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INVESTIGATIONS OF ANGIOSPERMS FROM THE EOCENE OF SOUTHEASTERN NORTH AMERICA: PHILODENDRON LEAF REMAINS[1]

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ABSTRACT

Large leaves, new to the fossil record, from the Claiborne Formation in western Tennessee have been collected and analyzed. Careful analyses of venation and cuticular anatomy indicate that these fossil leaves contain specific characters found in modern species of the genus *Philodendron* subgenus *Meconostigma.* Features of venation were taxonomically more useful than other features. Reports of fossils of the Araceae are scarce and those few fossils assigned to the family frequently have been inadequately studied. This report establishes a reliable and carefully documented occurrence of the Araceae in the fossil record, and provides information concerning the differentiation of the family in time and the distributions of the genus *Philodendron.*

THE REINVESTIGATION of the Middle Eocene floras of southeastern North America (Dilcher, 1971) not only has provided a basis for the revisions of existing taxa (Berry, 1916, 1930, 1941) but also has yielded new plant fossils. Collections of fossil material have been made from over 25 plant-bearing localities (Potter, 1976) in western Kentucky and Tennessee. One large, new leaf type found is of particular interest because it (Daghlian and Dilcher, 1971) provides information concerning the evolution and distribution of the Araceae. Compressions of leaves about 75 cm wide in which taxonomically useful characters are well preserved, were collected from clay pits in Henry Co., Tennessee. Based upon vegetative characters the fossil leaves can be assigned to a particular subgenus of *Philodendron, Meconostigma.* This is the first fossil record of this genus.

The Araceae is generally considered to be a well-defined and natural grouping of plants (Engler and Krause, 1905–1920; Arber, 1925). The origin of the Arales is thought to be associated with a divergence of the Arecales, Cyclanthales, and Pandanales from a similar ancestral stock of the Liliales (Takhtajan, 1969). Doyle (1973) indicates that plant organs such as pollen and leaves with characteristic monocotyledonous features are first observed in basal Potomac Group (Aptian?) sediments of Maryland and Virginia. He further suggests that the earliest evidence in the pollen and megafossil record for palms (Arecales) is in the Senonian of the Upper Cretaceous. The fossil record of the Araceae, as reported in this paper, supports a differentiation of the subclass Arecidae (Cronquist, 1968) during the Cretaceous and the subsequent evolution of extant families prior to the Paleocene. A more precise time of differentiation must await fossil evidence from Cretaceous age sediments.

METHODS AND MATERIALS—The techniques used in this investigation are those discussed by Dilcher (1974). The gross form and venation, fine venation, and cuticular anatomy of the fossil material and several modern leaves were studied.

Analysis of numerous pieces of leaf compressions rather than any individual whole leaves provides the basis for this report. Thirty fragments of large leaves were analyzed: 19 specimens from the Rancho clay pit, six specimens from the Bandy Tan clay pit, and five specimens from the Young clay pit[3], Henry Co. Tennessee (Dilcher, 1971; Potter, 1976). One large leaf fragment includes the middle two-thirds of a leaf (R728) (Fig. 1) and another large leaf fragment includes one basal lobe (R1685) (Fig. 2). The other leaf fragments include various parts of the leaves; however, no leaf apex was collected. Leaves of 13 extant genera including 28 species of Araceae were also examined. These were all species which had leaves superficially similar to the fossil material.

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[3] The Young clay pit is newly opened 4 miles south of Como, Tennessee.

SYSTEMATICS

Family: Araceae Juss.
Genus: *Philodendron* Schott.
Subgenus: *Meconostigma*
Philodendron **limnestis** sp. n.

DESCRIPTION—Leaves wide ovate to very wide ovate, base sagittate, margin entire. Broad midrib and secondary veins taper distally. Secondary veins branch 35° basally to 65° distally. Tertiary veins branch 45° from secondary veins towards leaf margin. Secondary and tertiary veins form submarginal vein. No median vein formed from tertiary veins.

