

ON *POROSTROBUS ZEILLERI* NATHORST AND ITS SPORES  
WITH REMARKS ON THE SYSTEMATIC POSITION OF  
*P. BENNHOLDI* BODE AND THE PHYLOGENY OF  
*DENSOSPORITES* BERRY\*

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ABSTRACT

This paper contains results of a reinvestigation of *Porostrobos zeilleri* Nathorst., a fructification from the Lower Carboniferous of Spitzbergen and, based thereupon, remarks on the systematic position of *P. bennholdi* Bode and the phylogeny of *Densosporites* Berry.

The cone studied represents the lower portion including a part of the stalk. The cone shows rhomboid sporangia arranged spirally, sporangial wall very thin so that spore masses appear naked, sporophylls not visible but fine delicate hairs, apparently sporophylls, seen on the matrix along one of the sides of the cone. Megasporate and microsporate sporangia occur intermixed. Megaspores are sack-like, bottom heavy and gulate or vestibuled with verrucose ornamentation of the exine. Microspores are cingulate, roundly triangular with spinose ornamentation. Inner body has 3 inter-ray papillae.

*Porostrobos* shows lepidodendroid as well as sigillarioid characters.

*Porostrobos bennholdi* Bode is shown not to be a *Porostrobos* at all. It is provisionally referred to *Lepidocarpon*.

The microspores of *Porostrobos* agree morphologically as well as stratigraphically to the genotype of the dispersed spore genus *Densosporites* Berry. In view of the fact that *Densosporites* also occurs in strata where *Porostrobos* has never been found, it is postulated that presently circumscribed *Densosporites* contains spores of cone genera other than *Porostrobos* as well.

PS. *Porostrobos* is considered distinct from *Selaginellites* and *S. canonbiensis* Chaloner is advised inclusion in *Bothrostrobos* (Nath.) Sew.

INTRODUCTION

WHILE searching through literature to gather information regarding *in situ* spores from fructifications, I came across the description and illustrations of *Porostrobos zeilleri* Nathorst, by Nathorst (1914, p. 70, Pl. 5, Figs. 12-16). The description of *Porostrobos*, of which *P. zeilleri* is the type, is in itself very interesting as it shows significant deviation from the well-known fructification genus *Lepidostrobos*, but the spores, though badly reproduced and

still scantily described, appeared of greater interest and value. From the figures of microspores (NATHORST, loc. cit. Figs. 15, 16) I suspected that they correspond to *Densosporites* Berry, a genus of dispersed spores which is of stratigraphical value (BHARDWAJ, 1955) yet whose parentage has so far been shrouded in mystery. The illustration of megaspores by Nathorst (Figs. 13, 14) do not convey any information regarding their shape, organization or sculpture and in their description also besides the size nothing has been said. Thus realizing the need for a reinvestigation of this fructification I requested Prof. O. H. Selling, Director, Botany Dept., Riksmuseum, Stockholm, to loan me the type specimen of *P. zeilleri* for study and he so very kindly sent the same for which I am thankful to him.

MATERIAL

The fructification which formed the basis of present investigation was described and figured by Nathorst (1894, p. 42, Pl. 12, Fig. 8) as *Lepidostrobos zeilleri* n. sp. Subsequently, Nathorst (1914) created a new genus *Porostrobos* to include this fructification and thus renamed it as *Porostrobos zeilleri*.

The specimens studied consist of (1) a compressed piece of fructification separated from the matrix and (2) the matrix bearing the imprint of one of the faces of the compressed fructification.

The material was collected by Nathorst in 1882 out of a carbonaceous shale mixed with coal, from Pyramidenberg in Spitzbergen. This bed occurs in the lower reaches of the hill (NATHORST, 1914, Figs. 2, 3) unconformably overlying the Devonian strata and overlaid by the Kulm (Lower Carboniferous) sandstone which too is rich in plant remains.

\*Paper read at the 10th Scientific Meeting of the Palaeobotanical Society on 22 January 1958.

†Same as D. C. Bhardwaj.

## METHOD

The gross morphological features of the fructification, compression as well as impression were studied dry, under reflected light. The mega- and microspores were examined after macerating small pieces of the fructification containing two or more mega- or microsporulate sporangia. The sporangia are very small and so it was not possible to isolate a single sporangium without the risk of damaging the type specimen. Maceration was done by keeping the pieces in fuming  $\text{HNO}_3$  for 36 hours followed by a treatment of the acid-free material with 5 per cent KOH solution for 24 hours. In this particular case the procedure described above gave excellent results. Slides were prepared in glycerine-jelly and sealed with Gold-seal. Megaspores were recovered by sieving (0.1 Müllergaze). Some were dried on a filter paper and kept in cardboard cavity slides and others were stored in 50 per cent glycerine for study with transmitted light.

