
Evolutionary significance of the Late Devonian lycopsids of the northcentral America

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The paper focusses on the evolutionary characters revealed by the lycopsid axes and cones of North America. Highlighted especially are the specimens collected from the Late Devonian greyish-black shale of Greater Cleveland, Ohio and from the Late Devonian silty shale of Venango Formation in Erie County and Pennsylvania. Axes and cones are very large in dimensions comparable to those of Carboniferous. Dominance of many different kinds of lycopsids in the collection suggests that the coastal marshes of Late Devonian sea had forests of respectable size lycopsid trees. *Clevelandodendron ohioensis*, a slender, unbranched plant with an apical heterosporous cone and short, basal appendages, shows isotalean growth habit similar to a few Carboniferous genera and Triassic *Pleurometa*-like forms. This, coupled with presence of *Skullioctrobus*-like cones from the Triassic of Australia and Tasmania, suggest lineage of Triassic lycopsids from the Late Devonian forms of the Cleveland Shale.

Key-words—Lycopsids, Evolution, Late Devonian, Northcentral America.

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सारांश

उत्तर केन्द्रीय अमेरिका के अनंतिम डिवोनी लाइकोप्सिडों का विकासीय महत्व

शिया चितले

उत्तरी अमेरिका में प्राप्त लाइकोप्सिड अक्षों और कोनों के विकासीय लक्षणों का अध्ययन किया गया है। ओहियो में ग्रेटर क्लीवलैंड के अनंतिम डिवोनी काले भूरे रंग के शैलों तथा एरीकाउन्टी और पेन्सिलवानिया के वीनांगो शैल-समूह के अनंतिम डिवोनी कल्प के शैलों से एकत्रित प्रादर्शों पर विशेष ध्यान दिया गया है। कार्बोनिफेरस कल्प की अपेक्षा अक्ष और कोन आकार में बड़े हैं। विभिन्न प्रकार के लाइकोप्सिडों की बाहुल्यता से प्रस्तावित होता है कि अनंतिम डिवोनी समुद्र के तटों पर लाइकोप्सिड वृक्षों के वन थे। *क्लीवलैन्डोडेन्ड्रॉन ओहियोएन्सिस* कुछ कार्बोनिफेरस प्रजातियों तथा ट्राएसिक *प्लूमेरिया* सदृश प्रारूपों के समान आइसोडेटेली वनस्पति का द्योतक है। आस्ट्रेलिया और तस्मानिया के ट्राएसिक कल्प से *स्कुलिओस्ट्रोबस* सदृश कोनों की उपस्थिति के साथ-साथ यह क्लीवलैंड शैल के अनंतिम डिवोनी प्रारूपों से ट्राएसिक लाइकोप्सिडों का उद्भव इंगित करता है।

A FEW lycopsids have been described earlier from the Upper Devonian rocks of North America exposed at different places many miles apart from each other. From Erie County Pennsylvania, Chitale and McGregor (1988) described *Bisporangiostrobus harrisii*, a specimen showing two cigar-size and shaped heterosporous cones on a small, forked axis. Later, from the same place, a piece of slender permineralized lycopsid axis, *Lycopodites mckenziei* (Chitale, 1989) was described suggesting a possibility of its

being a piece of the forked axis which bore cones of *Bisporangiostrobus harrisii*.

Arnold (1933, 1935, 1939) collected compressed lycopsid specimens from McKean County of Pennsylvania which he described under the names *Prolepidodendron breviinternodum*, a vegetative axis with leafy appendages, and *Lepidostrobus galloyi*, a cone which, according to him, might belong to the former shoot. However, the age of the locality from where these two were collected is controversial, whether Upper Devonian or Lower Mississippian

(Gensel & Andrews, 1984), although for the time these authors approved of its being the Upper Devonian.

A few more lycopsids, *Drepanophycus colophyllus*, *Haskinsia colophylla* and *Archaeosigillaria vanuzemi* (Göppert) Kidston have been described by Grierson and Banks (1963) from the Upper Devonian of New York State. Others have been *Lepidosigillaria whitei* (Kräusel & Weyland 1949) and *Colpodexylon deatsii* (Banks 1944).