Upper epidermal cells rectangular to oval, 24 μm × 18 μm (ranging 14–33 μm long × 11–28 μm wide). Outer portion of anticlinal walls and outer periclinal walls cutinized. Slightly elongate cuticular thickening located centrally on epidermal cells. Inner surface of cuticle granular, subsidiary cells lack granular deposits. Two brachyparacytic (i.e., not completely enclosing guard cells as in paracytic), subsidiary cells 30 μm × 12 μm (ranging 26–34 μm long × 10–14 μm wide). Guard cells level with the epidermis, anticlinal walls adjacent to and extending into substomatal chamber, well cutinized and flared apart. Guard cells 22 μm × 7 μm (ranging 15–29 μm long × 5–9 μm wide).

Lower epidermal cells rectangular to oval, 23 μm × 17 μm (ranging 12–30 μm long × 11–24 μm wide). Outer portion of anticlinal walls and outer periclinal walls cutinized. Outer periclinal walls evaginate outwards forming conspicuous papillae which terminate as rounded irregular ridges of thickened cuticle located centrally over each epidermal cell. Inner surface of cuticle granular except for subsidiary cells. Subsidiary cells papillate with papillae directed over guard cells. Two brachyparacytic subsidiary cells 19 μm × 11 μm (ranging 14–22 μm long × 8–14 μm wide). Guard cells level with the epidermal cells. Anticlinal walls adjacent to the stoma well cutinized.

Type—Specimen R728 is designated as the holotype. Paratype is R1685.

Stratigraphic occurrence—Claiborne Formation, Middle Eocene, Henry Co., Tennessee.

Source of name—*limnestis* (Gr.) = a marsh plant. Substantive used as an epithet.

DISCUSSION—*Leaf form and venation*—The secondary and tertiary veins are important in the systematic positioning of the fossil leaf, *Philodendron limnestis*. They course towards the margins and eventually bend to form fine continuous submarginal veins (Fig. 3, 5, 7, 8). Submarginal veins formed from the coalescing of the distal ends of the secondary and tertiary veins are common to only a few extant species of the Araceae (Fig. 6). The tertiary veins branch at about 45° from the secondary veins, sweeping towards the leaf margins (Fig. 5, 7) where some join with the submarginal veins at angles of 60° to 90° (Fig. 3, 5, 8). The tertiary veins arch towards the center of the leaf blade between the secondary veins. They do not fuse to form a median vein as found in some extant leaf forms in the Araceae. Only the secondary veins of the prominent basal lobes branch repeatedly to produce four or five short prominent veins which extend to the submarginal veins of the lobes (Fig. 2, 8). The submarginal venation, combined with the features of nonreticulate tertiary veins, the lack of intercostal veins, the presence of pronounced basal lobes, and a triangular leaf shape are characters found in common in the genus *Philodendron*, subgenus *Meconostigma* and the fossil leaves.

A comparison of leaf size of fossil and extant leaves showed the fosssil leaves to be generally larger than the herbarium specimens examined or leaves recorded in the literature (Engler and Krause, 1905–1920) from herbarium specimens. Commonly, juvenile leaves have been collected and mounted as herbarium specimens, perhaps to avoid the problems of drying and mounting mature leaves which may be 1–2 m in length. The modern leaves examined in this study (except for greenhouse specimens) and the leaves discussed by Engler and Krause (1905–1920) were often not typical of mature foliage. The fossil leaves are not considered to be abnormally large, rather they represent normal mature foliage generally not available in most collections of extant *Philodendron* species.

Epidermal anatomy—Both the upper and lower epidermis are well preserved and the leaf is amphistomatic. Carefully oriented cuticular peels of the compressed leaves were examined, and by relating these peels to the orientation of the leaf compression, we were able to determine which epidermis was the upper and which was the lower.

Upper epidermal preparations were successfully made from all the leaf fragments collected. However, lower epidermal preparations were successfully made from only a few leaf fragments; in these preparations the lower epidermis appears to be as heavily cutinized as the upper epidermis and it is not obvious to the investigators why it often was absent in the cuticular preparations.

The stomata are frequently, but not consistently, oriented with the long axis more or less parallel with other stomata and with the venation of the leaf (Fig. 9, 10, 13, 14). This is characteristic of both the upper and lower epidermis. This feature is observed consistently in many monocotyledons which have numerous parallel tertiary veins, and is a feature of some extant *Philodendron* species (Fig. 4).

