has been accepted here as the differences on spore morphology, in some cases amongst the different genera advocated by various authors are very subtle. It may be recalled here that KNOX (1950) made an interesting effort to compare the fossil spores recovered from the Carboniferous coal of England with the extant lycopod. Her investigation revealed that the Palaeozoic spore genera *Triquitrites* (Wilson & Coe) Sullivan & Neves (1964) and *Tripartites* Schemel (1950) resemble the spores of *Lycopodium selago* in shape and in possession of thickened truncated corners. The former genus is, however, distinguished by its absenece of pitted ornamentation characterstic of the living species. She also remarked that many spores assigned to the genera *Microreticulatisporites* (Knox) Potonié & Kremp (1954) and *Reticulatisporites* (Ibrahim) Potonié & Kremp (1954) are of *Lycopodium* affinity except *Reticulatisporites polygonalis* and *R. fibriatus* which show resemblance with *Selaginella* in ornamentational pattern. The Mesozoic spore genus *Trilobosporites* (Pant) Potonié (1956) also resembles the spores of *Lycopodium selago* in general characters and thickening in the auriculate region but is also distinguished from the living species by its laevigate exine.

The spores of *Lycopodium* (*s. l.*) as detailed earlier are so varied that it is difficult to place them in one genus. However, *Lycopodiumsporites* Thiergart *ex* Delcourt & Sprumont (1955) is the best known fossil genus for accommodating dispersed fossil, reticulate spores having lycopodian affinities. It may be mentioned here that some other members of Lycopodiaceae, viz. *Phylloglossum,* possess reticulate, trilete spores. The microspores of *Selaginella* and *Isoetes* according to KNOX (1950) are very much different from that of *Lycopodium* as the exospore of those two genera possess acicular, spinose, warty, tuberculate or rod like protuberances besides membraneous extension of the wall to form the zona or the equatorial flange.

The genus *Lycopodiacidites* originally proposed by COUPER (1953) and subsequently emended by POTONIÉ (1956) is characterized by muri which do not anastomose to form perfect reticulate pattern. Though COUPER (1953) advocated for its *Lycopodium* affinity, it shows more resemblance with *Selaginella* than *Lycopodium* as the muri project haphazardly in all directions without forming true reticulation. However, some species, viz. *Lycopodium cernuum* have more or less this type of ornamentation.

DETTMANN (1963) instituted *Sestrosporites* for the triangular, trilete spores with differentially thickened exine, crassitude in the interradial area and foveolate to foveoreticulate sculpture. According to DETTMANN (1963) the spores of *Lycopodium manii*

Hillebr described by SELLING (1946) and those of *L. laterale* R. Br. figured by HARRIS (1955) are comparable to this genus. However, the form is not comparable to any of the Indian species.

Foveotriletes van der Hammen *ex* Potonié (1956) and *Foveosporites* Balme (1957) are both triangular-subtriangular spores with foveolate-foveoreticulate ornamentation. In the opinion of DETTMANN (1963), *Foveotriletes* is distinguished from *Foveosporites* in the presence of concavely triangular shape. *Microfoveolatisporis* Krutzsch (1959) is also comparable to *Foveosporites* Balme (1957) but nothing can be said with certainty as the illustration of the type species of *Microfoveolatisporis* does not depict the nature of ornamentation clearly. However, the spores assignable to *Foveotriletes* and *Foveosporites* are comparable to the spores of *Lycopodium verticillatum* group of KNOX (1950).

Foraminisporis Krutzsch (1959) apparently resembles the spores of *Lycopodium* in shape, size and negative reticulate pattern but is distinctly spinose with a few irregularly scattered foveola. DETTMANN (1963) thinks that this genus resembles the living hepatic species *Notothylas breutelii* Gottsche and *Phaeoceros bulbiculosus* Brotero.