This paper highlights especially the evolutionary characters observed in the lycopsid specimens of the Northcentral America.

Focussed are the specimens discovered in the Late Devonian black shale of Greater Cleveland, Ohio and found in the silty sediments of Venango Formation exposed at the Union City Dam, Erie County, Pennsylvania. From these areas collections of varied plant life from algae to pteridophytes and progymnosperms were made. Both the collections have one common plant—*Callixylon*—the wood of a progymnosperm tree, *Archaeopteris*. It marks the Upper Devonian stratum. Lycopsids dominate in both these silty shales. Most of the specimens from Cleveland shale are compressions whereas the Pennsylvanian specimens from the Venango Formation are permineralizations.

Although there are many specimens collected of lycopsid tree barks and cones showing different characters from each other, for the purpose of this paper, only few of them are selected for illustrations. There are over 20 different kinds of large axes, meaning there were so many different lycopsid trees growing during the Late Devonian Period on the Cleveland sea coastal wetland. The diameter of the pieces of axes varies from 3 - 50 cm, displaying the tree habit of those lycopsids to which they belonged. Ten cones of different shapes and sizes, with different kinds of

sporophylls and spores collected from the same silty shales also support the presence of arborescent habit in lycopsids grown 363 million years (Harland *et al.*, 1990) ago. They are unusually large for Devonian age and have a woody appearance.

The Cleveland Shale is the uppermost member of the Ohio black shale (Hansen, 1994). This greyish-black shale was known to have preserved fishes and sharks (Hyde, 1926, 1928, 1965). When these were collected by geologists and paleontologists, plant specimens were also collected by them since 1920 and were being stored in the Cleveland Museum of Natural History under the name, "Plants," without being identified.

Since 1980, many Cleveland Shale exposures in the vicinity of Greater Cleveland, like Big Creek, Rocky River, Skinners Run (Chitale, 1992a) were visited frequently for fresh collections. Though most of the better preserved specimens were salvaged when I-71 interstate route was being constructed through Cleveland, exposing fresh shale on the roadside cuts. A short report on some of the plant fossils collected from here was published by Chitale (1982). Since then the investigation of the Cleveland Shale flora is being continued and published by Chitale (1985, 1986, 1988, 1989, 1989a, 1991, 1992, 1992a, 1996) to understand the biodiversity and dominance of certain groups observed, in relation to environment in these Late Devonian plants. The Cleveland Museum of Natural History is the only repository of this valuable Cleveland Shale flora of America.

Different methods were used to prepare the compressed and permineralized specimens. Usually compressed ones were studied directly under incident light under low and high magnifications. Also acetate film transfers were made with some barks, and cone scales were macerated in Schulzes solution for spores

PLATE 1

Bar scales are in centimeters unless otherwise stated.

1. A lycopsid cone, found in part and counterpart (counterpart shown here). P-2994
2. *Clevelandodendron ohioensis*, gen. et sp. nov. An entire, slender unbranched tree with an apical cone. P-2975.
3. Cone of *C. ohioensis* enlarged. P-2975.
4. A lycopsid elongated cone. P-4207
- 5, 6. Part and counterpart of a lycopsid globular cone with appearance and size of *Skulliostrobus*. P-2985, P-2986 and P-2987.
7. *Bisporangiostrobus harrisi* gen. et sp. nov. Two cones on a forked axis. P-3180.
8. A lycopsid cone found in part and counterpart. Part is seen here. P-2972.
9. An ovoid lycopsid cone with appearance and size of *Skulliostrobus*. P-1696.