The amphistomatic condition is a conspicuous feature of the fossil leaf (Fig. 9–18). Both the upper and lower epidermis have cuticular thick-


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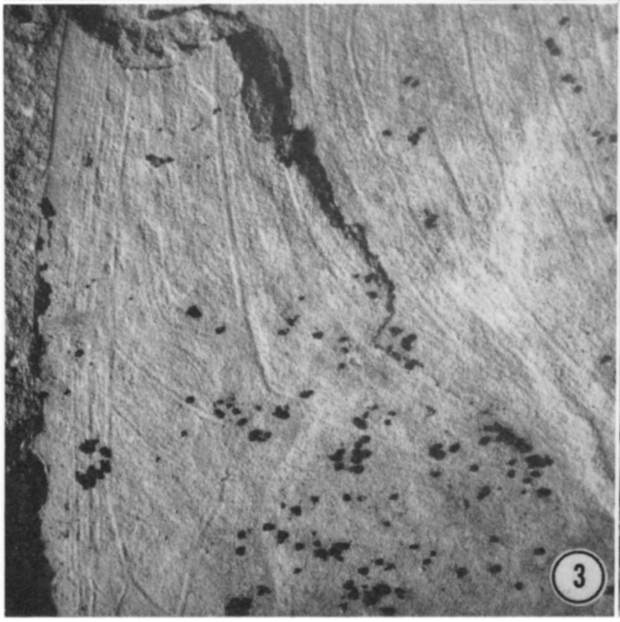
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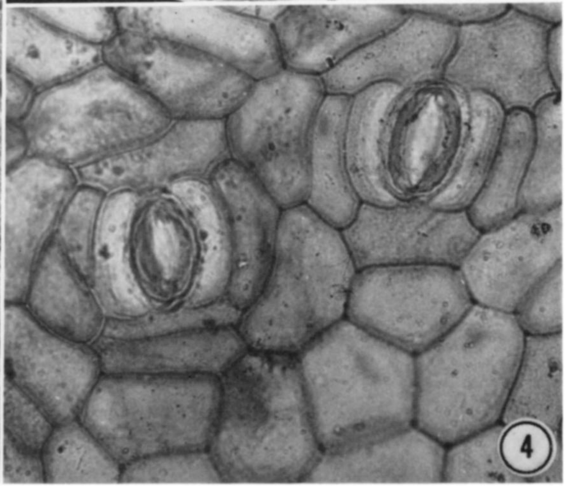
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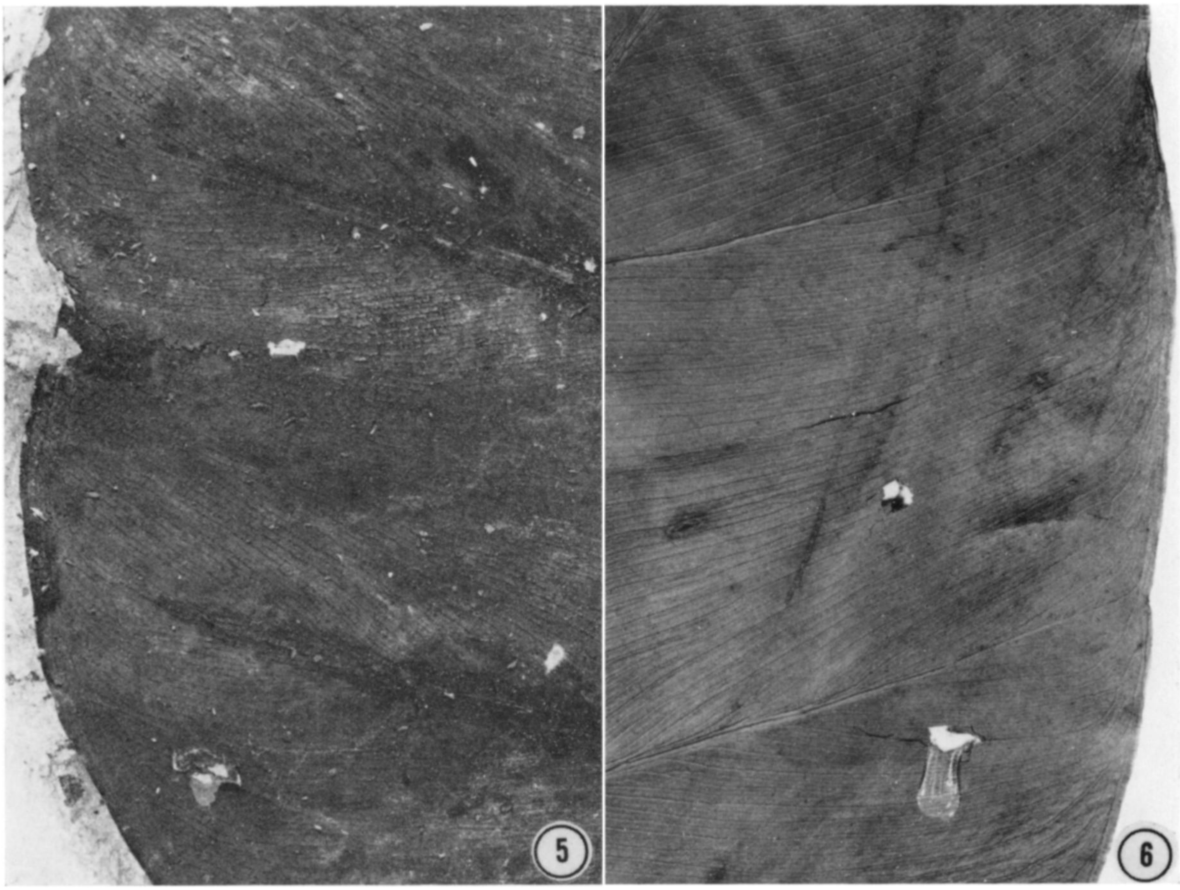

