A review of some Late Devonian lycopods from north-central United States

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Lycopod axes and strobili from the Upper Devonian Cleveland Shale of Cuyahoga County, Ohio and siltstone of Venango Formation, Erie County, Pennsylvania, U.S.A. are reviewed. Most of the specimens from the Cleveland Shale are compressions and those from the Venago Formation are petrifactions. The specimens illustrate the presence of the arborescent habit and the heterospory, both well-established by Late Devonian time. A specimen of small unbranched lycopod tree with basal root-like appendages and an apical lepidostroboid strobilus, is remarkably significant in indicating a possible evolutionary trend to the Triassic lycopod tree, *Pleuromeia* corda, from Lepidostroboid stock of Late Devonian age.

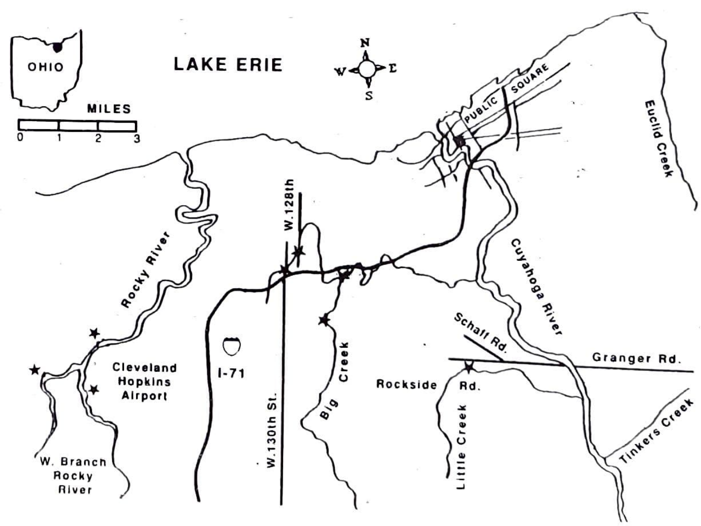
Key-words—Lycopods, *Pleuromeia*, Late Devonian, Ohio, Pennsylvania, U.S.A.

INTRODUCTION

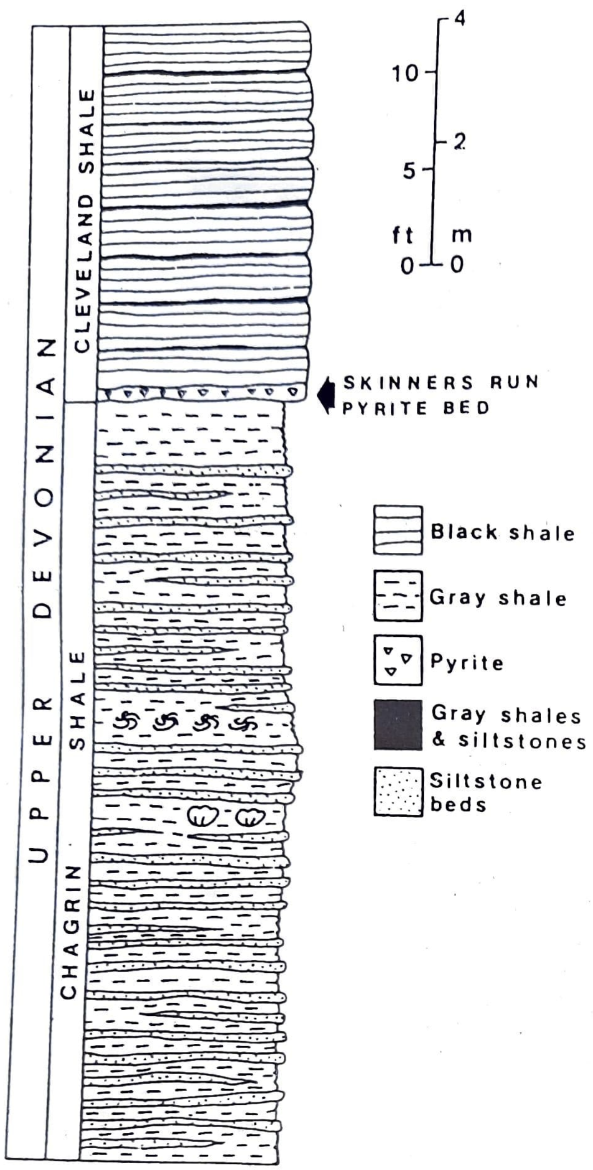
QUITE a few lycopods have been described from the Upper Devonian rocks of eastern and north-central United States. The best known are *Drepanophycus colophyllus* Grierson & Banks 1963, *Archaeosigillaria vanuxemi* (Göppert) Kidston (Grierson & Banks, 1963), *Lepidosigillaria whitei* Kräusel & Weyland 1949, *Colpodexylon deatsii* Banks 1944, *Haskinsia colophylla* Grierson & Banks 1983, *Knorria chemungensis* (Hall) Arnold 1939 and *Bisporangiostrobus harrisii* Chitaley & McGregor 1988. Another early lycopod, *Lycopodites mckenziei* Chitaley 1989, is a small specimen of a permineralized axis, possibly the stalk of a strobilus similar to *B. harrisii*.