Some of the other genera which come close to lycopodiaceous spores are *Klukisporites* Couper (1958), *Ceratosporites* Cookson & Dettmann (1958), *Camarozonosporites* (Pant) Klaus (1960), *Rugulatisporites* THOMSON & Pflug (1953) *Corrugatisporites* Weyland & Greifild (1953), *Grassoretitriletes* Germeraad, Hopping & Muller (1968) and *Auriculiretisporites* Venkatachala & Rawat (1971). Spores assignable to *Klukisporites* Couper (1958) have been described by VENKATACHALA (1969) from the Bhuj Formation (Lower Cretaceous), VENKATACHALA *et al.* (1968) from the Katrol (Upper Jurassic) of Kachchh, VENKATACHALA AND JAIN (1970) from the Lower Cretaceous of Cauvery basin and SAH AND SINGH (1980) from the Upper Cretaceous of Meghalaya. The reticulation in *Klukisporites* is broad, squarish and thick and it is quite unlike from present day *Lycopodium* spores.

The genus *Ceratosporites* Cookson & Dettmann (1958) has been recorded by SAH and JAIN (1964) from Rajmahal Hills (Upper Jurassic), VENKATACHALA (1969) from Bhuj Formation (Lower Cretaceous), VENKATACHALA AND JAIN (1970) from the subsurface samples of Cauvery basin (Lower Cretaceous) and others. This genus is easily distinguished from the living spores of *Lycopodium* in the presence of laevigate exine on the proximal side and variously ornamented on the distal side by clavae, setulae and capillae. COOKSON AND DETTMANN (1958) compared the type species of this genus with the extant spores of the *Selaginella latifrous* group of KNOX (1950). The genus *Camarozonosporites* (Pant) Klaus (1960), *Rugulatisporites* Thomson & Pflug (1953) and *Corrugatisporites* Weyland & Greifeld (1953) do not possess distinct reticulation with the baculi/muri and hence are easily separated from the *Lycopodium* spores.

GERMERAAD *et al.* (1968) instituted *Grassoretitriletes* to accommodate spherical, trilete, with coarsely reticulate undulated muri. KAR AND JAIN (1981) observed that in this genus muri on the proximal side are comparatively few than the distal one and they never form perfect reticulum. The muri on the distal side, however, anastomose to form perfect reticulum. This genus by its presence of very thick muri and imperfect reticulum on the proximal side readily distinguishes from the spores of *Lycopodium.* It may be mentioned here that GERMERADD *et al.* (1968) postulated the affinity of *Crassoretitriletes* with the living spores of *Lygodium microphyllum.*

A good number of fossil miospore genera resemble the spores of extant *Lycopodium.* The spores of *Lycopodium* as has already been stated possess mainly three types of ornamentation reticulate, pitted and rugulate. The reticulate sculpture in living

Lycopodium is quite rigid but the fossil reticulate spores exhibit diversified types of reticulation. The reticulate, trilete fossil spores resembling the living spores of *Lycopodium* are generally described as *Lycopodiumsporites* Thiergart *ex* Delcourt & Sprumont (1955). This genus has very wide geological and geographical distribution and is known from Permian to Pliocene in India. BHARADWAJ (1962) and BHARADWAJ AND SALUJHA (1964) reported this genus from the Raniganj Formation (Upper Permian) of Raniganj Coalfield, W. Bengal. MAHESHWARI AND KUMARAN (1979) subsequently recorded it from the Tikki Formation (Triassic) of South Rewa Gondwana basin, Madhya Pradesh. SUKH-DEV (1961) found this genus from Jabalpur Series (Lower Cretaceous) of Madhya Pradesh. VISHNU-MITTRE (1955) and SAH AND JAIN (1964) described spores assignable to this genus from the Rajmahal Hills (Jurassic) of Bihar. VENKATACHALA (1969), VENKATACHALA *et al.* (1969) recovered this genus from the Bhuj (Lower Cretaceous) and Katrol (Upper Jurassic) of Kachchh, Gujarat.