Fig. 5, 6. The distal end of two secondary veins with tertiary and marginal veins in fossil and modern *Philodendron* leaves. **5.** *P. limnestis.* × 1.7. I.U.P.C. #R1685. **6.** *P. brasiliense.* × 1.6. I.U.P.C. #1297.

enings located centrally on the epidermal cells. Those on the lower epidermis form short papillae which are evaginations of the outer periclinal cell walls (Fig. 10, 12, 16). The inner surfaces of the outer periclinal walls of the epidermis are granular on both leaf surfaces except for those of the subsidiary cells (Fig. 13, 14). The cuticle has a number of easily recognized features and has been used to identify small fragments of otherwise undistinguishable fossil leaf material.

CONCLUSIONS—Analysis of venation and cuticular characters in the fossil material and in several extant genera of the Araceae indicates that for this family, and in particular the genus *Philodendron*, venation is more useful in taxonomic identification than is cuticle.

Comparison of leaf venation suggests a close relationship of the fossil material to *Philodendron* subgenus *Meconostigma.* Cuticle of six species in this subgenus was examined: *P. brasiliense, P. corcovadense, P. minarum, P. speciosum, P. tweedianum,* and *P. undulatum.* All except *P. corcovadense* and *P. speciosum* were found to be amphistomatic; thus, this character is variable even within the subgenus *Meconostigma.* Subsidiary cell number and arrangement of these six species are similar to that of the fossil material

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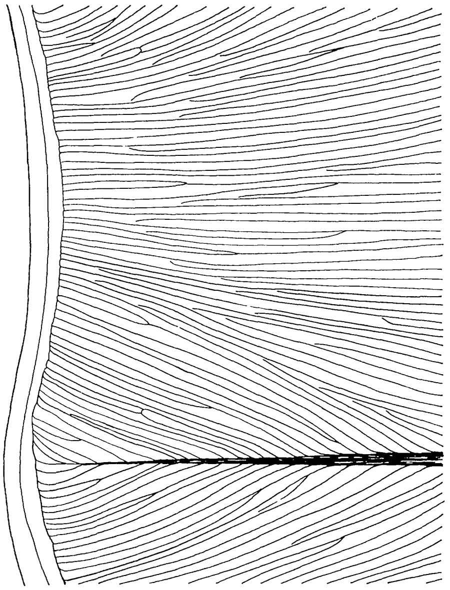
Fig. 1–4.—Fig. 1–3. *Philodendron limnestis.* **1.** Middle portion of a large leaf showing the midrib, secondary veins, and leaf margin on the left. Arrows indicate broken edge of the large leaf exposed to the left and a different *P. limenestis* leaf exposed to the right. See text for explanation. × 0.075. Ind. Univ. Palaeonbot. Collection #R728. **2.** Basal lobe of leaf. Arrows indicate broken edge of leaf exposing another leaf, see text. × 0.3. I.U.P.C. #R1685. **3.** Enlarged portion along the leaf margin showing the marginal venation and a few tertiary veins. × 4. I.U.P.C. #R728. **4.** *Philodendron speciosum,* lower epidermis showing the stomatal complex each with two parallel subsidiary cells. × 425. I.U. Reference Collection #1288.