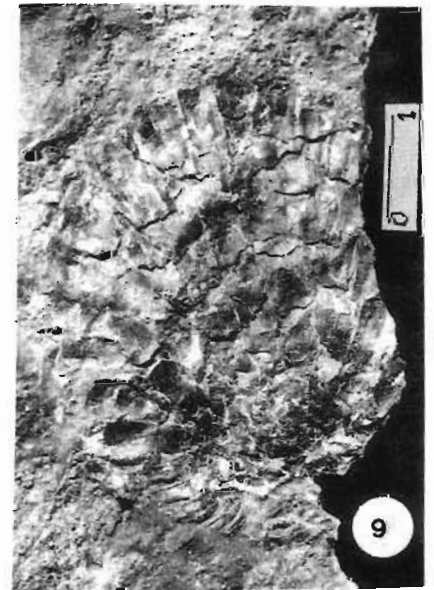
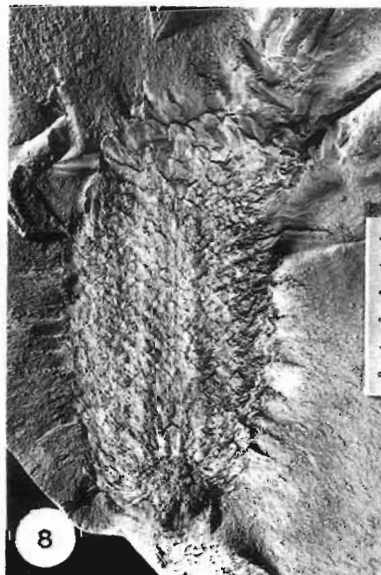
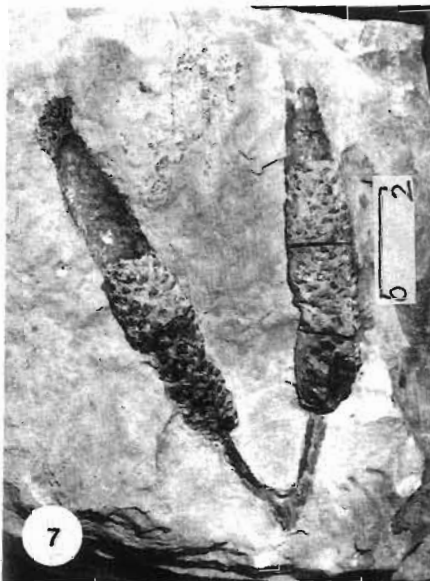
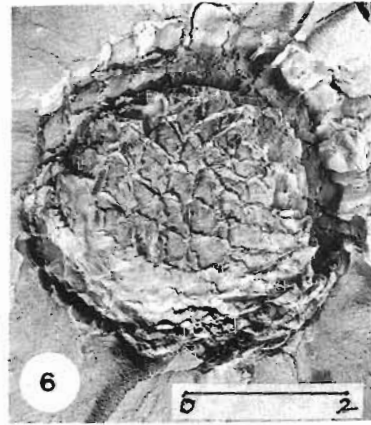
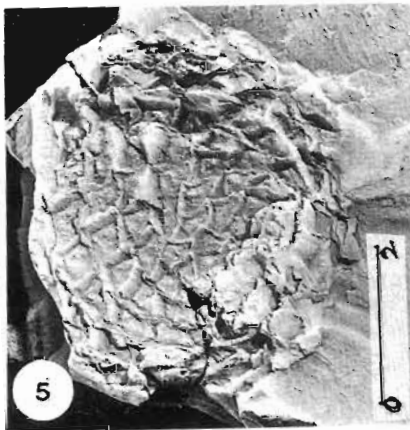


PLATE 1

and cuticles. The permineralized specimens usually with pyrite and silica were treated first with 45 per cent hydrofluoric acid, followed by 45 per cent nitric acid for etching the required smoothed surfaces, and then washed with sodium bicarbonate, followed by flowing water. After drying them well, the surfaces were flooded with acetone and covered with cellulose acetate film. The dry film was pulled off as a peel carrying a thin section with it. The treatment time, strength of acids and the thickness of the acetate film vary with different specimens. Additional ground thin sections of microscopic transparency were prepared to study some of the permineralized specimens.

The specimens used in this paper are stored with their preparations in the Paleobotany Department of the Cleveland Museum of Natural History, Ohio, USA. They bear the following numbers: P-2994, P-2975, P-4207, P-2985, P-2986, P-2987, P-3180, P-2972, P-1696, P-3676, P-4281, P-3893, P-3905, P-3889-92, P-3879-80, P-3880.