Tertiary sediments particularly of Assam and Meghalaya are rich in *Lycopodiumsporites*. SAH AND DUTTA (1966) and DUTTA AND SAH (1970) instituted a number of species of this genus from Cherra Sandstone (Palaeocene) of Meghalaya. SINGH (1974) and SINGH AND SINGH (1978) also reported various species of *Lycopodiumsporites* from the Tura Formation (Palaeocene-Eocene) of Garo Hills, Meghalaya. DUTTA AND SINGH (1980) recorded this genus from the Tertiaries of Arunachal Pradesh. MEHROTRA AND SAH (1980) recovered some very interesting spores of *Lycopodium*-type from the Mikir Formation (Palaeocene-Eocene) of Assam. RAMANUJAM (1967) reported them from Cuddalore Series (Micocene) of Tamil Nadu. POTONIÉ AND SAH (1960), KAR AND JAIN (1978) recorded them from Quilon and Warkala beds (Micocene) of Kerala. RAMANUJAM AND RAO (1980), and BAKSHI AND DEB (1981) encountered them in the subsurface samples of Andhra Pradesh and W. Bengal respectively.

It is interesting to note that some of the fossil spores described by these authors under *Lycopodiumsporites* resemble the living spores of *Lycopodium* and *Diphasium* in shape, size-range, nature of the trilete rays and ornamentational pattern. For example, *Lycopodiumsporites austroclavatidites* (Cookson) Potonié (1956) described by SAH AND JAIN (1964, pl. 2, figs, 61-63) from the Rajmahal Hills (Jurassic), Bihar are very much similar to the living reticulate spores of *Lycopodium clavatum.* The spores placed by DETTMANN (1963, pl. 7, figs. 1-3) under *L. austroclavatidites* from the Upper Mesozoic strata of Australia are very much close to *Lycopodium clavatum* and allied forms. MEHROTRA AND SAH (1980) described *Lycopodiumsporites assamicus* from the Mikir Formation of Assam. This species comes very close to the living spores of *Lycopodium veitchii.* This species, at present, is found in the hills of Eastern Himalayas.

Some of the species hitherto placed under *Lycopodiumsporites* Thiergart *ex* Delcourt & Sprumont (1955) do not show the same ornamentational pattern as the type species. This genus is basically for the triangular-subtriangular, trilete, reticulate spores. The reticulation on the distal side is more regular. However, some of the later workers placed many species under *Lycopodiumsporites* with fossulate, foveolate or other types of ornamentation. MEHROTRA AND SAH (1980) described trilete, triangular, foveolate spores as *Lycopodiumsporites foveolatus* while *Lycopodiumsporites* sp. illustrated by SINGH (1974) is fossulate. If these forms are accommodated in *Lycopodiumsporites* then it goes against the original diagnosis of the genus. For this reason, it would be better if these are transferred to some other genera. It may be recalled here that POTONIÉ (1934) described some spores originally as *Sporites agathoecus* from the Eocene brown coal. This species was designated later as type species of *Lycopodiumspori-*

tes by THIERGART (1938) and DELCOURT AND SPRUMONT (1955). The illustration provided by POTONIÉ (1934, pl. 1, fig. 25) for *Sporites agathoecus* seems to be broken specimen without any distinct trilete mark. Some parts of proximal surface (?) also seems to be adhered along the equatorial margin. POTONIÉ (1956, pl. 5, fig. 52) while provided the text-figure of the same showed the trilete mark but did not say anything about the nature of ornamentation on the proximal side. Moreover, the text-figure is not the exact representation of the type species illustrated by him earlier.

DELCOURT AND SPRUMONT (1955) described several species of *Lycopodiumsporites* from the Wealden of Belgium. One of the species viz. *L. triarcuatus* (DELCOURT & SPRUMONT, 1955, pl. 3, fig. 1) is typified by a broken specimen showing triangular shape, trilete mark and reticulation both on proximal and distal surfaces. But from the illustration and description of POTONIÉ (1934, 1956) it is not clear whether the reticulation is also present on the proximal side. Though most of the living spores of *Lycopodium* have got reticulation on both sides but in two species viz. *L. veitchii* and *L. volubile* where the reticulation is restricted only to the distal side. So the type species of *Lycopodiumsporites* should be critically examined to ascertain whether it has got reticulation on one or both surfaces.

MEHROTRA AND SAH (1980) proposed *Assamiasporites* to accommodate triangular-subtriangular trilete spores with reticulate ornamentation on both proximal and distal surfaces. According to them *Lycopodiumsporites* should include only those spores which have distal reticulation and they transferred many species of hitherto known *Lycopodiumsporites* into *Assamiasporites*. MEHROTRA AND SAH (1980) while instituting the genus did not mention anything about *Reticulatisporites* (Ibrahim) Potonié & Kremp (1954). This genus has also reticulate ornamentation and it seems that reticulation is present on both sides. The shape is generally triangular and the trilete mark is also distinct. So in all probability, *Assamiasporites* seems to be a junior synonym of *Reticulatisporites* if not of *Lycopodiumsporites*.