Two more specimens are worth mentioning, since they are from the United States. *Prolepidodendron breviinternodum* Arnold 1939 and *Lepidostrobus gallowayi* Arnold 1933, 1935 were collected from the Pocono Sandstone at Campbell Hollow, 1.5 miles northeast of Port Allegheny, McKean Count, Pennsylvania. There is some doubt regarding the age of the horizon from which they were collected, whether the sandstone is Devonian or basal Mississippian. Nevertheless, assuming that it is of latest Devonian as Gensel and Andrews (1984) concluded, then these two species should be added to the list of Upper Devonian lycopods.

This paper gives a review of some of the fossil lycopods collected from the two Upper Devonian Formations in north-central United States. One is the Cleveland Shale from the vicinity of Clevleland, Ohio, and the other is the Venango Formation exposed in Erie County, Pennsylvania. The Cleveland Shale contains an abundance of fossilized lycopod axes and cones. This shale crops out at many sites along the creeks and rivers of Greater Cleveland (Text-fig. 1). Plant specimens have been col-

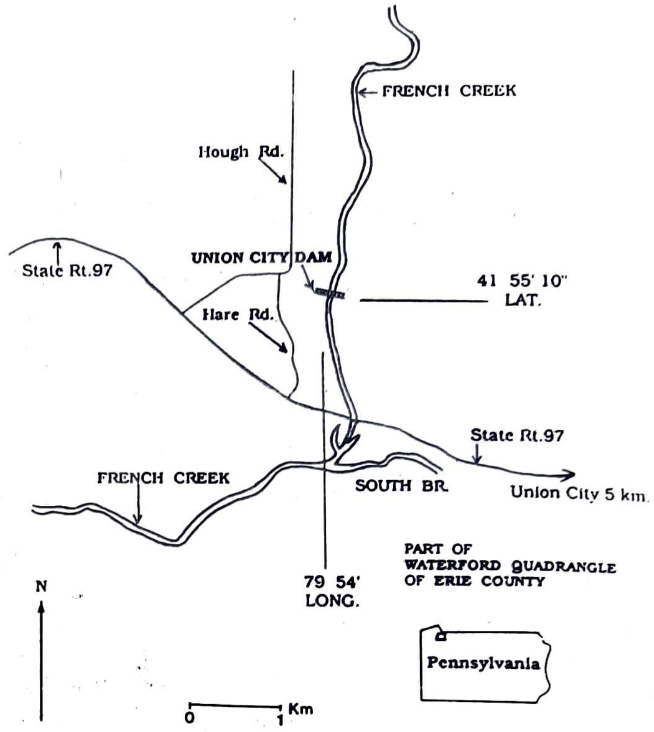


Text-figure 1. A sketch map of part of the Greater Cleveland area, showing Cleveland Shale outcrops; the best ones are marked(*).