EVOLUTIONARY SIGNIFICANCE

The two essential basic characters to be found in land plants to justify their evolutionary significance are the presence of arborescent habit and the heterosporous reproductive organs. This condition is distinct in the Late Devonian lycopsids collected from the Northcentral rocks of America.

Arnold as early as 1933 and 1935 described a cone, *Lepidostrobus gallowayi* (*Flemingites gallowayi* (Arnold) (Brack-Hans & Thomas 1983) having two kind of spores. He later suggested that the associated vegetative remains of *Prolepidodendron breviinternodum* described by him as an arborescent form (Arnold, 1939; Gensel & Andrews, 1984) might have borne the *L. gallowayi* cone.

Besides these early records, there was no other lycopsid described in detail from the Late Devonian

of Northcentral America until 1988 when Chitaley and McGregor (1988) published on *Bisporangiostrobus harrisii* (Pl. 1, fig. 7), a structurally preserved lycopsid cone from the Late Devonian of Pennsylvania. The specimen with two cones each 7.2 cm long, upright, elliptical, 1.4 cm wide, had a short axis of 0.9 cm long and 0.5 wide. Eligulate lanceolate sporophylls with a lobed heel were helically borne on a slender protostelic axis. The cones were heterosporous, the spores borne in two separate sporangia, megasporangia with *Duosporites* megaspores and microsporangia with *Geminospore* microspores. The appearance of the cone was woody. This was the first record of a structurally preserved lycopsid cone from the Late Devonian of Northcentral America. This specimen is very valuable in illustrating the evolutionary significance of the lycopods grown in Late Devonian of Northcentral America. The woody appearance and the size of the cone suggests arborescent habit of the plant on which it was borne. The absence of ligule in this heterosporous cone is interesting, since it sets aside the age-old belief of the two going together.

Both micro- and megaspores give new records of their age. The Givetian microspore genus, *Geminospore*, is extended into the Late Devonian, being found in *B. harrisii*, and the *in situ* *Duosporites* megaspores found in this cone push back their occurrence from Late Carboniferous to Late Devonian.

Clevelandodendron ohioensis gen. et sp. nov. (Pl. 1, figs 2, 3), a compressed specimen mentioned in earlier reports, is now described in detail (Chitaley & Pigg, 1996). It is unique in that it is found preserved as an entire, slender unbranched lycopsid tree with basal appendages and an erect, ovoid apical cone 9 cm long and up to 6 cm wide, robust in appearance. It has two kinds of spores in separate sporangia, megasporangia conical with a narrow base and a wider apex containing spherical laevigate megaspores with moderately thick trilete mark with

PLATE 2

Bar scales are in centimeters unless otherwise stated.