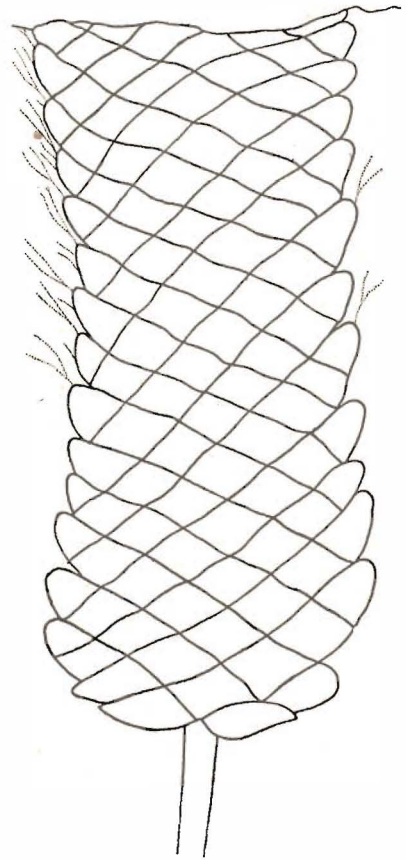
## DESCRIPTION

*Porostrobus zeilleri* Nathorst 1914

Syn. *Lepidostrobus zeilleri* Nath. 1894

*Cone* — The piece of cone separated from its matrix is 13 mm. long and *ca.* 6 mm. broad. Being broken at both ends it evidently does not represent the whole cone (PL. 1, FIG. 1). The basal portion of the cone, about 3 mm. in length, is still attached to the matrix (PL. 1, FIG. 2; TEXT-FIG. 1). The cone base is broadly rounded and is attached to a slender stalk, *ca.* 1 mm. broad and 5 mm. long. Apparently the stalk is devoid of any distinguishable structures (PL. 1, FIG. 3; TEXT-FIG. 1).

A cursory examination of the cone or its impression suggests that it consists of successive rows of cushions directed obliquely from a median region upwards along its length (PL. 1, FIGS. 1, 2). But actually each of these cushions consists of a row of small rhomboid units arranged obliquely upon the cone axis suggesting their spiral arrangement (PL. 1, FIG. 3). Each of these rhomboid units are sporangia, containing either mega- or microspores (PL. 1, FIG. 5). There does not appear to have been any substantial sporangial membrane covering the spores as the latter can be seen as distinctly



TEXT-FIG. 1 — Impression of *P. zeilleri* showing stalk, base, rhomboid sporangia and the acicular sporophyll ends.  $\times 6$ .

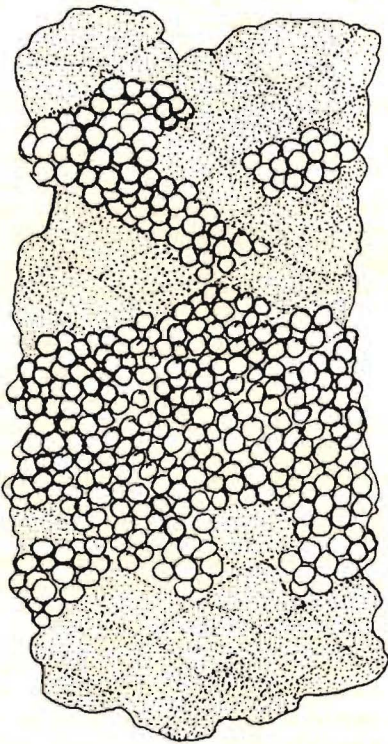
in surface examination as if they were naked (PL. 1, FIGS. 6, 7; mega-, micro-). The sporangia containing megaspores are evident by virtue of their unmistakable contents but such others as show a matted or granulated surface are the sporangia containing microspores.

In the isolated cone part, there is no indication if the sporangia were borne on sporophylls. However, in the maceration the fragmentary cuticular remains, presumably of the sporophylls, could be identified. In the cone-impression (PL. 1, FIG. 3; TEXT-FIG. 1), along one of the margins, there is a suggestion of the occurrence of small, narrow, bifid, acicular structures arising from, and turning away upwards from, the cone which could as well have been the sporophyllends. In

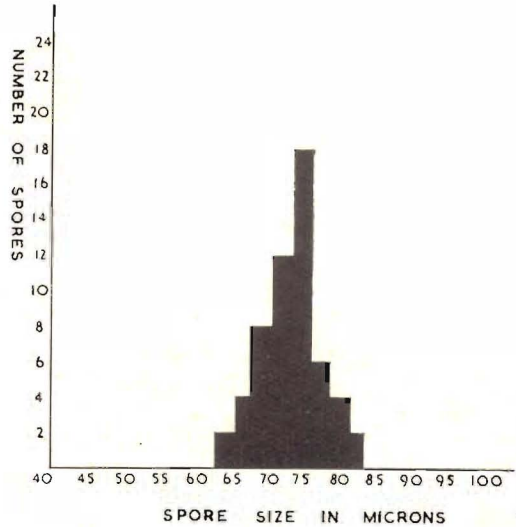
view of the impressions of these being faint and these too clearly seen mostly on one side (PL. 1, FIG. 3, left) of the cone, it appears that these were delicate and could easily escape being preserved as encrustation or even imprinted on the matrix.