Text-figure 2. Stratigraphical column showing major rock units in the vicinity of Greater Cleveland. (Reproduced by courtsey of Hannibal & Feldmann, 1983)

lected from these outcrops since 1920. They were stored in The Cleveland Museum of Natural History. The study of these plants began in 1980 when the Paleobotany Department was created at the Museum with the appointment of a paleobotanist to the staff. The first publication on this collection was a preliminary report on some outstanding specimens from these localities (Chitaley, 1982).



Text-figure 3. Geographic location of the Union City Dam, Erie Co., Pennsylvania

From a new locality in the Upper Devonian Venango Formation (Text-fig. 3), a superb specimen of a lycopod strobilus (Chitaley & McGregor, 1988) and many lycopod axes have been collected. *Bisporangiostrobus harrisii* (Chitaley & McGregor, 1988) is the first report on the fossil plants from this locality emphasizing the arborescent habit and clear heterospory. A unique specimen of plant fossil from the Cleveland Shale suggests a possible line to the Triassic lycopod *Pleuromeia corda*.

STRATIGRAPHY

Cleveland Shale—The Cleveland Shale of Cuyahoga County was named by Newberry in 1870. It was considered by some (Szmue, 1970) to be a member of the Ohio Shale. It is greyish black in colour and flaky. Interbedded with this fissile shale are siltstones in which the plant parts are better preserved. There are many

Plate 1 →

Bar scales are in centimeters unless otherwise stated.

1-12. Compressions of lycopod axes from the Cleveland Shale, Ohio. ? *Cyclostigma*, figs 1-3, P-2966 and P-3876-77, respectively.

3. Leaf scars magnified from fig. 2.

5,6, 12. ? *Bothrodendron/Cyclostigma*, P-3880, P-3889-92.

6. Leaf scars magnified from fig. 5, P-3880.

4,7,9, Protolepidodendropsis, P-3900, P-3066, P-3901-03

8. stigmarioid, P-3002.

10. ? *Lepidosigillaria*, P-4835.

