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 Porostrobus 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.

Porostrobus shows lepidodendroid as well as sigillarioid characters. Porostrobus bennholdi Bode is shown not to be a Porostrobus at all. It is provisionally referred to Lepidocarpon.

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

PS. Porostrobus is considered distinct from Selaginelloides and S. canoniensis Chaloner is advised inclusion in Bothrostrobus (Nath.) Sew.

INTRODUCTION

While searching through literature to gather information regarding in situ spores from fructifications, I came across the description and illustrations of Porostrobus zeilleri Nathorst, by Nathorst (1914, p. 70, Pl. 5, Figs. 12-16). The description of Porostrobus, of which P. zeilleri is the type, is in itself very interesting as it shows significant deviation from the well-known fructification genus Lepidostrobus, 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 (BHARADWAJ, 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 Lepidostrobus zeilleri n. sp. Subsequently, Nathorst (1914) created a new genus Porostrobus to include this fructification and thus renamed it as Porostrobus 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.

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METHOD

The gross morphological features of the fructification, compression as well as impres­
sion were studied dry, under reflected light. The mega- and microspores were examined
after macerating small pieces of the fructi­
fication containing two or more mega- or
microsporate 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. Macera­
tion was done by keeping the pieces in
fuming HNO₃ 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 Mullergaze). Some were dried
on a filter paper and kept in cardboard
avity slides and others were stored in 50
per cent glycerine for study with transmitt­
ed 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 evi­
dently 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 suc­
cessive 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 sub­
stantial sporangial membrane covering the
spores as the latter can be seen as distinctly
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 granu­
lated surface are the sporangia containing
microspores.

In the isolated cone part, there is no indi­
cation if the sporangia were borne on sporo­
phylls. However, in the maceration the frag­
mentary 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 sugges­
tion 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 megaspore 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 ± 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 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 megasporangium 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), ±5 µ in width as compared to those elsewhere which are ±10 µ in width. The verrucae have a broad base and bluntly conical or rounded apex.

Text-Fig. 2 — Compression of P. zeilleri showing predominantly mega- or microsporate zones. × 5.

Text-Fig. 3 — Histogram depicting the range of variation in the size of the microspores of P. zeilleri.
The size of wet megaspores (mounted in glycerine-jelly) in meridional plane ranges from 350 X 300 \(\mu\) to 480 X 400 \(\mu\), and in equatorial plane 360 X 320 \(\mu\). Dry megaspores are smaller and measure up to 400 X 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 dumbbell 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 \(\pm \frac{3}{8}\) 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 zeilleri 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 microsporate or megasporate 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 microsporate sporangia followed by a zone containing mostly megasporate sporangia which in turn is again followed by a region richer in microsporate sporangia. It is not definitely known if this alternation of micro- and megasporate sporangial zones was continued in the remaining, missing upper part of the cone.

As compared to the other heterosporous lycopsid cones, Porostrobus is distinct from all others in one or more respects. Lepidostrobus and Lepidocarpon differ from Porostrobus mainly in the intermixed occurrence of micro- and megasporate sporangia in the latter as compared to the isolation of megasporate sporangia in the basal region and microsporate 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 megasporate sporangia in Porostrobus was a prelude or otherwise parallel to the condition met with in Lepidostrobus and Lepidocarpon. Porostrobus is bisexual but Mazocarpon and Sigillariostrous are unisexual. Between these cone genera Lepidostrobus appears to be nearer to Porostrobus as is borne by the testimony of the morphology of the megaspores. The megaspores of Porostrobus are gulate as are the megaspores of Lepidostrobus (Chaloner, 1953). These, however, do not conform in sculpture. The megaspores of Lepidocarpon are not gulate as in Porostrobus and are much bigger in size and differ in sculpture of the exoexine. The megaspores of Mazocarpon or Sigillariostrous (Schoff, 1941; Chaloner, 1953b) are scarcer shaped, without gula, and laevigate or tuberculate quite unlike Porostrobus. The microspores of Porostrobus though strikingly different in external morphology approach those of Mazocarpon (Schoff, 1941) and Lepidostrobus sea 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 Porostrobus shows a mixture of lepidodendroid and sigillarioid features yet is distinct from Lepidostrobus, Lepidocarpon, Sigillariostrous 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 Porostrobus, Mazocarpon and Lepidostrobus sea (now transferred by Chaloner* to Polysporia).