The mega- or microsporate sporangia are not strictly regionally segregated. In the basal region of the cone occur the microsporate sporangia followed by a belt of megasporate sporangia which in turn is again succeeded by a region of microsporate sporangia. But none of these regions are purely mega- or microsporate because in between the sporangia of one kind the other kind also occur (PL. 1, FIGS. 5-7; TEXT-FIGS. 2, 3) frequently.

*Spores* — The isolated cone compression was very convenient to provide material for maceration that could be considered  $\pm$  free from contamination. The parts selected for maceration were carefully examined under a lens to avoid any piece of the matrix sticking to them. As the mega- or microsporate sporangia are hardly more than 1 mm. in



TEXT-FIG. 2 — Compression of *P. zeilleri* showing predominantly mega- or microsporate zones.  $\times 5$ .



TEXT-FIG. 3 — Histogram depicting the range of variation in the size of the microspores of *P. zeilleri*.

size, small pieces containing 2-4 sporangia were carefully removed and macerated. The macerates yielded mega- as well as microspores, both being only of one type each.

*Megaspores* — Each megasporate sporangium contains some megaspore tetrads. The isolated megaspores are usually to be seen lying in meridional plane (PL. 2, FIGS. 18-22) but occasionally some are seen in equatorial plane also. The specimens in meridional view are pitcher-like in shape with a roundly conical bottom, widest middle region and sharply convergent apical part leading to a protruding neck or *gula*. The specimens in equatorial view show a roundly triangular or subcircular equator and subequatorial, thick, arcuate ridges enclosing the Y-mark whose rays are progressively elevated towards the vertex (proximal pole).

The exoexine is densely ornamented by *verrucae*. These are usually coalesced with their adjacent ones, forming short, usually curved ridges. In between the ridges the exine is finely granulose (PL. 2, FIG. 23) and occasionally, isolated *verrucae* are found as if filling the gaps. The *verrucae* occur all over but those in the *area contagionis* are smaller (PL. 2, FIG. 23),  $\pm 5 \mu$  in width as compared to those elsewhere which are  $\pm 10 \mu$  in width. The *verrucae* have a broad base and bluntly conical or rounded apex.

The size of wet megaspores (mounted in glycerine-jelly) in meridional plane ranges from  $350 \times 300 \mu$  to  $480 \times 400 \mu$ , and in equatorial plane  $360 \times 320 \mu$ . Dry megaspores are smaller and measure up to  $400 \times 360 \mu$ , in meridional plane *gula* protrudes  $50-70 \mu$  high above the rays. Ray length is  $\pm 170 \mu$  and the median depth of each lobe of *area contagionis* is  $\pm 200 \mu$  in wet specimens.

*Microspores* — Normally macerated microspores are triangular in polar view (PL. 2, FIGS. 8-12), but sphaeropyramidal or dumb-bell shaped in lateral view. The angle in the triangular forms are normally bluntly conical. The central body, which is much more hyaline than the dark brown *cingulum* surrounding it, is also roundly triangular in shape.

The proximal exoexine is granulose ornamented (PL. 2, FIGS. 11, 12) but the distal exoexine is spinose ornamented (PL. 2, FIGS. 9, 10). The spines are sparsely and not so regularly distributed. They are fewer and hyaline on the central body but copious and dark coloured on the *cingulum*. Closely surrounding the central body, in the *cingulum*, rows of spines are radially arranged forming the thickest and most dense region of the *cingulum*. Beyond this, up to the equator, the *cingulum* is less dense but not forming a thin flange. The *extrema lineamenta* is finely granular. Y-mark is usually distinct on the central body if viewed from proximal side. The extensions of the rays over the *cingulum* are very often discernible as thick ridges reaching the equator of the angles (PL. 2, FIG. 11).

The overall size of the microspores ranges from  $84$  to  $63 \mu$  with  $76 \mu$  as mean (TEXT-FIG. 3). The size of the central body ranges from  $37$  to  $26 \mu$  with  $31 \mu$  as mean. The *cingulum* is usually  $\pm \frac{2}{3}$  of the radius of the microspores.

*Overmacerated Microspores* — In one of the macerations the material was allowed to get overmacerated by longer treatment with KOH solution. The overmacerated microspores looked so different from the normal ones that at first sight one would easily suppose that they belong to a different species. However, one could easily find the whole range of variations from the normal in that macerate.