It has been observed that some authors while placing the fossil species under *Lycopodiumsporites* also advocated their affinity with some of the living species. While describing *Lycopodiumsporites speciosus* from the Cherra Sandstone (Palaeocene) of Meghalaya DUTTA AND SAH (1970) remarked that this species compared well with the living spores of *Lycopodium phlegmeria*. However, the spores of latter species have typical foveolate pattern and so is very distinct from the fossil species described by them. DUTTA AND SAH (1970) also described *Lycopodiumsporites umstewensis* from the Cherra Sandstone. This species is characterized by a better developed distal reticulum and a comparatively reduced one on the proximal side. They thought that this species resembles the modern spores of *Lycopodium clavatum*. This contention is, unfortunately, not correct as the spores of *L. clavatum* possesses broad reticulum which is not found in the specimens described and illustrated by them (DUTTA & SAH, 1970, pl. 2, figs. 47-48).

In comparison to the reticulate *Lycopodium*-like spores, the pitted or fossulate forms are less recorded from the different geological horizons. The fossil genera comparable to the extant spores of *Lycopodium* are *Foveotriletes* (van der Hammen) Potonié (1956), *Trilobosporites* (Pant) Potonié (1956), *Foveosporites* Balme (1957), and *Auriculiretisporites* Venkatachala & Rawat (1971).

Foveotriletes according to POTONIÉ (1956) is finely reticulate but later workers (DETTMANN, 1963, pl. 6, figs. 8-13) also included foveolate to foveo-reticulate forms under this genus. Various species assignable to *Foveotriletes* have been described by

SINGH (1966) from the Jabalpur Stage (Upper Jurassic), VENKATACHALA *et al.* (1968) from the Katrols (Upper Jurassic) of Kachchh, VENKATACHALA (1969) from the Bhuj Formation (Lower Cretaceous) of Kachchh and VENKATACHALA AND JAIN (1970) from the subsurface Lower Cretaceous of Cauvery basin. From the Tertiary sediments, RAMANUJAM (1967) reported this genus from Neyveli lignite and DUTTA AND SAH (1970) from the Cherra Sandstone (Palaeocene).

Foveosporites Balme (1957) is distinguished from *Foveotriletes* by foveolate sculpture and a circular to convexly triangular shape. BALME (1957) observed that *Foveosporites canalis*, the type species of the genus, resembles the spores of *Lycopodium verticillatum* group of KNOX (1950). SAH AND JAIN (1964), VENKATACHALA (1969), VENKATACHALA AND JAIN (1970) reported this genus from the various Mesozoic sediments of India while from the Tertiary, SAH AND KAR (1969), DUTTA AND SAH (1970), MEHROTRA AND SAH (1980) and KAR AND JAIN (1981) described it.

Trilobosporites Pant *ex* Potonié (1956) is characterized by triangular shape with thickening at the apicular region and microreticulate ornamentation. Some of the species, with verrucose ornamentation have also been included in this genus (DELCOURT *et al.* 1963). VENKATACHALA *et al.* (1969) and VENKATACHALA AND JAIN (1970) reported this genus from the Mesozoic while SAH AND KAR (1969) illustrated it from the Lower Eocene of Kachchh.

Trilobosporites is unique in its apicular thickening and comes close to the living spores of *Lycopodium selago* type where the apicular regions are lobed and the exine is foveolate. It may be mentioned here that auricular thickening at the apices is found in a number of Palaeozoic genera. *Tripartites* Schemel (1950) has thickening of the exine at the apices which is characteristically folded on the distal surface. *Triquitrites* (Wilson & Coe) Sullivan & Neves (1964) has a narrow equatorial zone which is wider but not appreciably thicker at the apices. It seems that the lobes, apices and its different manifestation is a very primitive character in Lycopsida. *Auriculiretisporites* Venkatachala & Rawat (1971) from the Oligocene-Miocene of Cauvery basin has also thickening at the apices, laevigate exine on the proximal and reticulate on the distal side.