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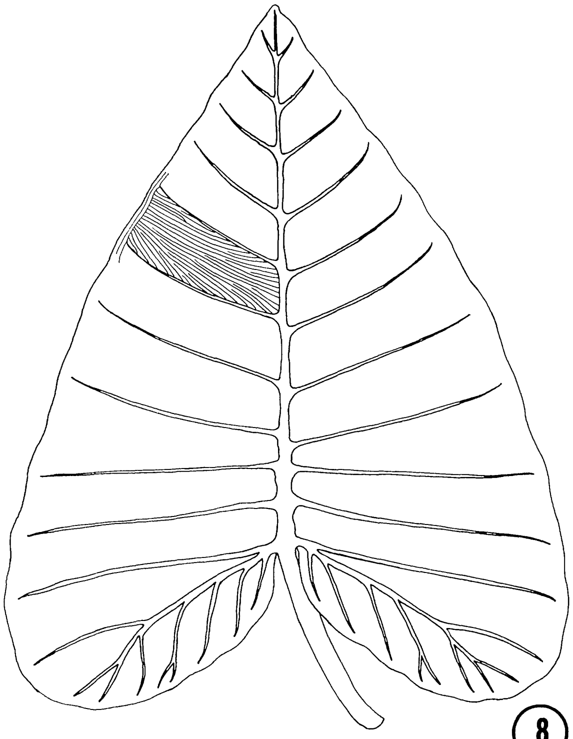

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Fig. 7, 8. **7.** Typical fine venation of the fossil along the leaf margin where a secondary vein terminates. **8.** Reconstruction of the leaf, *Philodendron limnestis.*

but no cuticular thickenings or papillae were present in the extant species examined (Fig. 4). Epidermal cell sizes and guard cell sizes are nearly twice as large as those observed in the fossil material. Cuticular characters of *Philodendron* are not unique to this taxon nor easily distinguished from the cuticular features common to various species of the aroids. The fossil cuticular material is typical of that found in the Araceae but otherwise is of little use in determining a more exact taxonomic designation.

Webber (1960) analyzed several epidermal characters of extant aroids and noted that the placement and type of stomatal apparatus may vary from species to species within an extant genus. Webber suggested six basic variations. He established groups based upon the position of the stomata (hypostomatic vs. amphistomatic), uniformity of the subsidary cell number in the two layers of amphistomatic leaves, and subsidiary cell number. This resulted in an unworkable listing of genera and species; *Philodendron* has species listed in four groups (Webber, 1960) and we found another extant species which would belong to yet a fifth group. The major problem is that the primary character used by Webber, hypostomatic vs. amphistomatic, is variable within genera of the Araceae. The amphistomtic condition relates more to leaf thickness than to taxonomic affinity. Subsidiary cell arrangement, found to be of systematic importance, was given lowest priority in Webber's system.

The cuticular anatomy of fossil leaves has been misinterpreted or misused by some investigators to indicate or suggest affinities with the Araceae (*Pistia nordenskioldii,* Berry, 1920; *Anthurium,* Weyland, 1957; *Limnobiophyllum scutatum,* Krassilov, 1973). Krassilov relied upon the work of Stebbins and Khush (1961) when suggesting that the cuticular anatomy of *Limnobiophyllum* from the Maastrichtian-Danian of Amur Province, USSR, was similar to that found in extant genera of the Araceae. Tomlinson (1974), in a critical review of the literature on the stomatal complex of monocotyledons, considers much of the published record, including Stebbins and Khush (1961), to be speculative and superficial. The results obtained in this research agree with Tomlinson's conclusions and extreme care must be exercised by anyone using cuticular anatomy as the major basis for referring fossil leaf material to the Araceae.