Overmaceration results into significant changes in the morphography as well as the size of the microspores. These overmacerated spores become more rounded, sometimes

almost circular, losing their triangular outline. The margin becomes more translucent and thin, frequently irregularly upturned. The spines on the distal face become thinner and sparser or even completely obliterated (PL. 2, FIGS. 13, 14). The ring of radially thickened rods around the central body lose all their individuality and this zone becomes of lighter brown colour, gradually merging with the yellowish, thin exine nearer the margin of the spores. The granular sculpture of the proximal face remains unaltered. The size of the overmacerated microspores may increase to as much as double the normal ones. The Y-mark becomes more easily discernible as composed of thin, dark brown lines so that the normal height and thickness of its labra is considerably reduced. In many cases the rays are distinct on the central body (PL. 2, FIG. 13) and a *papilla* is seen in each of the inter-ray areas. The central body also increases in size and in so doing assumes more rounded than triangular or oval shape. In the centre of such extended central bodies another subcircular or oval body is discernible (PL. 2, FIGS. 13, 14). This is the inner body which does not expand with the rest of the spore exine and thus is left in the centre. A number of these inner bodies which got free from the spores have also been found lying in the same macerate (PL. 2, FIGS. 15, 16). These are roundly triangular, bear hair-thin rays extending up to the equator and in each of the three inter-ray areas a *papilla* (circular darker spot) is apparent. In a few cases (PL. 2, FIG. 17) the inner body has been found within a thin body-wall.

## DISCUSSION

*Porostrobus zeileri* appears to have been a slender cone with spirally arranged sporophylls bearing the sporangia. The sporophylls apparently ended in slender, delicate, acicular, hair-like structures. The sporangia were rhomboidal in cross-section, massive as compared to the sporophylls and occupying all the space between adjacent sporangia (TEXT-FIG. 1).

The recognition of the basal part of the cone with its attached stalk suggests that the material studied represents the lower part of the cone which is  $16$  mm. in length and  $6$  mm. in width. The cone had, evidently, already attained maturity in view of the mature spores contained in the sporangia.

The cone is heterosporous, the sporangia containing either microspores or megaspores. The microsporite or megasporite sporangia are, in general, diffused, i.e. occurring intermixed together, yet the richness of one sort or the other in some regions, leads to the recognition of three zones in the portion of the cone studied. The part of the cone, closest to the base, contains mostly microsporite sporangia followed by a zone containing mostly megasporite sporangia which in turn is again followed by a region richer in microsporite sporangia. It is not definitely known if this alternation of micro- and megasporite sporangial zones was continued in the remaining, missing upper part of the cone.

As compared to the other heterosporous lycopsid cones, *Porostrobos* is distinct from all others in one or more respects. *Lepidostrobos* and *Lepidocarpon* differ from *Porostrobos* mainly in the intermixed occurrence of micro- and megasporite sporangia in the latter as compared to the isolation of megasporite sporangia in the basal region and microsporite sporangia in the apical region in the former two genera. However, even in this respect the apparently alternate zonation mitigates the difference to some extent suggesting as if this particular distribution of micro- and the megasporite sporangia in *Porostrobos* was a prelude or otherwise parallel to the condition met with in *Lepidostrobos* and *Lepidocarpon*. *Porostrobos* is bisexual but *Mazocarpon* and *Sigillariostrobus* are unisexual. Between these cone genera *Lepidostrobos* appears to be nearer to *Porostrobos* as is borne by the testimony of the morphology of the megaspores. The megaspores of *Porostrobos* are gulate as are the megaspores of *Lepidostrobos* (CHALONER, 1953). These, however, do not conform in sculpture. The megaspores of *Lepidocarpon* are not gulate as in *Porostrobos* and are much bigger in size and differ in sculpture of the exoexine. The megaspores of *Mazocarpon* or *Sigillariostrobus* (SCHOPF, 1941; CHALONER, 1953b) are saucer shaped, without gula, and laevigate or tuberculate quite unlike *Porostrobos*. The microspores of *Porostrobos* though strikingly different in external morphology approach those of *Mazocarpon* (SCHOPF, 1941) and *Lepidostrobos zea* Chaloner (1953a) more than those of any other lycopsid cone genus especially due to the presence of three inter-ray papillae.

It is apparent that *Porostrobos* shows a mixture of lepidodendroid and sigillarioid

features yet is distinct from *Lepidostrobos*, *Lepidocarpon*, *Sigillariostrobus* and *Mazocarpon*. It, apparently, differs from the sigillarioid cone genera in more respects than with the lepidodendroid ones, although in the lepidodendroid cones the inner body of the microspores does not possess the three inter-ray papillae, the like of which are found in the microspores of *Porostrobos*, *Mazocarpon* and *Lepidostrobos zea* (now transferred by CHALONER\* to *Polysporia*).

The diagnosis of *Porostrobos* Nath. is emended thus:

*Porostrobos* Nathorst 1914 emend.

Genotype — *Porostrobos zeilleri* Nath.