Apart from the shape, the pitted sculptured pattern of the present day spores of *Lycopodium* is not most closely comparable to the foveolate, foveo-reticulate fossil genera because the pits in the spores of extant *Lycopodium* are generally widely placed whereas in the fossil ones they are comparatively closely placed to provide a small meshed pseudoreticulate pattern. *Triancoraesporites* Schulz (1962) described from the Triassic is, however, quite similar to the living spores of *L. selago* and *L. serratum* in the presence of truncated apices and sculptural pattern.

Fossil spores with rugulate ornamentation as exhibited in the living spores of *Lycopodium cernuum* and *L. inundatum* group are poorly represented. Some of the species assigned to *Camarozonosporites* (Pant) Klaus (1960) and *Coronatispora* Dettmann (1963) are comparable to this type. *Camarozonosporites cretaceus* (Weyland & Krieger) Potonié (1956), the type species of the genus, is cingulate and the exine is somewhat laevigate. *Coronatispora* has no doubt foveolate to reticulate ornamentation but the exine is differentially thickened in equatorial, interradial regions where carssitudes are developed. Distal hemisphere in this genus according to DETTMANN (1963) is with a circumpolar ridge which concentrically encircles a polar thickening. As this type of organisation is not found in *L. cernuum* and *L. inundatum* types so these spores are not closely comparable to those two fossil genera.

DISCUSSION

It has become obvious from the present investigation that reticulate type of spores assignable to *Lycopodiumsporites* Thiergart *ex* Delcourt & Sprumont (1955) was more prevalent than the foveolate-fossulate type particularly during the Tertiary. Some of the species described under this genus are strikingly similar to the spores of living *Lycopodium* (*s. s.*). *Lycopodiumsporites austroclavatidities* (Cookson) Potonié (1955) described by Sah and Jain (1964) from the Rajmahal Hills resembles very much the spores of *Lycopodium clavatum*. Similarly, *Lycopodiumsporites assamicus* Mehrotra & Sah (1980) reported from the Mikir Formation, Assam is very much similar to the extant species of *Lycopodium veitchii* which even today grows in the region. It seems that the foveolate-fossulate type of spore producing *Lycopodium* came in north-east India much later than the first type.

In this connection, it may be mentioned that Harris (1974), Kemp (1974) and Kemp and Harris (1975, 1977) investigated the palynology of the bore cores of the Deep Sea Drilling Project Site nos. 214 and 254. The sites are situated on the Ninety east Ridge in Indian Ocean. They observed that during Palaeocene, the sites were occupied by more or less cold loving plants and they have good similarity with the early Tertiary vegetation of Australia, New Zealand and Antarctica. According to McKenzie and Sclater (1971), India migrated north-wards through the Ninety east Ridge, during the Upper Cretaceous and Lower Tertiary. It is possible that while passing through this zone, some cold loving *Lycopodium* inhabitated in north-east India or the spores came from the neighbouring islands, long submerged in the present day Indian ocean.

Mahabale and Satyanarayana (1977, 1978) described two species of *Taxaceoxylon* Kräusel & Jain (1964) and one petrified wood of *Ginkgo* from the Deccan Intertrappean beds of Kateru and Pangidi, near Rajahmundry, Andhra Pradesh, respectively. The presence of these woods in Palaeocene-Eocene time in Andhra Pradesh indicates that this region was enjoying a temperate climate during that period. As Assam, Meghalaya and Andhra Pradesh were almost in the same latitude during that time (*vide* McKenzie & Sclater, 1971) so the presence of cold loving *Lycopodium* in north-east India seems to be natural.

North-east India, it appears since the dawn of Tertiary was the home of lycopodiaceous plants. Most of the species of *Lycopodiumsporites* has been reported from this region and are also commonly met within the percentage count. Out of 27 living species, about 20 are concentrated in this region. The favourable climate and the proximity of the Malayan region perhaps responsible for this kind of eccentric distribution.