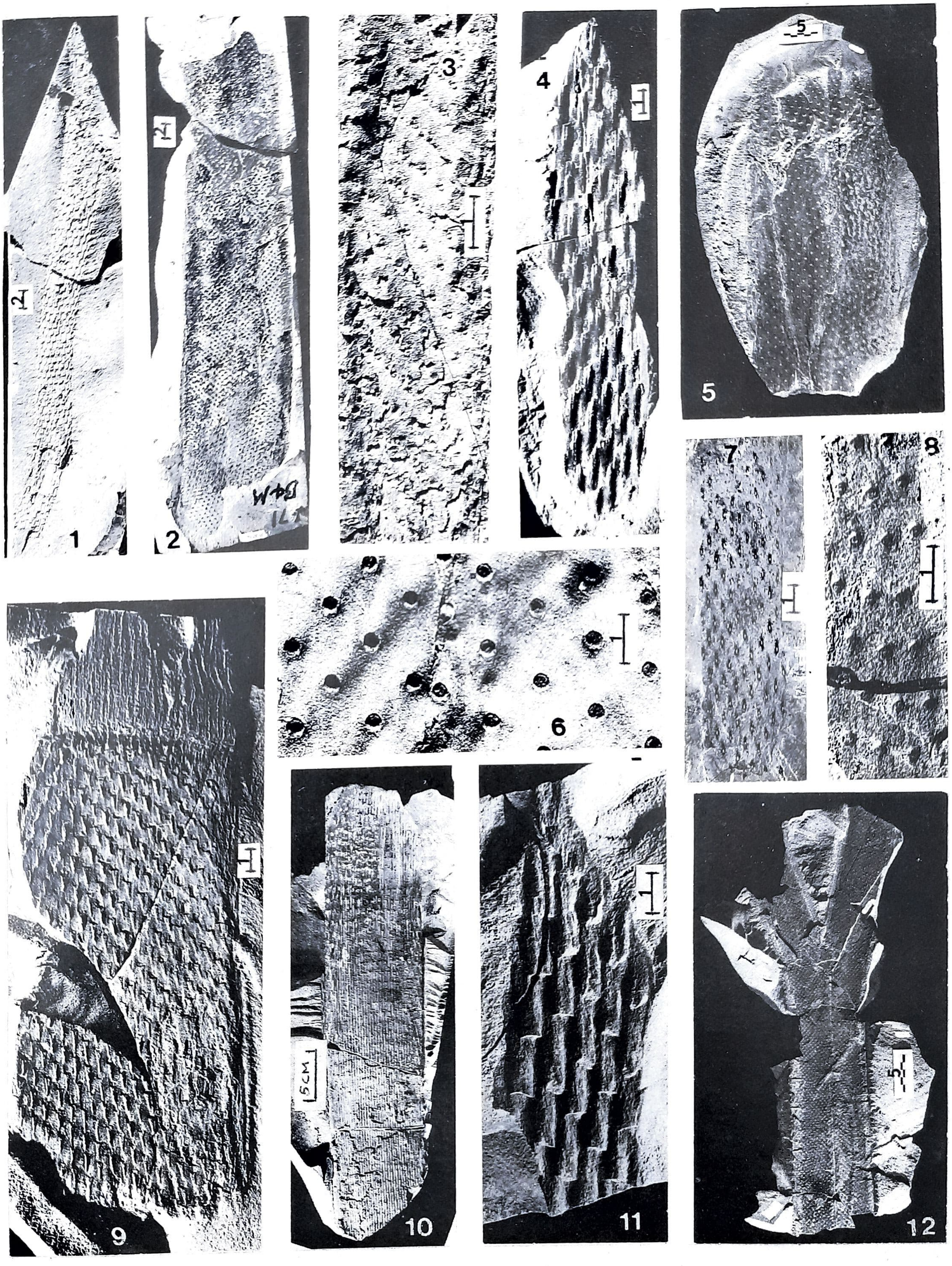
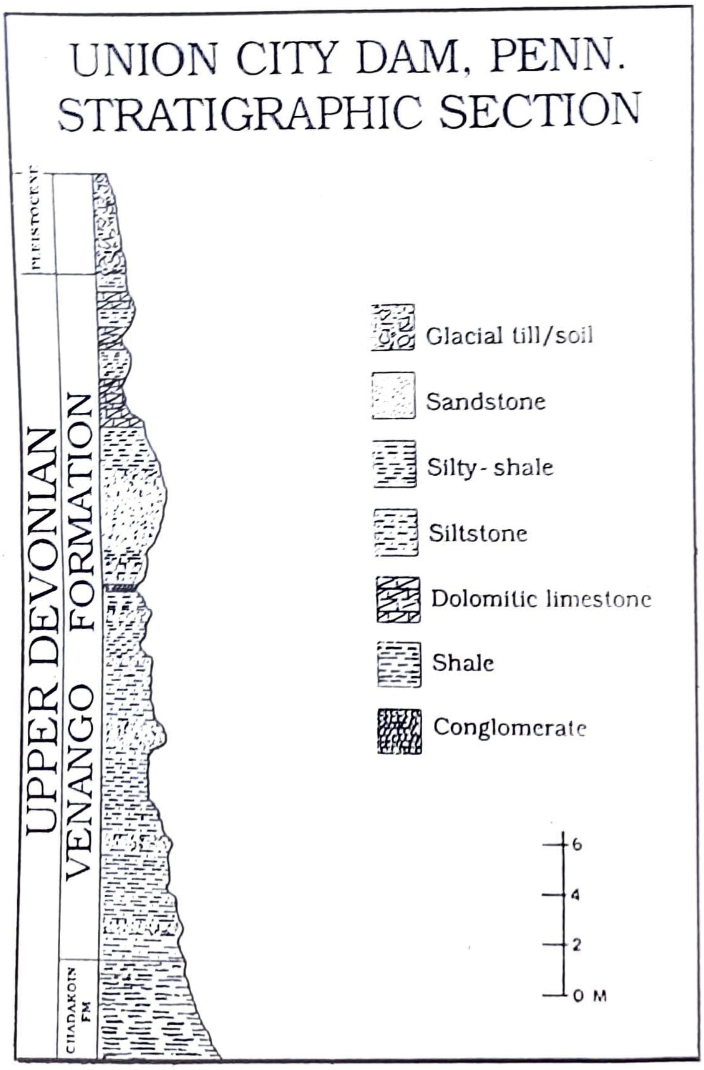


