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POROSTROBUS NATHORSTII SP. NOV.: A NEW SPECIES OF LYCOPSID CONE FROM THE EARLY PENNSYLVANIAN OF ILLINOIS

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ABSTRACT

Thirty-one specimens of a small megasporangiate lycopsid cone referable to the genus Porostrobus Nathorst and abundant associated dispersed megaspores have been collected from Early Pennsylvanian strata in the Allied Stone Company quarry, Milan, Illinois. Based on other elements in the flora, the deposit is considered to be part of the Morrowan Caseyville Formation and probably of Namurian age. This is the first reported occurrence of Porostrobus in North America and the cones are recognized as a new species, P. nathorstii. The environment of deposition indicates that the cones may have been transported from the parent plant prior to preservation. Cones are preserved as coalesced compressions measuring 15-36 mm long by 2.5-7 mm wide, and are characterized by an apical tuft of leaves up to 20 mm long. Sporophylls are spirally arranged on a narrow cone axis, lack a heel or keel, and have a long distal lamina. Sporangia contain a single functional megaspore tetrad. Mature megaspores are 750-1,150 μm in diameter, have prominent trilete sutures raised to form a gula, and have numerous branched hairs confined to an equatorial band. Megaspores correspond to the dispersed form Setosisporites praetextus (Zerndt) Potonie and Kremp. Porostrobus nathorstii is the only species of the genus described to date that is monosporangiate.

IN RECENT YEARS, several sites in western Illinois have yielded significant information about Early Pennsylvanian nonsamp floras, both on their overall composition and on individual taxa within the floras. The Allied Stone Company quarry in Milan, Illinois (Leary, 1981) has been a major collecting site for nearly ten years and continues to yield new species as well as new data on known taxa. Among the abundant and well preserved fossil plants from the Allied quarry deposits are thirty-one specimens of small lycopsid cone referable to the genus Porostrobus Nathorst and numerous dispersed associated megaspores of the Setosisporites Potonie and Kremp (1955) type.

Porostrobus was originally erected by Nathorst (1914) based on a single specimen which he had previously described as a new species, Lepidostrobus zeilleri, from the Lower Carboniferous of Spitzbergen (Nathorst, 1894). Nathorst reassigned this cone in the belief that it was associated with Porodendron stems from the same locality. This association has been questioned because it is based solely on a single, unattached cone (Chaloner, 1967). Bharadwaj (1958) reexamined P. zeilleri and more fully described megaspores and microspores contained within the cone. Chaloner (1967) states that the megaspores are of the Setosisporites hirsutus var. brevispora (Zerndt) Potonie and Kremp (1955) type. Playford (1963) describes dispersed microspores from Spitzbergen that closely resemble those described for P. zeilleri (Bharadwaj, 1958), and designates them as Densoisporites spitzbergenensis.

Chaloner (1962) named a second species of Porostrobus, P. canoniensis, based on a single cone from the Westphalian of Scotland which he had previously named Selaginellites canoniensis (Chaloner, 1958). Chaloner (1958) describes the megaspores as being of the S. hirsutus type and the microspores as being of the Densoisporites loricatus type.

The cones described in this report represent a new species, Porostrobus nathorstii, and constitute the largest known suite of specimens of the genus known to date. This is also the first reported occurrence of this genus in North America. The discovery of these cones provides an opportunity to expand the generic concept of Porostrobus to include monosporangiate cones.

MATERIALS AND METHODS-Study material includes thirty-one cones and cone fragments

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plus numerous slabs with abundant megaspores, preserved as coalified compressions and impressions (Schopf, 1975). Cone specimens were studied using light microscopy. Dispersed megaspores were removed from the shale matrix by first placing them in heated dilute HCl (Doher, 1980), then in concentrated HF to remove adhering dolomitic and siliceous mineral matter. Spores were then placed on SEM stubs and coated with gold/palladium alloy for observation by scanning electron microscopy (SEM). Specimens are housed in the Geology Collections of the Illinois State Museum, Springfield, Illinois, as ISM 417032–417049.