Lycopodiumsporites Thiergart *ex* Delcourt & Sprumont (1955) is a cosmopolitan genus but not properly understood by most of the workers. The inherent drawback lies in the selection of a bad specimen as the type species and its inadequate description. A lot of confusion may be removed and nomenclatural problem solved if the nature of reticulation and its presence on one or both sides in the type species is known.

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EXPLANATION OF PLATES

(All slides are preserved at the herbarium of Birbal Sahni Institute of Palaeobotany. All figures are magnified *ca* ×500).

PLATE-1

1- 2. *Huperzia selago* (L.) Bernh. ex Schrank & Mar. Fig. 1. Showing foveolate distal surface. Fig. 2. Shows laevigate proximal surface. Slide no. 10295.

3- 4. *H. serrata* (Thunb.) Rothmaler. Fig. 3. Shows hexagonal shape, truncated corners and foveolate distal surface. Fig. 4. Shows proximal laevigate surface. Slide no. 10296.

5-6 . *H. herteriana* (Kümm.) Sen & Sen. Fig. 5. Showing laevigate proximal surface. Fig. 6. Depicting elongated foveola on distal surface. Slide no. 10297.

7. *H. carinata* (Desv.) Rothmaler. Showing foveolate distal surface. Slide no. 10298.

8. *H. laxa* (Presl.) Sen & Sen. Shows foveolate distal surface. Slide no. 10317.

9-10. *Phlegmariurus phlegmarius* (L.) Rauschert. Fig. 9. Shows foveolate distal surface. Fig. 10. Note the tapering trilete mark on the laevigate proximal side. Slide no. 10308.

11. *P. phyllanthus* (Hook. et Arn.) Löve & Holub ex Holub. Showing foveolate distal surface. Slide no. 10309.

12. *Huperzia squarrosa* (Forst.) Rothmaler. Distal surface showing union of few pits. Slide no. 10299.

13-14. *H. hamiltonii* (Spring ex Hook. & Grev.) Sen & Sen. Fig. 13. Showing distally foveolate-fossulate sculpture.

15. *H. fordii* (Baker) Mandal & Sen. Showing foveolate distal surface. Slide no. 10305.

16. *H. subulifolia* var. *assamica* Mandal & Sen. Showing foveolate distal surface and fusion of few pits. Slide no. 10307.

17-18. *Lycopodium clavatum* Linnaeus. Fig. 17. Note the complete reticulation on distal surface. Fig. 18. Depicts irregular polygons around trilete mark on the proximal surface.

19-20. *Diphasium complanatum* (L.) Rothmaler. Fig. 19. Showing proximal surface. Fig. 20. Note the complete reticulation on distal slide. Slide no. 10312.

PLATE-2

21. *Huperzia obtusifolia* (Swartz) Rothmaler. Showing ornamentation on distal side. Slide no. 10302