Plate 1



Text-figure 4. Stratigraphic column showing the major rock units at the Union City Dam in Pennsylvania.

outcrops of this shale in the vicinity of the Greater Cleveland areas. These occur along Rocky River, Big Creek, Skinners Run (Little Creek) as shown in text-figure 1, and also northeast of Cleveland along Tinkers Creek, a tributary of the Cuyahoga River. Better preserved specimens of plants have been collected from the sites on Big Creek and Skinners Run. However, the best specimens were salvaged by the Museum staff during the 1965-68 construction of U.S. Interstate Route I-71 passing through Cleveland at the intersection of West 130th street (Text-fig. 1). Since the specimens came from a fresh exposure, weathering was reduced and structural details are thus better preserved.

The major rock units present in the vicinity of Cleveland in northeastern Ohio are illustrated in text-figure 2. The thickness of the Cleveland Shale varies locally from 2.5 m to 34 m (Banks & Feldmann, 1970).

Venango Formation—The Upper Devonian rocks are well exposed at the Union City Dam on French Creek in the Waterford Quadrangle of Erie County, Pennsylvania (Text-fig. 3). The spillway of the dam exposes the upper part of the Chadakoin Formation and the lower part of the Venango Formation. Both are of Late Devonian age (Berg & Dodge, 1981).

The lower part of the Venango Formation is comprised of shale and bluish-brownish-grey siltstone (Text-fig. 4), whereas its upper part consists of sandstone. Many lycopod axes, branched and unbranched, have been collected from both sections of this formation. Most of them have secondary xylem. Only one strobilus of an arborescent lycopod has been collected from the lower part of the Venango at a site near the Union City Dam.

MATERIAL AND METHOD

Most of the specimens of strobili and axes collected from the Cleveland Shale are compressions. A few, small axes are permineralized with pyrite and silica. The outcrop at the Union City Dam, on the other hand, has yielded many permineralized axes, branched and unbranched. A strobilus has also been collected. Compressions of axes are rare at this locality.

Compressions were studied by routine methods of clearing, viewing and making transfers. In some cases, macerations of some sporophylls for spores were made. Pyritic permineralized specimens were prepared using the techniques developed by Chitaley (1985). Almost all of the pyritized petrifactions are mixed with silica. Therefore, to etch away the rock matrix, both hydrofluoric and nitric acid of commercial strengths were used, one following the other. After washing and drying, the desired surface of the specimen was flooded with acetone and a piece of cellulose acetate paper was gently placed upon it. It takes 20-30 minutes to dry the film, and after the acetate paper film was pulled from the surface, it was mounted in permount resin under a cover glass on a microslide.

All the specimens figured on plates 1-3 are stored in the Paleobotany Department of The Cleveland Museum

Plate 2 →

1-3, 5-6 Permineralized axes from the Cleveland Shale, Ohio.

1-2 Opposite surfaces of the same specimen, P-3733.

3. P-2892.

5. P-3379.

6. P-2893.

4, 8-12. Compressed cones from the Cleveland Shale, Ohio, P-2990, P-1696, P-4207, P-2981, P-2974, P-2973, respectively.