The apparent relationship of the Middle Eocene *Philodendron limnestis* to an extant genus and subgenus is of particular interest from an evolutionary perspective. Several fossil leaves, fruits, and flowers of dicotyledonous plants from the same sediments have been studied and given new generic names (Dilcher, 1973; Crepet, Dilcher, and Potter, 1975; Dilcher, Potter, and Crepet, 1976). In addition to the *Philodendron,* fossil palms (*Sabal* sp.) are common monocotyledonous elements of this flora (Dilcher, 1968; Daghlian and Dilcher, 1971). It is interesting to note that by careful analysis of anatomy and morphology, the monocotyledonous fossils are found to be extremely similar to, if not identical with, extant genera (e.g., *Sabal*, *Philodendron*, subgenus *Meconostigma*), while the dicotyledonous fossils from the same deposits do not show such close relationships. Most fossil dicotyledons studied can be related to extant families and often to sections within those families but not to extant genera. This is understandable when we consider that taxa such as the family or the genus of extant monocotyledons are not comparable with the same taxa in extant dicotyledons. There is no evidence to indicate a rapid modernization of monocotyledons through time; rather, the different levels at which relationships with extant taxa can be determined for Middle Eocene fossil monocotyledons and dicotyledons represent the lack of evolutionary parallelism between the taxonomic units established for these two groups of plants. As a result of careful analysis of the angiosperm fossil record we should expect to see further evidence demonstrating this basic difference between the systematics of monocotyledons and dicotyledons.

The fossil record of the Araceae is very incomplete and in need of revision. Much of the record in North America has been established from spadix-like remains that have been assigned to such genera as *Acorus* (Berry, 1930), *Araceaites* (Berry, 1916), *Lysichiton* (Berry, 1931), and *Orontium* (Cockerell, 1926) in North America. These are published with comments such as "interpretation must be accepted with due reserve" (Berry, 1916) and "appears to be part of a crushed spadix of some aroid" (Berry, 1931). Some of the supposed spadices, *Spathyema* (= *Symplocarpus*) have since been recognized as rhizomes of a water lily by Brown (1937) and renamed *Nymphaeites*. However, not all records of fossil spadices should be disregarded. Recent work on the anatomy of an Eocene spadix by William L. Crepet provides reliable confirmation of Berry's earlier designation of the fossil *Acorus heeri* as an araceous spadix (W. L. Crepet, personal communication).

Few fossil remains of aroid leaf material have been found. Fossil leaves assigned to the extant genus *Pistia* were reported by Berry (1910, 1916, 1920) and Lesquereux (1874) from Upper Cretaceous and Eocene sediments in North America. These records are certainly questionable. Rasky (1964) assigned leaf material to *Araceophyllum* from Tertiary sediments in Hungary. Only incomplete fragments of the leaves were found and it is impossible to say more than that they probably represent large monocotyledonous leaves. *Caladiosoma* (Berry, 1925, 1937), *Araceophyllum*, and *Anthuriophyllum* (Weyland, 1957) are from Miocene sediments. It would seem reasonable to accept these as valid reports of aroid leaves, although the evidence for reliable generic designations is weak. *Nitophyllites zaisanica* (Fedotov, 1975) was described from Paleocene sediments in Kazakhstan, and from Eocene sediments in Amur Province, U.S.S.R. Only fragments, the largest being 12 cm × 13 cm, were collected and the general appearance of the leaves was provisionally reconstructed by analogy with extant members of the Araceae, especially species of *Alocasia* and *Colocasia*. It is reasonable to accept this report from the Paleocene and Eocene of the U.S.S.R. and to hope that further collections will permit a more thorough investigation of its possible relationship with extant taxa in the Araceae. Both the venation (marginal veins interconnected by numerous anastomoses) and the cuticle (stomata rarely found on the upper epidermis, epidermis lacks papillae) of the fossils from the U.S.S.R. differ from the fossil material reported here.

The *Philodendron* leaf reported here is the only fossil record of this genus. Careful comparison of the anatomy and morphology of the fossil leaf to that of numerous extant genera provides a sound and reliable basis upon which to accept this fossil record. This fossil leaf provides not only an initial record of the genus *Philodendron*, but also demonstrates the degree of differentiation (evolution) that had occurred already within the genus by the Middle Eocene. It indicates that the Araceae must have had an earlier origin and radiation in order for the subgenus *Meconostigma* to be represented in the Northern Hemisphere during the Middle Eocene.