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|---|---|
| <ol style="list-style-type: none"> 1. A lycopsid axis with <i>Lepidostigillar</i> leaf scars. P-3676. 2. A lycopsid displaying growth habit. P-4281. 3. A lycopsid with corrugated bark and indistinct leaf scars. P-3893. 4. A lycopsid bark, ribbed. P-3905. 5. A forked lycopsid axis displaying <i>Cyclostigmar</i> leaf scars in close helicals. P-3889-92. | <ol style="list-style-type: none"> 6. Enlarged from figure 2. 7. A lycopsid axis with leaf scars in close helicals. Found in two parts, one part seen here. P-3880. 8. Enlarged from figure 8 to show details of leaf scar. 9, 10. Details of bark with leaf cushions and leaf scars. Enlarged from figure 7. |
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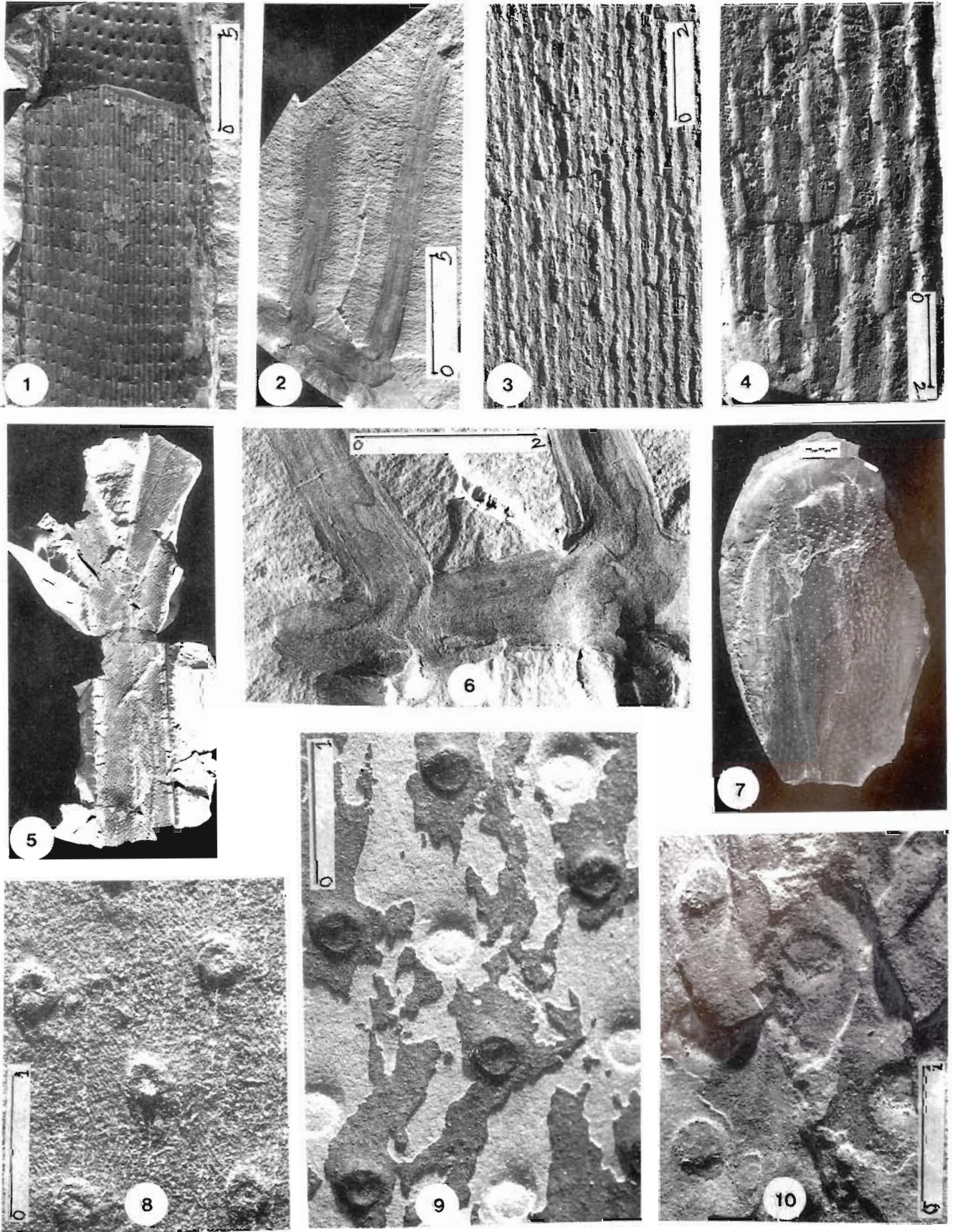


PLATE 2

three wide radii or laesurae. Microsporangia with thin sporangial wall having small round microspores with trilete mark and indistinctly punctate wall, very much like *Calamospora* or *Punctatisporites*.

C. ohioensis is very significant in lycopsid phylogeny. It demonstrates that unbranched slender monopodial plants with isoteleian growth habit similar to the Carboniferous genera *Chaloneria* and *Sporangiostrobus* and Triassic *Pleuromeia*-like forms were present as early as the Late Devonian.