Diagnosis — Pedunculate, compact heterosporous cone with sporangia spirally arranged round the axis; sporophylls not to be seen but for their hair-like free ends; megasporite and microsporite sporangia occurring in alternating zones with the admixture of one type into the zone of the other, basal zone consisting of microsporite sporangia. Megasporite sporangia containing a number of tetrads, megaspores gulate, sac-like with the exoexine verrucose; microspores cingulate with broad uniformly thick, ornamented cingulum, inner body having 3 inter-ray papillae.

#### Systematic Position of *Porostrobos bennholdi* Bode

In 1929 Bode described a fructification from the Lower Carboniferous brown coals of Moscow as *Porostrobos bennholdi* n. sp. He diagnosed his species as follows:

“Grösse wechselnd, 10-22 mm. breit und z.T. mehr als 60 mm. lang. Im innern des Zapfens auf den Sporophyllen nur Mikrosporangien, wahrscheinlich in grösserer Zahl, je vier Mikrosporen enthaltend; am Ende jedes Sporophylls je ein Makrosporangium, wahrscheinlich je vier Makrosporen enthaltend. Die Sporen werden frei durch zerfall der Sporangiumwand. Grösse der Makrosporen im Mittel 3-3.5 mm. die der Mikrosporen 0.8-1.0 mm. Beide Sporenarten völlig glatt, jedoch mit deutlicher Tetradenzeichnung, nach der sie meistens aufgeplatzt sind. Durch die Art und die Grösse der Sporen und durch die Grösse des Zapfens selbst von *Porostrobos zeilleri* unterschieden, sonst in der Organization weitgehend mit ihm übereinstimmend.”

(Translated by the present author) “Size variable, 10-22 mm. broad and in parts more

\*Personal communication by Dr. Chaloner dated 5 February 1958.

than 60 mm. long. In the interior of the fructification microsporangia on the sporophylls, probably in larger number, each containing four microspores; at the end of each sporophyll a macrosporangium, probably each containing four macrospores. The spores liberated through disintegration of the sporangial wall. Average size of the macrospores 3.3-5 mm., of the microspores  $0.8 \times 1.0$  mm. Both kinds of spores fully smooth, however, with distinct tetrad-mark along which they are mostly burst open. Through the type and the size of the spores and through the size of the cone itself distinct from *Porostrobus zeilleri*, otherwise mostly agreeing with it in organization."

As compared to the details of *Porostrobus zeilleri* now known, the cone described by Bode (loc. cit.) as *P. bennholdi* differs in some fundamental aspects. *P. zeilleri* is bisexual but *P. bennholdi* is unisexual in so far as can be gathered from the description by Bode (loc. cit.) because what have been interpreted by Bode as microspores are really the immature megaspores (BODE, loc. cit., PL. 21, FIG. 20) both in organization and size. The figure given by Bode is absolutely clear to convince any worker on Carboniferous megaspores that these so-called microspores are in reality those immature megaspores, at whose cost one megaspore out of each tetrad develops fully. So, as a matter of fact that part of the cone which Bode investigated appears to have contained only megasporate sporangia. It is not known if any microsporate sporangia occurred on that cone in any other or the missing part. There is no evidence to suggest that the micro- and the megasporate sporangia occur diffused or inter-mixed in *P. bennholdi* — a feature which characterizes *Porostrobus*. Besides this the size and the sculpture of the megaspores in *P. bennholdi* is different from those of *P. zeilleri*. The megaspores of *P. bennholdi* are smooth, lack the characteristic *gula* and are nearly six times as big as those of *P. zeilleri*. Such big-sized megaspores as those of *P. bennholdi* are known only from *Lepidocarpon* (BOCHENSKI, 1936; CHALONER, 1952) and are designated as seed-megaspores. The likeness of the megaspores of *P. bennholdi* to those of *Lepidocarpon* has already been accepted by Dijkstra (1946) who has referred such dispersed forms as a species of *Cystosporites* Schopf., *C. bennholdi* (according to POTONIÉ & KREMP, 1956, p. 150, the dispersed megaspores of *P. bennholdi*-type

should not be named as *C. bennholdi* but be given a new specific name under *Cystosporites*). It is thus apparent that the cone described by Bode cannot be assigned to *Porostrobus*. At the same time in view of the features of its megaspores it may be assigned provisionally to *Lepidocarpon* as *Lepidocarpon bennholdi* (Bode) emend., till further investigations may confirm this emendation or otherwise.

***Lepidocarpon bennholdi* (Bode) emend.**

Syn. *Porostrobus bennholdi* Bode 1929

*Emended Diagnosis* — Grösse wechselnd, 10-22 mm. breit und z.T. mehr als 60 mm. lang. Auf den Sporophyllen nur Makrosporangien. Die Sporen werden frei durch zerfall der Sporangiumwand. Makrosporen mit Polachse länger als der Äquatorialachse, Grösse der Makrospore im Mittel 3-3.5 mm., die der jugend oder Abortive Makrosporen 0.8-1.0 mm. Beide sporenart völlig glatt, jedoch mit deutlicher Tetradenzeichnung, nach der sie meistens aufgeplatzt sind.