7. Better preserved part of a cone, P-2995.

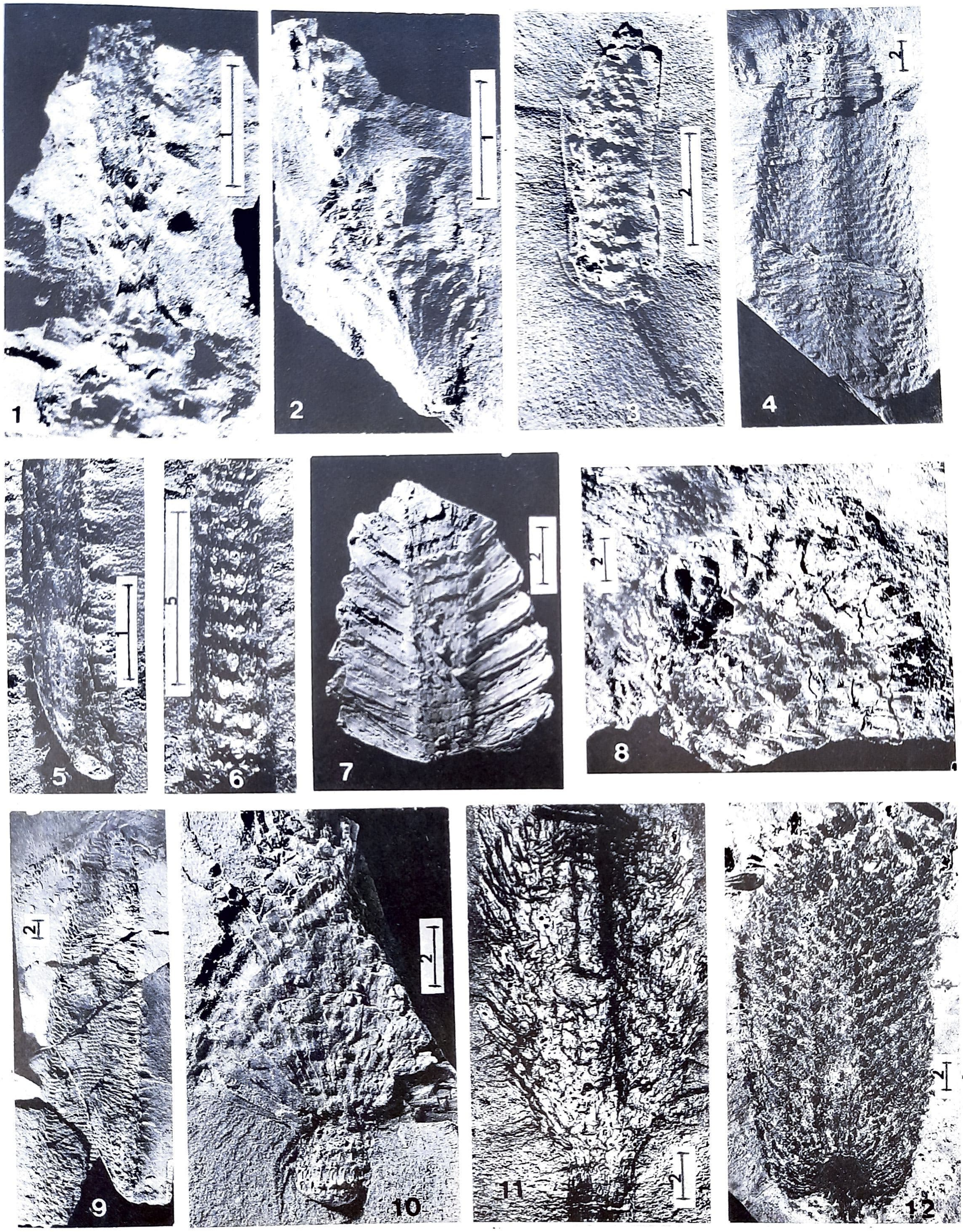


Plate 2

of Natural History, Cleveland, Ohio.