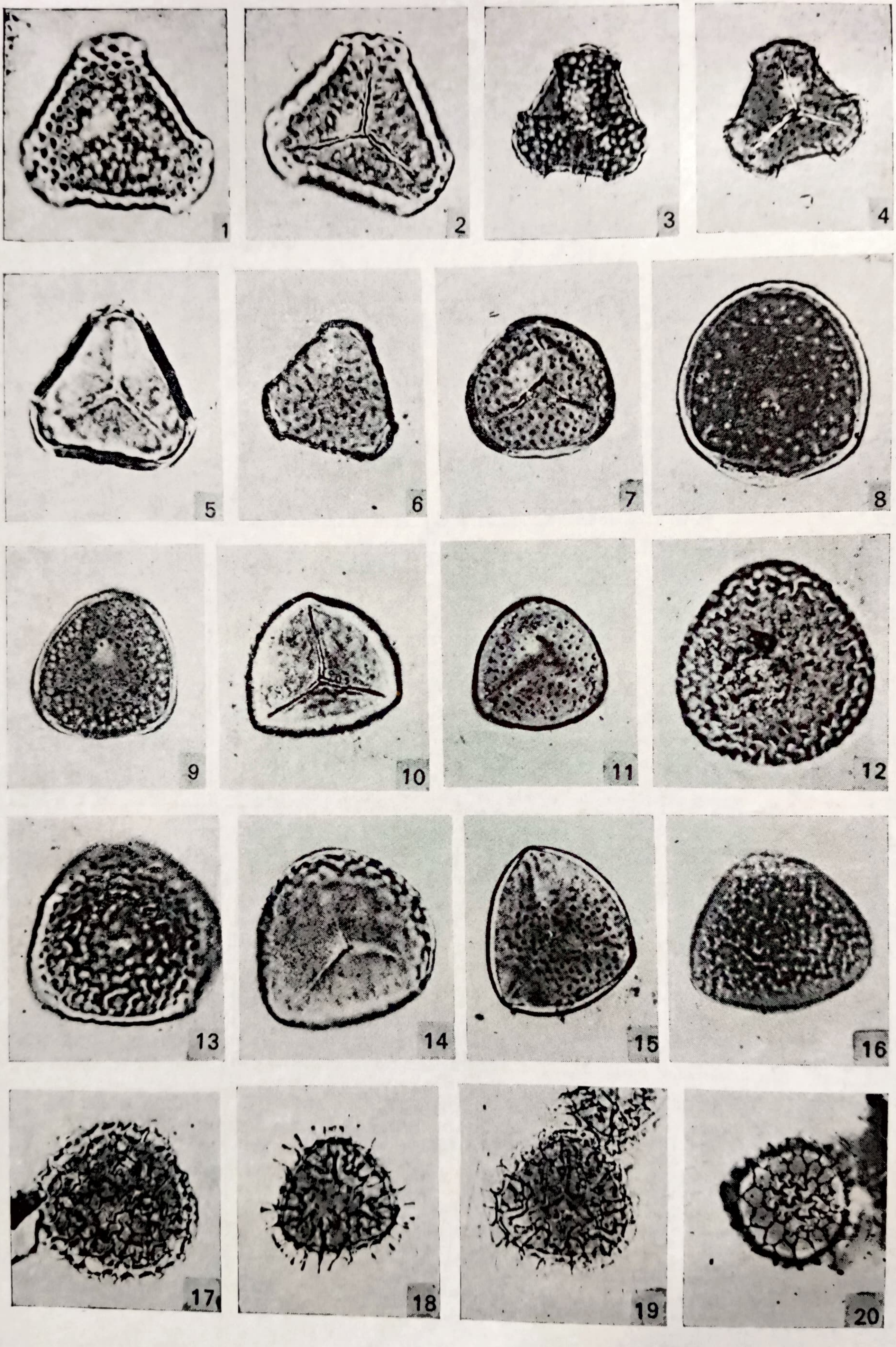
22. *H. tetrastychya* (L.) Presl. Depicts typically foveolate ornamentation on distal surface. Slide no. 10306.

23. *H. gnidioids* (L. fil). Rothmaler. Showing foveolate distal surface. Slide no. 10303.

24. *H. subulifolia* (Wall. ex Hook. & Grev.) Mandal & Sen. Shows foveolate-fossulate ornamentation on distal surface. Slide no. 10302.

25-26, 39. *H. pulcherima* (Wall. *ex* Hook. & Grev.) Pic. Ser. Figs. 25 & 39. Shows typical fossulate ornamentation on distal surface. Fig. 26. Note the narrow trilete mark on the proximal surface. Slide no. 10300.