Specimens were collected from sediments which fill channels eroded in Devonian Cedar Valley Limestone (Leary, 1981). These channels are 6 m deep, 8 to 30 m wide, steep-sided, and flat-bottomed. They are exposed in the Allied Stone Company quarry, Milan, Rock Island County, Illinois (Fig. 1). The fossil-bearing strata consist of shale, siltstone, sandstone, and occasional thin conglomerates (Fig. 2). Conglomerate is most common at the base of the section, although it sometimes caps the channel fill. The amount of sandstone present increases downward in the section.

Stratigraphically, the age of the fossil-bearing shale is difficult to determine. The shale is underlain by upper Middle Devonian Cedar Valley Limestone. Pleistocene erosion has removed nearly all overlying Pennsylvanian strata in the quarry, but at a few points clean white to buff sandstone is present above the fossil-bearing shale. This sandstone contains

Stigmaria casts and, on this basis, has been correlated with the "Stigmarian Sandstone" or Babylon Sandstone. Across the Rock River from the quarry, the same sandstone is interlayered with shale, carbonaceous shale, and impure coals. Using palynomorphs, these strata have been dated as Caseyville and probably lower Westphalian A (R. Peppers, personal communication).

Based on spores present, the Allied quarry shale deposit is considered to be of Late Namurian age (R. Peppers, personal communication). Macrofossils also indicate a Namurian age (Leary, 1981). Some of the taxa present have ranges extending from Namurian B or C through the Westphalian (Table 1), others are restricted to the Namurian. Some Namurian taxa, such as Gulpenia, are rare in the Allied quarry flora; others, such as Sphenophyllum tenerimum and Mesocalamites cistiformis, are abundant.

**Diagnosis**—Generic diagnosis emend. — *Porostrobus* Nathorst 1914: Compressed cones small, compact, heterosporous, and pedunculate; with sporangia spirally arranged around the axis. Sporophylls have hairlike distal ends or a distal lamina. Megaspores trilete, gulate,
and radial, with numerous branched hairs on equatorial or distal surfaces; of the *Setosisporites* Potonie and Kremp type. Microspores tri-lete with broad, uniformly thick, ornamented cingulum; of the *Densosporites* Berry type.

**Type species:** *P. zeilleri* Nathorst 1914.

**Specific diagnosis**—*Porostrobus nathorstii*, sp. nov.: Megasporangiate cones up to 25 mm long and 7 mm in diameter, tapering slightly distally. Central axis up to 1 mm in diameter. Sporophylls lack a heel or keel, and possess a distal lamina up to 6 mm long. Tuft of leaves up to 20 mm long present at cone apex. Sporangia containing a single megaspore tetrad and decreasing in size distally. Megaspores 750-1,150 μm in diameter with prominent trilete arms; gulate; possessing branched hairs confined to an equatorial band; of the *Setosisporites praetextus* (Zerndt) Potonie and Kremp type.

**Holotype:** ISM 417032, Geological Collections, Illinois State Museum, Springfield; Fig. 3.

**Paratypes:** ISM 417033–417043, Geological Collections, Illinois State Museum, Springfield; Fig. 4–6.

**Collecting locality:** Shale deposits in the Allied Stone Company quarry, Milan, Rock Island County, Illinois (SE ¼ sec. 14, T. 17 N., R. 2 W., Milan Quadrangle).

**Stratigraphic position:** Probably Caseyville Formation, Morrowan Series.

**Age:** Early Pennsylvanian.

**Etymology:** The specific epithet honors A. G. Nathorst, who first described the genus in 1914.

**Description of specimens**—Cones of *P. nathorstii* are elongate, tapering slightly toward the apex. Incomplete preservation of many of the specimens prevents accurate determination of the total length and width. The body of the cone ranges from 8 to more than 26 mm long and from 2.5 to 7 mm wide. A prominent tuft of leaves at the distal tip extends as much as 20 mm beyond the body apex (Fig. 4). Whether the distal tuft represents immature distal sporophylls or a region of vegetative leaves distal to the fertile region is uncertain.

Megasporophylls are attached to an axis which has a maximum observed width of 1 mm. Two of the cones are attached to pedicels which are up to 2.5 mm wide and extend about 6 cm from the cone base (Fig. 5). The pedicels are bare with neither appendages nor leaf scars apparent. In one instance, two cones were attached to a common pedicel (Fig. 6).