DESCRIPTION

All description (except of those from the Venango Formation) are based on preliminary observations made of the specimens, giving a general idea of their form and structure. The specimens from the Cleveland Shale fall into two categories :

1. Lycopod axes
   a. compressions
   b. permineralized
2. Lycopod strobili compressed

1. Lycopod axes (a) compressions—Pieces of the compressed axes are large, measuring 2-25 cm in diameter (Pl. 1, figs 1-2, 4-5, 7-12). Their surfaces show leaf scars that lack in supporting leaf cushions. The scars vary in shape and size in different specimens. They also vary in the distance between the two successsive scars and their arrangement on the axis. One of the specimens is dichotomously branched (Pl. 1, fig. 12)

(b) Permineralized—Only a few axes have been found structurally preserved. They are small, around 6 mm in diameter, 3-6 cm long, showing leaf scars on their surface (Pl. 2, figs 1-3, 5-6). They are included here to document their presence in the Cleveland Shale. Their internal structure has not yet been studied.

2. Lycopod strobili compressions—There are eight lycopod strobili preserved as compressions (Pl. 2, figs 4, 7-12; Pl. 3, fig. 3). The general structure of each strobilus is as follows: They have a central axis with sporophyll/sporangium complexes arranged in close helixes. Their sporangia are elongated and adaxial on the sporophyll. The strobili differ from one another in size, shape, and the angle of their sporophyll attachment to the axis. In some, the sporophylls bend downwards from the axis and then turn upwards distally (Pl. 3, fig. 3). Whereas in others, they turn upwards from the axis at a 45° angle (Pl. 2, figs 7-8, 10-12), and in still others they are first seen at right angle to the axis (Pl. 2, figs 4,9) and then turned upwards distally.

The specimen of cone (Pl. 3, figs 1-3) is unique in the sense that its strobilus is borne on an unbranched, long stem having basal appendages. The stem is 2.5 cm wide at its base, tapering to 1.5 cm. at its apex. It is 120 cm long, bears scaly leaves on its edges, and elongated scars on its surface. The basal end bears moderately thick, elongated appendages (Pl. 3, fig. 2) tapering like roots. The apical end of this unbranched stem terminated into an erect ovate cone (Pl. 3, fig. 3). The axis of the cone bears sporophyll/sporangium complexes in close helicals. Sporophylls turn downward first from the axis and then the distal laminar ends turn upward.

Spores have not been studied, therefore their homo- or heterosporous condition is unknown.

The fossils found in the spillway of the Union City Dam include several permineralized branched and unbranched axes, possibly of lycopods, and an excellent specimen of *Bisporangiostrobus harrisii*, which consisted of two structurally preserved strobili erect on a small branched axis, one on each branch (Pl. 3, fig. 8) (Chitaley & McGregor, 1988). Each strobilus is cigar shaped and measures 7.2 cm in length and 1.4 cm in diameter. Each strobilus axis bears megasporophylls on its proximal end in close helicals with elongated, adaxially attached megasporangia, and on its distal end microsporopylls with adaxial microsporangia (Pl. 3, fig. 7). Ligules were not observed. There is a small transition zone between the mega-and-micro regions where both kinds of sporangia are in the same helix. Each sporophyll extends horizontally at right angles to the axis and develops a heel where the laminal end turns up. The megasporangia contain a few large spores of *Duosporites* type (Pl. 3, fig. 5) and the microsporangia have many small spores of the *Geminospora* type (Chitaley & McGregor, 1988).

The branched (Pl. 3, fig. 6) and unbranched axes are thick and woody. Plate 3, fig. 4 is a cross section of a small axis of *Lycopodites mckenziei* from the Venango Formation near the Union City Dam (Chitaley, 1989). This axis consists of a protostele having exarch xylem surrounded by a primary parenchymatous cortex. It might be a piece of a cone stalk of *Bisporangiostrobus harrisii*.

CONCLUSIONS

It is evident from the above information that the

Plate 3 →

1-3. Compressed specimen, P-2975, of a lycopod tree from the Cleveland Shale, Ohio.
  1. Entire specimen.
  2. Basal region enlarged.
  3. Apical cone enlarged.