**Phylogeny of *Densosporites* (Berry)  
Pot. & Kr.**

The microspores of *Porostrobus* if found as *Sporae dispersae* would unmistakably be referred to the spore-genus *Densosporites* Berry, by virtue of their characteristically broad *cingulum* and comparatively small body. Berry (1937) created *Densosporites* to include broadly cingulate miospores from Lower Carboniferous coals and *Porostrobus zeilleri* also belongs to Lower Carboniferous age. It seems that morphologically as well as stratigraphically the specimens referred to the genotype of *Densosporites*, *D. covensis* Berry could have belonged to *Porostrobus* rather than any other cone genus. However, in recent years, spores referable to *Densosporites* have also been reported from many horizons of Upper Carboniferous, thus extending the continuous distribution of this genus from Lower Carboniferous to Westphalian C and occasionally in Stephanian C (BHARDWAJ & VENKATACHALA, 1958). But *Porostrobus* has not been reported from all these horizons extending from Lower Carboniferous to Westphalian C and even Stephanian C, and hence the question automatically arises, where have these miospores, morphographically similar(?) to those of *Porostrobus*, come from? In view of the fact,

that *Porostrobos* has not been collected or described from all the horizons where *Densosporites* has been reported to occur it is more probable that microspores of some other cone genus or genera are included in the genus *Densosporites*.

#### POSTSCRIPT

In a recent paper by Chaloner (1958b) an observation questioning the advisability of retaining *Porostrobos* as a distinct lycopodiaceous cone genus other than *Selaginellites* has been made. From the reinvestigation of *Porostrobos* by me, hardly any doubt remains that *Porostrobos* is quite distinct in its organization as well as in the spore morphology from *Lepidostrobos*, *Lepidocarpon*, *Sigillariostrobus* and *Mazocarpon*. However, comparison is needed now with the other two detached heterosporous cone genera, *Polysporia* and *Selaginellites*.

Recently Chaloner (1958a) has merged his species *Lepidostrobos zea* into *Polysporia mirabilis* which has a distinct megasporate basal region and microsporate apical region as opposed to the roughly alternating, mixed mega- and microsporate zones in *Porostrobos*. In addition to this the mega- and microspore morphology in these two genera is also substantially different. Thus *Porostrobos* stands out distinct as compared to *Polysporia* in spite of the only similarity, i.e. the occurrence of 3 inter-ray papillae on the inner body of the microspores in both the genera.

*Selaginellites* was instituted by Zeiller (1906) to include *S. suissei* Zeiller, a shoot with *Selaginella*-like vegetative habit and a fertile heterosporous cone containing megaspores of the type now included in the spore genus *Triangulatisporites* Pot. & Kr. and microspores as of the spore genus *Cirratriradites* Wils. & Coe (ZEILLER, 1906, CHALONER, 1954). Subsequently, Halle (1907) described *Selaginellites primaevus* (Goldenberg) Halle containing megaspores of *Triangulatisporites*-type and Hoskins & Abbott (1956) have described a petrified, detached cone, *Selaginellites crassicinctus*, containing megaspores referable to *Triangulatisporites* and microspores to *Cirratriradites* as in *S. suissei* Zeiller, the type species of *Selaginellites*.

In my opinion the taxonomic position ascribed by Halle (loc. cit.) as well as Hoskins & Abbott (loc. cit.) to their cones is justified in view of the agreement in the morpho-

graphy of their spores with type of the genus even if in the latter case the vegetative nature of the parent plant is unknown and the fossil is a petrification unlike the type of the genus *Selaginellites*. Although, had *S. crassicinctus* been described early in the present century, it might have been placed in a separate genus because of its petrified nature as at that time spores were not held to be of much value for taxonomic purposes. As compared to these species of *Selaginellites*, e.g. *S. suissei*, *S. primaevus* or *S. crassicinctus*, *Porostrobos zeilleri* differs in having mixed zones of mega- and microsporate sporangia from the base upwards and also in the morphology of its mega- as well as microspores.