27. *Phlegmariurus phyllanthus* (Hook. & Arn.) Löve & Holub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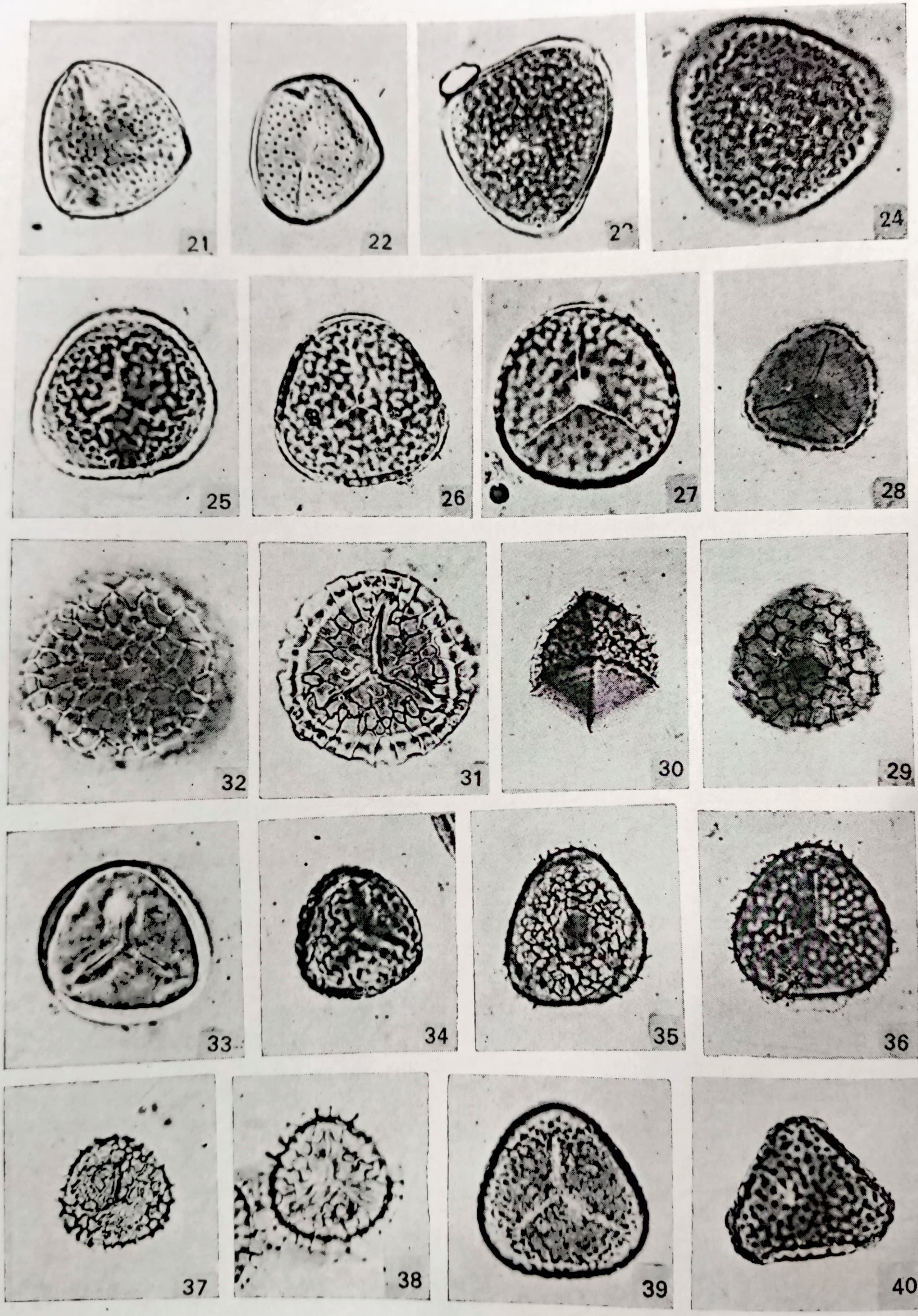
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28-29 & 37. *Lycopodium veitchii* Christ, Fig. 28 depicts laevigate proximal surface. Figs. 29 & 37. Note reticulation on distal surface. Slide no. 10314.

30, 35-36. *Lycopodium volubile* Linnaeus, Fig. 30. Equatorially preserved spore showing reticulate distal surface and laevigate proximal surface. Fig. 35. Shows broken polygons on distal surface. Fig. 36. Depicts laevigate proximal ornamentation. Slide no. 10315.

31-32. *Diphasium wightianum* (Wall. *ex* Grev. & Hook.) Pic. Ser. Fig. 31. Shows complete reticulation on distal surface. Fig. 32. Note the nature of reticulation on proximal surface. Slide no. 10311.

33-34. *Palhinhaea cernua* Franco & Vasc. Fig. 33. Shows trilete mark rests in a groove. Fig. 34. Note the distal rugulate ornamentation. Slide no. 10316.

38. *Diphasium alpinum* (L.) Rothmaler. Showing incomplete reticulation around trilete mark. Slide no. 10310.

40. *Huperzia serrata* (Thunb.) Rothmaler. Showing distal foveolate ornamentation. Slide no. 10296.