4-8. Specimens from Venango Formation, Union City Dam, Pennsylvania.
  4. Cross section of a permineralized axis, P - 3170.
  5. Cross section of *Bisporangiostrobus harrisii* strobilus, P-3180, x 6.
  6. Permineralized branched axes, P-5079.
  7. Part of longitudinal section of *B. harrisii* strobilus, P-3180, x 7.5.
  8. *B. harrisii* strobili, P-3180.

Plate 3

different axes from the Cleveland Shale and from the siltstone of Venango Formation are lycopods. It is true that in the compressed condition, unless the leaf cushions are distinctly visible, the generic identification and assignment of axes to different genera is difficult, if not impossible, and at times their assignment may not be correct (Chaloner & Boureau, 1967). These axes probably never had any leaf cushions. However, the shape, size and arrangement of the scars not having leaf-cushions may be the next best set of characters for tentative groupings of the lycopod axes. Using these criteria, the axes described in this paper are tentatively recognized as most similar to some of the better known lycopod genera such as *Cyclostigma* Haughton (1859) (Pl. 1, figs 1-3, 12), *Lepidosigillaria* Kräusel & Weyland (1949) (Pl. 1, fig. 10), Bothrodendron/Cyclostigma (Pl. 1, figs 5.6), *Protolepidodendropsis* Høeg (1942) (Pl. 1, figs 4, 7, 9, 11) and (Pl. 1, fig. 8) a stigmarioid. The general woody appearance and large size of the strobili suggest an arborescent habit for the plants on which the strobili were borne. No herbaceous, trailing lycopods are known to have such huge fructifications. The specimens from Cleveland, Ohio and from Erie, Pennsylvania contribute to a substantial support to the statement that the Late Devonian was marked by the presence of lycopod trees. The arborescent habit in lycopods was well established by the Late Devonian time. The big axes and strobili closely resemble the lepidodendrons and leipodostrobi of the Carboniferous Period, thereby illustrating the gradual natural change in vegetation from Late Devonian to Lower Carboniferous.

An important condition in the evolution of vascular plants is the presence of heterospory, a purported antecedent to seed habit. This condition was remarkabley well-achieved in lycopods by the end of the Late Devonian as exhibited by *Cylostigma* Haughton (Chaloner, 1968) and now strongly supported by the lycopod strobilus *Bisporangiostrobus harrisii*.

The strobili of *B. harrisii* from the Venango Formation reveal another interesting condition of a ligule probably not being present in these heterosporous strobili. This condition, with the previous record of the homosporous ligulate lycopod *Leclercqia complexa* (Banks et al., 1972; Grierson, 1976; Grierson & Bonamo, 1979), refutes the age-old belief that heterospory and ligule go together.

Spores related to the microspore genus *Geminospora* in *B. harrisii* is a new record for the former genus. It extends this Givetian genus into the Late Devonian. Also, the *in situ Duosporites* megaspores found in these strobili push back their earliest occurrence from Late Carboniferous to Late Devonian.

It is obvious that the specimen of a long, unbranched stem with root-like basal appendages and bearing a lepidostroboid strobilus erect on the stem tip from the Cleveland Shale is similar to *Pleuromeia corda*, a small tree of Triassic age. The architectural similarities between the two suggest a lineage of the Triassic *Pleuromeia* from this Late Devonian lycopod specimen through *Chaloneria* of Pennsylvanian age.

The form and structure of the lycopods found in the Cleveland Shale of Ohio and in the Venango Formation of Pennsylvania, suggest that the Late Devonian flora of north-central United States was formed basically of arborescent lycopods. These trees grew around the Devonian Sea and were drifted down to the marine sediments. It can be surmised that the climate prevalent during that short time of a few million years in the Late Devonian was warm and humid, favouring the luxuriant growth of such lycopods with huge lepidostroboid srtobili typically comparable with those of Carboniferous age.

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