The other lycopsid cones are woody in appearance, large and heterosporous, recorded in brief by Chitaley (1982, 1986, 1989, 1992). The cone seen in Pl. 1 fig. 1 is large with central axis bearing sporophyll sporangia complexes in close helicals, directed upwards at an angle of 30°. Spores are of one kind, but big enough to be megaspores though not mature. Pl. 1, fig. 4 is a long heterosporous cone. It measures 7 cm wide in widest region and 30 cm long as seen preserved, but likely to be much longer. It is heterosporous with two kinds of spores, smaller with triradiate marks with shiny wall and larger with triradiate mark with smooth walls. The sporophyll sporangia complexes are in close helicals, and attached almost at right angles to the central cone axis. Pl. 1, fig. 8 is a cone preserved in part and counterpart (only one half is seen here). The oval, large cone with sporophyll sporangia complexes in close helicals on the central axis, is also heterosporous. The whole appearance of the cone and shape of the individual leaf is reminiscent of the Carboniferous cone, *Bothrodendrostrobus* Hirmer (Chaloner, 1967). The two (part and counterpart) pieces of a globular cone figured in Pl. 1, figs 5, 6 and another similar cone Pl. 1, fig. 9 have central axis on which the sporophyll sporangia complexes are in close helicals. They are wedge-shaped with long horizontal limbs directed upwards. Since they are not yet macerated for separating the spores, it is not known whether they are heterosporous or homosporous. However, their presence in the Upper Devonian Cleveland Shale is intriguing. They are almost identical in appearance and size as that of *Skillioostrobus* cones (Ash, 1979) described from the Early Triassic of Australia and Tasmania.

Detail study later might bring forth many other noteworthy characters. However, right now, the two

evolutionary features, arborescence and heterospory, are distinctly observed well developed in these large cones of unusual size for the Late Devonian age.

A few lycopsid axes are illustrated here from our big collection of over 20 specimens. The specimens are pieces of big tree trunks with a different kind of bark pattern, suggesting the large number of lycopsid species present in the coastal Cleveland Shale. These pieces of compressed woods vary in diameter from 2-50 cm, unlike the modern lycopods. Almost all of them are decorticated so as not to reveal the cushioned leaf bases. However, the leaf scars are distinct. They are of different sizes and shapes, and reveal vascular traces. One of the compressed decorticated specimens (Pl. 2, fig. 5) is a specimen of a branched trunk and though without leaf cushions, the leaf scars are elevated, round, with thick border and with a central vascular trace (Pl. 2, fig. 8) like in *Cyclostigma* (Haughton, 1859; Johnson, 1913). Another specimen (Pl. 2, fig. 7) is equally interesting. It is collected as part and counterpart, of which one half is in the photograph. These pieces exhibit the remnants of leaf cushions (Pl. 2, figs 9, 10) which are diagonally elongated with leaf scars on the upper end (Andrews, 1961). Each scar is more or less concave with vascular trace scar in the centre and two upper parichnos scars on the two sides. This piece of trunk also is a reminiscent of the Carboniferous genus *Bothrodendron* Lindley & Hutton. The shape of the leaf scar with vascular and parichnos scars is very much similar to that of *B. kuianum* Lee (Chaloner, 1967). Ligule scar is not observed.

This lycopsid specimen (Pl. 2, fig. 2), also a compression, has an underground, elongated rhizome with few rhizoids on its abaxial side and two vertical shoots on its adaxial side. The specimen is totally decorticated, but is useful in showing its growth habit. The other pieces of decorticated tree trunks (Pl. 2, figs 1, 3, 4) show vertically ribbed architecture of the bark similar to *Lepidosigilaria* (Kräusel & Weyland, 1949). The rafted leaf scars are indistinct in the specimens (Pl. 2, figs 3, 4), but distinct in the specimen (Pl. 2, fig. 1).

Without hesitation, it can thus be concluded from the above illustrations of axes and cones, that sufficient evidence is brought forth to signify that by Late

Devonian the lycopsids had achieved arborescent habit of having respectable size trees with heterosporous cones. The architectural similarities between *Clevelandodendron ohioensis* and Triassic *Pleuromeia*-like forms, and the presence of other two globular cones in the Cleveland Shale, almost identical in appearance and size with Triassic *Skulliostrobus* described from Australia and Tasmania, suggest a lineage of Triassic lycopsids from the Late Devonian forms of the Cleveland Shale.

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