Sporophylls are spirally arranged and bear only megasporangia throughout the cone. The sporophyll lamina lacks both a heel and a keel and extends distally for up to 6 mm.

Megasporangia contain a single functional tetrad of megaspores (Fig. 7) and range in diameter from 1.85 mm basally to 1.2 mm distally. Maceration of distal sporangia released tetrads of smaller size which appeared to be immature, suggesting that sporangia matured acropetally.

Mature megaspores are 750 to 1,150 μm in diameter, and have prominent trilete sutures raised to form a gula which is approximately 120 μm high (Fig. 8, 9). Numerous branched or laterally fused hairs are confined to a narrow band around the equator (Fig. 8, 10, 12). The distal spore surface is glabrous (Fig. 10, 11). Contact faces are evenly covered with small coni approximately 5 μm high (Fig. 8). Sporoderm ultrastructure is very similar to that of specimens described by Stubblefield and Rothwell (1981) as *Setosisporites praetextus* forma minor (S. Stubblefield, personal communica-
Fig. 3-6. *Porostrobus nathorstii*. All figures ×5. 3. Cone showing arrangement of sporangia and tetrads. Holotype. ISM 417032. 4. Cone showing distal lamina of sporophyll. ISM 417036. 5. Cone showing tuft of leaves at apex. ISM 417036. 6. Two cones attached to a pedicle. ISM 417033.
Fig. 7–12. 7. Megaspore tetrads. ISM 417032. ×25. 8. Megaspore showing trilete mark and gula. SEM ×150. 9. Proximal face of megaspore showing trilete mark. SEM. Bar = 500 μm. 10. Distal face of megaspore. SEM. Bar = 100 μm. 11. Megaspore showing equatorial hairs. SEM. Bar = 500 μm. 12. Details of equatorial hairs. SEM. Bar = 50 μm.
tion). The megaspores of *P. nathorstii* correspond to the dispersed form *Setosisporites praetextus* (Zerndt) Potonie and Kremp (1955).

**Discussion—Comparisons—** Among known Carboniferous lycopod cones, *P. nathorstii* is most similar in morphology and spore type to *Porostrobus zeilleri* (Nathorst, 1894, 1914; Bharadwaj, 1958; Chaloner, 1967), *P. canonbiensis* (Chaloner, 1958, 1962, 1967), and *Bothrodenstrobus mundus* (Watson, 1908; Chaloner, 1967; Stubblefield and Rothwell, 1981). All four of these species are relatively small cones containing *Setosisporites*-type megaspores. *Porostrobus nathorstii* can be distinguished from each of the others in that it is monosporangiate and possesses a distal tuft of leaves, in contrast to the bisporangiate nature and lack of a tuft in the others. Further, *P. nathorstii* is delimited from *P. zeilleri* and *P. canonbiensis* based on megaspore type (Table 2): *P. nathorstii* sporangia contain *S. praetextus*-type megaspores, while *P. zeilleri* and *P. canonbiensis* have *S. hirsutus*-type megaspores.

**Taxonomic placement of *P. nathorstii*—** Stubblefield and Rothwell (1981) demonstrated that embryos attributable to *Bothrodenstrobus mundus* (found within the spore wall of megaspores of the *Setosisporites praetextus* forma *minor* type) displayed an Isoetalean developmental pattern. This data influenced Thomas and Brack-Hanes (1984) to include *Bothrodenstrobus* in Isoetales. In the same work, they place *Porostrobus* in Selaginellales. Based on the close similarity of unique megaspores in members of *Porostrobus* and *Bothrodenstrobus* (Bharadwaj, 1958; Chaloner, 1958, 1967; Stubblefield and Rothwell, 1981) and on the undoubted affinity of *Bothrodenstrobus* within the Isoetales (Stubblefield and Rothwell, 1981; Thomas and Brack-Hanes, 1984), the most appropriate ordinal classification for *Porostrobus* is within the Isoetales.