In addition to the above-named species, *Selaginellites* also includes a few other species such as *S. elongatus* (GOLDENBERG) Halle, (1907; SEWARD, 1910), and *S. canonbiensis* Chaloner (1958b) both of which possess spores of a morphographical type different from those of *S. suissei*, the type of the genus. As compared to *S. suissei*, the species *S. elongatus* has the megaspores referable to the spore genus *Bentziisporites* Pot. & Kr., and lacks also a compact strobilus, the sporangia occurring in the axils of vegetative leaves. In *S. canonbiensis* the megaspores are referable to the spore genus *Setosisporites* (Ibr.) Pot. & Kr., and the microspores are like those of the spore genus *Densosporites*. In view of the veritable difference in the spore morphology of *S. elongatus* and *S. canonbiensis* as compared to the type species *S. suissei*, it is apparent that the inclusion of the former two species in *Selaginellites* is only that of convenience, based on superficial resemblance. In my opinion it would be preferable to place *S. elongatus* in *Selginella*, if not in a new genus, as has also been done by Darrah (1938) for his *Selaginella*-like cone containing megaspores referable to the spore genus *Zonalesporites* (Ibr.) Pot. & Kr., and Lundblad (1950) for her *Selaginella*-like, heterosporous, detached cone. The living genus *Selaginella* with its over 600 species and varied spore types is apparently a suprageneric grouping and can easily accommodate all such fossil *Selaginella*-like remains which do not find a place in any known fossil cone genus. Likewise is the case of *S. canonbiensis* if, however, it must be denied a place in *Bothrostrobos*.

The name *Bothro(dendro)strobos* was suggested by Nathorst (1894, p. 43) for the fructi-

fication *Lepidostrobus zeilleri* Nath., which he assumed to be the cone of *Bothrodendron* (*Ex-Lepidodendron*) *tenerrimum* (A. & T.) Nath. (1894, p. 45). Subsequently, however, Nathorst (1914) made *Lepidostrobus zeilleri* as the type of *Porostrobus*. In the meantime Seward (1910) included a petrified cone described by Watson (1908) in *Bothrostrobus*. Watson (loc. cit.) attributed his cone as belonging to *Bothrodendron mundum* in view of the agreement in the anatomical characters of the stele of the cone-axis with that of the vegetative shoots and the constant association of the cone and the vegetative shoots in the bed. Seward (1910, p. 263) had little doubt that the cone was borne by a species of *Bothrodendron* and that is why he described Watson's cone under *Bothrostrobus*. Irrespective of the fact whether or not Watson's cone was borne by a *Bothrodendron*, it does seem to have contained megaspores closely comparable to the type found in *S. canonbiensis*. The megaspores in Watson's cone as usually seen in meridional section (SEWARD, 1910, FIG. 216) are characterized by a ring of long, branched hair in the equatorial region and a gulate projection on the proximal face. Chaloner (1953, p. 287) considered these spores as rather similar to *Setosisporites praetextus* (Zerndt) Pot. & Kr. Potonié & Kremp (1956, p. 72) also consider the megaspores in Watson's cone to be possessing the same organization as in *Setosisporites*. In a number of other megasporangia out of Williamson and Scott collections and in that of University College, Nottingham, investigated by Holden (1932) and assigned to *Bothrodendron mundum*, the megaspores are more like the spore species *Setosisporites hirsutus* (Loose) Ibr. with the branched hair extending from the equator all over the distal face. The megaspores of *S. canonbiensis* are unmistakably similar to *Setosisporites hirsutus*. The morphographical agreement of *Setosisporites praetextus* and *S. hirsutus*

as two species of *Setosisporites* can hardly be doubted thus a more pertinent place for *S. canonbiensis* would be in *Bothrostrobus* rather than in *Selaginella* irrespective of the fact that the type of *Bothrostrobus* is a petrified cone and *S. canonbiensis* a compression.

Considering the comparison between *Porostrobus zeilleri* and *S. canonbiensis* one can see that in their general morphology both are heterosporous with spirally arranged sporangia and both have the ends of the sporophyll lamina free. However, in *Porostrobus zeilleri* the ends of sporophyll lamina are only hair-like but those in *S. canonbiensis* are much more developed. In *P. zeilleri* there occurs a mixed, alternating zonation of mega- and microsporate sporangia beginning with the latter at the base, whereas in *S. canonbiensis* a lower zone of megasporate sporangia demarcated from an upper zone of microsporate sporangia, has been recognized. Some difference is also noticed in the morphology of the spores in the two cones. The megaspores in *P. zeilleri* are gulate, *Lagenicula*-type, usually lying in meridional view having verrucose ornamentation. In *S. canonbiensis* the megaspores are gulate but with less pronounced *gula*, usually dorsiventrally flattened and having long-branched hair for ornamentation. In the microspores of *Porostrobus* the *cingulum* is broad and thick all over and the inner body has 3 inter-ray *papillae* but in *S. canonbiensis* the broad *cingulum* has an inner thick, crassitudinous, part followed by an outer thin flange and the inner body is without any evidence of the 3 inter-ray *papillae*. If we were to take the disparity in the age of the two cones, *Porostrobus* being a Lower Carboniferous fructification and *S. canonbiensis* from the Upper Carboniferous, together with the morphological differences into account, the two are distinctly members of two different cone genera although they might be phylogenetically closer to each other as compared to other lycopsid cone genera.