The distribution of the subfamilies and genera of the Araceae is consistent with the history of angiosperm origin and dispersal documented by Raven and Axelrod (1975). Most genera are restricted either to the Old World or to the New World (Engler and Krause, 1920) and are represented by numerous species in the tropics and subtropics. *Philodendron* is limited to the New World, and the subgenus Meconostigma is presently restricted across South America to areas south of central Brazil to the middle of Argentina. The presence of this subgenus in western Tennessee during the Middle Eocene suggests that the range of species has been transient through time and space. The radiation of *Philodendron* may have been northward and contained in the New World as the continental plates moved apart during the Cretaceous and Paleogene. The abundant species of *Philodendron* observed today probably have their basis in the wide distribution of this genus in ancient times.

It is not necessary to assume a wet, tropical climate in a densely forested region (Berry, 1937; Rüffle, 1964) when leaf remains of aroids such

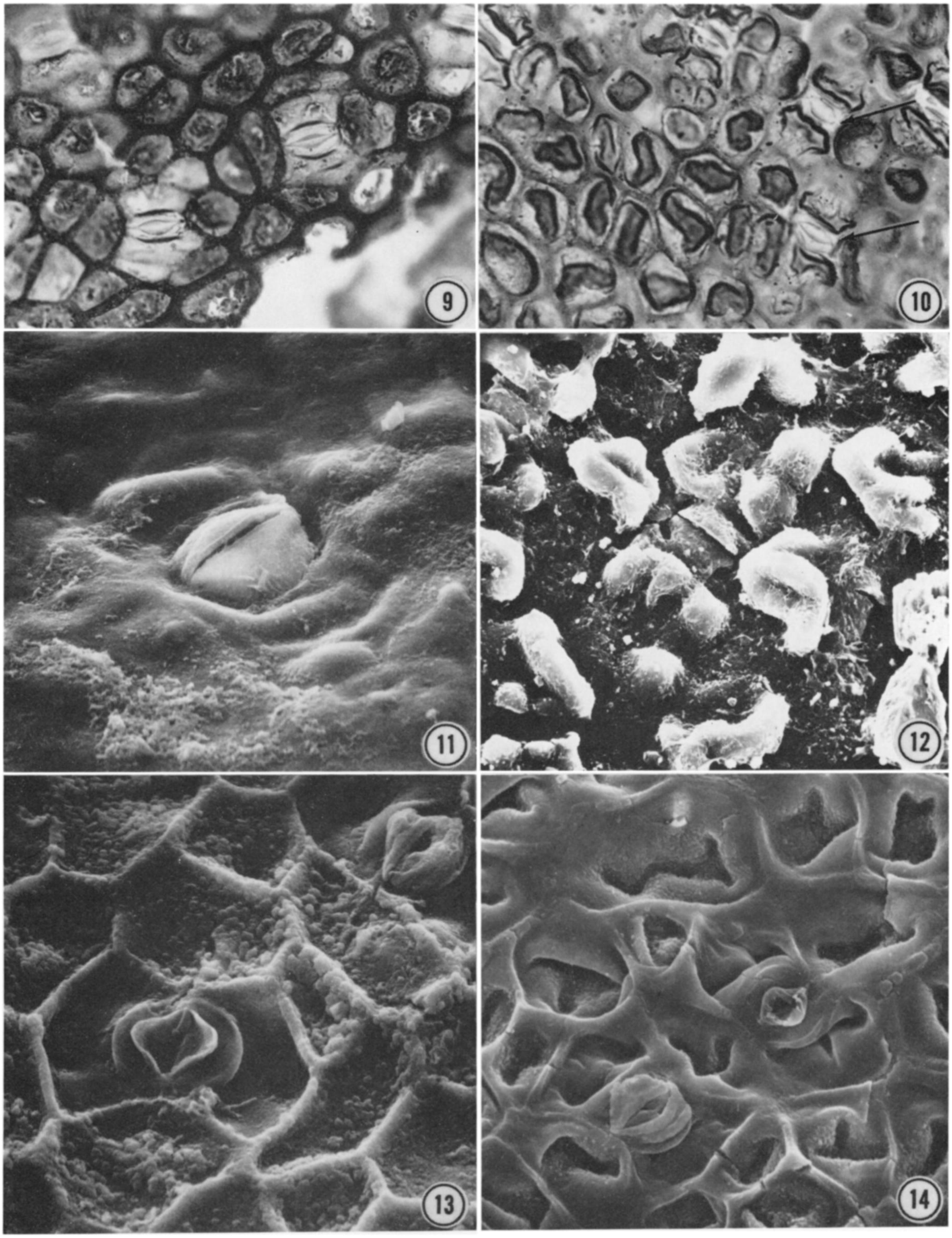

Fig. 9–14. Epidermis of *Philodendron limnestis* as prepared from I.U.P.C. #R728.—Fig. 9–10. Light microscopy.—Fig. 11–14. SEM. **9.** Upper epidermis. Cuticular thickenings on the epidermal cells evident. × 425. **10.** Lower epidermis. Evaginations of epidermal cells and cuticular thickenings evident. Stomata indicated by arrows. × 425. **11.** Upper epidermis showing two guard cells. Cuticular thickening over epidermal cells can be seen.

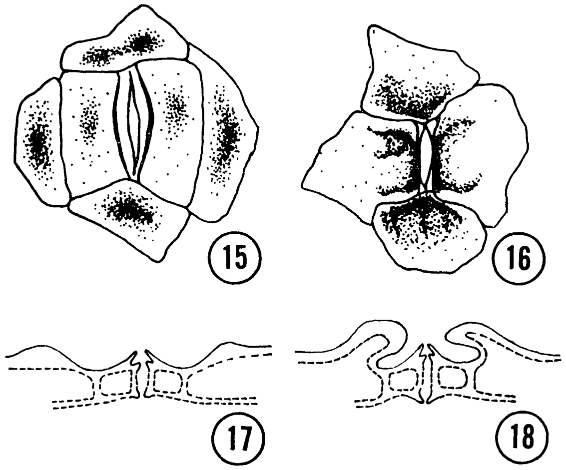

Fig. 15–18. Diagrams of cross section and surface views of the stomatal complex of *P. limnestis*. **15, 17.** Upper epidermis. **16, 18.** Lower epidermis.

as *Anthurium*, *Caladiosoma*, or *Philodendron* are found. The climate of western Tennessee during the Middle Eocene was seasonally dry, warm temperate to subtropical (Dilcher, 1973). The important feature of the climate is that it probably lacked any extensive cold season or hard freezes. The elements of the flora, such as *Philodendron*, that we now recognize as subtropical, could have ranged north into western Tennessee under such climatic conditions.