Pigg and Rothwell (1983) recognized three families of Isoetales: Isoetaceae for the Mesozoic and Cenozoic *Isoetes* and *Isoetaceae*-like plants, Pleurosemiaceae for the Mesozoic forms for which internal anatomy is little known, and Chaloneriacae for *Chaloneria* and similar Paleozoic forms, such as *Polysporia*. Thomas and Brack-Hanes (1984) recognized an additional family, Takhtajanodoxaceae, based on Triassic material described by Snigerevskaya (1980). Among these families, *Porostrobus* shows greatest affinities with the Chaloneriacae. Pigg and Rothwell (1984) circumscribe Chaloneriacae as having trilete megaspores with auric-
ulae or a cingulum and microspores possessing a saccus. Although similar in some respects, including general form of the microspores, megaspores of Porostrobus have equatorial or distal hairs and possess a prominent gula in contrast to the solid auriculae or cingulum and lack of a gula in members of the Chaloneriaceae. Because of the dissimilarities with circumscribed families in the Isoetales and in complete nature of specimens of known species, Porostrobus cannot be classified in any existing family, and must be considered as a form genus within Isoetales.

Environment of deposition — The fossil-bearing Early Pennsylvanian sediments occur in channels eroded in a nearly level limestone surface (Leary, 1981). Sediments completely fill these channels, and consist of a generally fining upward sequence of sandstone, siltstone, mudstone, gray shale, and black highly fissile shale. Although isolated S. praetextus megaspores occur occasionally throughout the sequence, primarily in thin, carbonaceous horizons containing little recognizable material, they are concentrated in the highly fissile black shale at the top of the sequence. Porostrobus nathorstii cones are restricted to these upper black shales. Almost none of the channel sediments are bioturbated, indicating that plants did not grow in the channels, even when the channels filled with sediments. This observation suggests that cones and megaspores were transported prior to burial.

Based on the associated flora in the upper black shales, with its overwhelming predominance of Mesocalamites and lycopod remains, as well as paleoenvironmental interpretations of the strata (Leary, 1981), the Porostrobus-bearing plant probably grew in swamps adjacent to the channels. As local water levels rose, the swamps increased their extent in the immediate area and Mesocalamites dominated the flora and the Porostrobus- and Lepidostrobus-bearing lycopods became more abundant.

Associated floral elements — The only species of lycopod axis commonly present in the sediments at the Allied quarry locality is Lepidodendron mannabachense (sensu Thomas, 1970) (= L. obovatum). Large Lepidostrobus cones are also abundant in the flora. Additional common elements in the flora include dispersed Lepidocarpon megasporophylls and Lepidophylloides leaves; Stigmaria and Lepidophloios are rarely found. No vegetative structures or microsporangiate cones unambiguously associated with P. nathorstii have been found.

Reproductive biology — Among living and fossil lycopsids, three mechanisms of spore dispersal are currently recognized. In the first mechanism, spores are shed from free-sporing dehiscent sporangia with the sporophyll or cone later shed from the plant. The majority of lycopsids would fall into this category (Bierhorst, 1971). In the second mechanism, entire megasporophyll/megasporangium/megaspore complexes are shed from cones as a single, seedlike unit, while microspores are free-sporing. Examples of this mechanism are Lepidocarpon and Achlamydocarpon and associated plants (Phillips, 1979). In the third mechanism, dehiscence does not occur. Rather, spores are released from the sporangium due to degradation of the sporangium by microorganisms. Isoetes is an example in which this mechanism occurs (Bierhorst, 1971).

The cones of P. nathorstii may indicate a fourth, previously unrecognized mechanism of dispersal among lycopsids. Cone specimens of P. nathorstii consist of two types. Some cones are essentially intact in that the sporangium is left covering mature megaspore tetrads, and the distal sporophyll laminae and tuft are intact. Other cone specimens consist of little more than megaspore tetrads in the positions of sporangia in a cone, but the sporangium, laminar tissue, and axis are not preserved. No specimens have been observed that appeared to have dehisced sporangia. Based on these observations and indications that the cones were transported, we speculate that whole cones of P. nathorstii were shed from the parent plant intact. Spores would have then been released by decay of the surrounding tissues.

LITERATURE CITED


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