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Micro

6

Mega

Museum paleont. botan. Stockholm

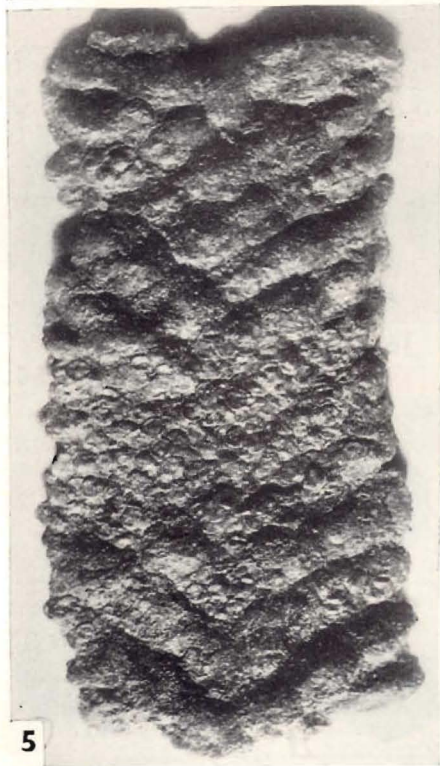
*Lepidostrobus Zielleri* Nath.

Nath: Z. pal. Fl. D. aelit. 2em XII, 5

Spitel. Pyrenae. Geopit

Geol. Lepidit. 1112

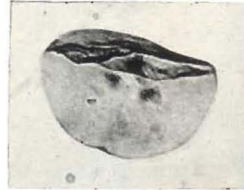
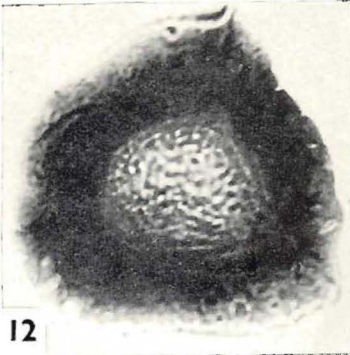
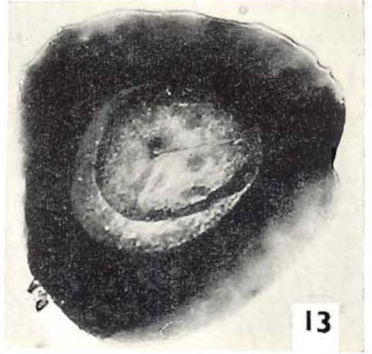
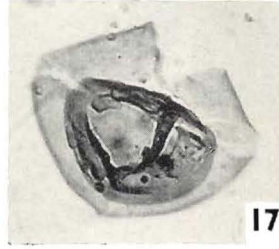
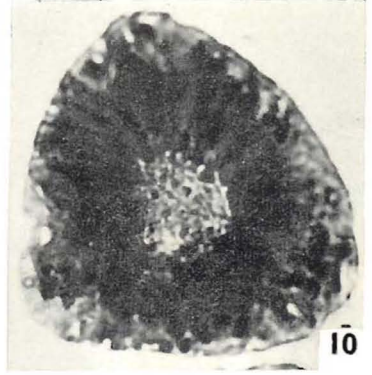
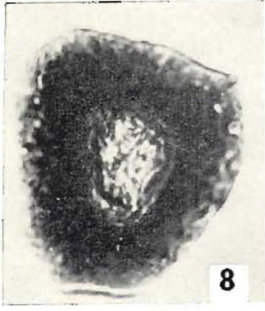
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5



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## EXPLANATION OF PLATES

## PLATE 1

1. Genoholotype of *Porostrobus zeilleri* Nath., Compression.  $\times 1$ .
2. Genoholotype of *Porostrobus zeilleri* Nath., Impression.  $\times 1$ .
3. Impression of *P. zeilleri* enlarged.  $\times 3$ .
4. Original label by Nathorst.
5. Compression of *P. zeilleri* enlarged.  $\times 7$ .
- 6, 7. Part of the compression of *P. zeilleri* further enlarged showing distribution of (mega and micro) sporangia.

## PLATE 2

- 8-11. Normally macerated microspores of *P. zeilleri*.  $\times 500$ .

12. Slightly overmacerated microspore of *P. zeilleri*.  $\times 500$ .
- 13, 14. Overmacerated microspores of *P. zeilleri*.  $\times 500$ .
- 15, 16. Inner body of the microspores showing 3 inter-ray papillae.  $\times 500$ .
17. Inner body enclosed in another outer membrane.  $\times 500$ .
18. A dry megaspore.  $\times 50$ .
19. Same megaspore as in Fig. 18.  $\times 108$ .
- 20, 21. Two dry megaspores.  $\times 50$ .
22. A wet megaspore.  $\times 50$ .
23. Exine sculpture of one of the inter-ray area in a megaspore.  $\times 200$ .