When living, the thickness of the leaf blade and veins of *Philodendron limnestis* was similar to that of extant related species. The leaf compressions of the midrib and secondary veins show a broad midrib tapering distally as broad secondary veins branch from it (Fig. 1). The broadness of these compressed veins suggests that they were thick, perhaps even fleshy, in life. In addition there is a strong correlation of leaf thickness with amphistomatism for known physiological reasons in several extant genera (David Parkhurst, personal communication).

The history of the clay deposits (Dilcher, 1971; Potter, 1976) in western Tennessee demonstrates that the area was a flood plain containing abandoned channels. These rapidly filled with fine grain sediments and changed their character from open lakes to swampy areas (Potter, 1976). The fossil leaves of *Philodendron* are often found grouped together with thin layers of clay between them (Fig. 1, 2). Further, the leaves are oriented in the same direction and, for such large leaves (75 cm wide), there was very little distortion or damage in deposition. This would suggest that several leaves from the same plant were deposited together in quiet water. We suggest that the fossil, *Philodendron limnestis*, grew as an herbaceous shrub in wet areas on the Middle Eocene flood plains of western Tennessee. During periods of flooding the plants were washed into the sediment-laden waters and incorporated in the clay deposits filling these ancient basins. *Philodendron limnestis* may not have been a common element of the floras because it is found in only three of over 30 clay deposits examined.

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× 1050. **12.** Lower epidermis, two guard cells. Papillate projections of subsidary cells and epidermal cells evident. × 1000. **13.** Inside upper epidermis showing anticlinal walls of the guard cells, subsidary, and epidermal cells. Granular nature of epidermal cells contrasts with smooth subsidary cells. × 1050. **14.** Inside lower epidermis showing anticlinal cell walls. The evaginations of the periclinal walls to form papillae are obvious. Subsidiary cells lack granular deposits. × 1000.

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