The diagnosis of Porostrobus Nath. is emended thus:

Porostrobus Nathorst 1914 emend.

Genotype — Porostrobus 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; megasporate and microsporate sporangia occurring in alternating zones with the admixture of one type into the zone of the other, basal zone consisting of microsporate sporangia. Megasporate sporangia containing a number of tetrads, megaspores gulate, sac-like with the exoexine verrucose; microspores cingular with broad uniformly thick, ornamented cingulum, inner body having 3 inter-ray papillae.

Systematic Position of Porostrobus bennholdi Bode

In 1929 Bode described a fructification from the Lower Carboniferous brown coals of Moscow as Porostrobus 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 Sporenparen völlig glatt, jedoch mit deutlicher Tetradenszeichnung, nach der sie meistens aufgeplattet sind. Durch die Art und die Grösse der Sporen und durch die Grösse des Zapfens selbst von Porostrobus zeilleri unterschieden, sonst in der Organisation 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.

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 X 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 megaspore 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 megasporangia 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 Schöpf., C. bennholdi (according to POTONIE & 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 Aquatorialachse, Grösse der Makrospore im Mittel 3-3.5 mm., 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. coevensis 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 (BHARWAJ & 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 *Porostrobus* 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 *Porostrobus* as a distinct lycopodiaceous cone genus other than *Selaginellites* has been made. From the reinvestigation of *Porostrobus* by me, hardly any doubt remains that *Porostrobus* is quite distinct in its organization as well as in the spore morphology from *Lepidostrbus*, *Lepidocarpon*, *Sigillariostrobus* and *Mazocarpod*. However, comparison is needed now with the other two detached heterosporous cone genera, *Polyspora* and *Selaginellites*.

Recently Chaloner (1958a) has merged his species *Lepidostrbus zeilleri* into *Polyspora mirabilis* which has a distinct megasporangia basal region and microsporangia apical region as opposed to the roughly alternating, mixed mega- and microspore zones in *Porostrobus*. In addition to this the mega- and microspore morphology in these two genera is also substantially different. Thus *Porostrobus* stands out distinct as compared to *Polyspora* 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. suisei* Zeiller, a shoot with *Selaginella*-like vegetative habit and a fertile heterosporous cone containing megasporangia of the type now included in the spore genus *Triangulatisporites* Pot. & Kr. and microsporangia as of the spore genus *Cirratriradites* Wils. & Coe (Zeiller, 1906, Chaloner, 1954). Subsequently, Halle (1907) described *Selaginellites primaevus* (Goldenberg) Halle containing megasporangia of *Triangulatisporites*-type and Hoskins & Abbott (1956) have described a petrified, detached cone, *Selaginellites crassicinctus*, containing megasporangia referable to *Triangulatisporites* and microspermatangia to *Cirratriradites* as in *S. suisei* 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 morphology 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. suisei*, *S. primaevus* or *S. crassicinctus*, *Porostrobus zeilleri* differs in having mixed zones of mega- and microsporangia from the base upwards and also in the morphography 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. canoniensis* Chaloner (1958b) both of which possess spores of a morphographical type different from those of *S. suisei*, the type of the genus. As compared to *S. suisei*, the species *S. elongatus* has the megasporangia referable to the spore genus *Bentisissporites* Pot. & Kr., and lacks also a compact strobilus, the sporangia occurring in the axils of vegetative leaves. In *S. canoniensis* the megasporangia are referable to the spore genus *Setosisporites* (Ibr.) Pot. & Kr., and the microsporangia are like those of the spore genus *Densosporites*. In view of the veritable difference in the spore morphography of *S. elongatus* and *S. canoniensis* as compared to the type species *S. suisei*, 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 megasporangia referable to the spore genus *Zonasporites* (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. canoniensis* if, however, it must be denied a place in *Bothrostrobus*.

The name *Bothrostrobus* 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 morphography of the spores in the two cones. The megaspores in P. zeilleri are gulate, Lageniculate 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.

REFERENCES


**EXPLANATION OF PLATES**

**PLATE 1**

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

**PLATE 2**

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