

2006

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Recommended Citation

Stockey, Ruth A. (2006) "The Fossil Record of Basal Monocots," *Aliso: A Journal of Systematic and Evolutionary Botany*: Vol. 22: Iss. 1, Article 8.

Available at: <http://scholarship.claremont.edu/aliso/vol22/iss1/8>

THE FOSSIL RECORD OF BASAL MONOCOTS

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ABSTRACT

The fossil record of basal monocots (Acorales and Alismatales) extends back to the Cretaceous in the Northern Hemisphere. While many fossils were originally assigned to these basal groups, rigorous paleobotanical studies show many of them to be misidentified. *Acorus* fossils have been reliably reported from the Eocene while those of Alismatales extend back to the early Cretaceous. The fossil record of basal monocots is usually represented by leaves, fruits, and seeds; however, some localities preserve stems with attached leaves and roots and even whole plants. A detailed examination of leaf venation patterns in alismatids has recently allowed the description of a new taxon from the Upper Cretaceous of Alberta based on leaves attributed to Limnocharitaceae. Anatomically preserved alismatid petioles (*Heleophyton helobiaeoides*) and well-preserved flowers/fruits are known from the Middle Eocene Princeton chert of British Columbia. A complete developmental sequence from flower to fruit is known, and this material has good possibilities for whole plant reconstruction. The extinct floating aquatic *Limnobiophyllum* (Araceae/Lemnoideae) and the genus *Pistia* have been the subject of morphological cladistic analyses and competing hypotheses of relationships among aroids and duckweeds. The fossil record and recent molecular studies support separate origins of *Pistia* and the duckweeds from within Araceae. The fossil taxon "*Pistia*" *corrugata* has been reexamined in light of new evidence and indicates the presence of a new genus that shows leaf morphology unlike that seen in extant *Pistia*, but with a similar growth habit. Fossil evidence indicates that the floating aquatic habit probably arose at least three times within Araceae.

Key words: Acorales, Alismatales, Araceae, Lemnaceae, *Limnobiophyllum*, Limnocharitaceae, *Pistia*.

INTRODUCTION

The fossil record of basal monocots (Acorales and Alismatales) extends back to the Cretaceous in the Northern Hemisphere. While many fossils were originally assigned to these basal groups, rigorous paleobotanical studies have shown many of them to be misidentified. The fossil record of monocots was reviewed by Daghljan (1981), and most recently by Herendeen and Crane (1995). The early Cretaceous record was later reviewed by Gandolfo et al. (2000). As Herendeen and Crane (1995) point out, there are difficulties in recognizing monocots as fossils due to the lack of synapomorphies for the clade and the types of morphological characters that might be seen in fossils. Furthermore, monocots make up only 22% of the total species diversity for flowering plants (Mabberley 1987; Herendeen and Crane 1995). Since most monocots are small and herbaceous and their flowers are mainly insect pollinated, potential for preservation of their pollen is especially low (Herendeen and Crane 1995). Nevertheless, good examples of monocots are present in the fossil record including flowers, pollen, fruits, seeds (some with embryos), leaves, stems (some with attached roots and leaves), and even whole plants are known in some cases (see Daghljan 1981; Muller 1981; Erwin and Stockey 1991, 1992, 1994; Herendeen and Crane 1995; Gandolfo et al. 2000; Smith and Stockey 2003). The fossil record suggests that monocots diversified rapidly in the Late Cretaceous but that their origins were much earlier (Gandolfo et al. 2000).

Phylogenetic analyses based on morphology (Dahlgren and Rasmussen 1983; Dahlgren et al. 1985; Donoghue and

Doyle 1989; Loconte and Stevenson 1991; Doyle and Donoghue 1992; Stevenson and Loconte 1995), those based on molecular characters (Chase et al. 1993, 2000; Duvall et al. 1993a, b; Qiu et al. 1993, 2000; Bharathan and Zimmer 1995; Davis 1995; Nadot et al. 1995; Nickrent and Soltis 1995; Davis et al. 1996, 1998; Rice et al. 1997; Soltis et al. 1997, 1998, 1999, 2000; Angiosperm Phylogeny Group (APG) 1998; Duvall 2000; Graham et al. 2000, 2006; Savolainen et al. 2000; APG II 2003; Borsch et al. 2003; Hilu 2003; Duvall and Ervin 2004; Tamura et al. 2004) and combined morphological and molecular analyses (Doyle et al. 1994; Chase et al. 1995; Doyle and Endress 2000; Stevenson et al. 2000) all indicate that the monocots are nested deeply within the angiosperms. The placement of monocots within angiosperm phylogeny as a whole varies with the taxa and genes that are included in an analysis. Despite these morphological and molecular analyses, the sister group of the monocots is still not completely resolved (Duvall 2001; Duvall and Ervin 2004). Nonetheless, most workers agree that the group is monophyletic, usually with *Acorus* at the base of the monocot clade, based on molecular characters (e.g., Duvall et al. 1993b, 2001). However, morphological analyses have often conflicted with this interpretation and several molecular studies do not place *Acorus* in the basal position definitively (Nadot et al. 1995; Soltis et al. 1997; Qiu et al. 2000; Stevenson et al. 2000; Duvall 2001; Duvall and Ervin 2004).

The fossil record has the potential to provide important data for first occurrences of major monocot groups. Remembering that first occurrences in the fossil record provide min-

imal dates for the antiquity of monocot taxa, one can assume that groups were present prior to their first occurrence as fossils. It is, therefore, very important that fossil plants be studied rigorously and that the data they provide be used cautiously when estimating dates of first occurrence. Each fossil has a certain amount of morphological, and sometimes ecological, data to impart and it is important that we pay attention to the signals these fossils provide. Ideally, we should aim for whole plant reconstructions. While such reconstructions are often tedious and time consuming, the data that they provide, about character evolution and the complex nature of character changes with time, are vital for resolving the overall pattern of phylogeny and for understanding the evolutionary pathways that have led to extant lineages. Such data provide the crucial link between the paleobotanist and neobotanist that is needed to develop more robust phylogenies.

The goal of this paper is to review the fossil record of basal monocots, Acorales and Alismatales (including Araceae), and evaluate the characters used to assign the fossils to these groups. New fossil evidence is also presented for Cretaceous aquatic plants from North America from several different localities based on leaves, infructescences and whole plants. The importance of fossils in our understanding of monocot evolution, and for dating the nodes in cladistic analyses are explored.

Acorales

The earliest report of fossil *Acorus* L. was that of Heer (1870) from the Miocene of Spitsbergen. *Acorus brachystachys* Heer was thought to represent an inflorescence or spadix that was attached to and jutting out at an angle from a leaf-like spathe (Fig. 1). Closer examination of these specimens (Bogner 2001) showed that they were not *Acorus* inflorescences, and flowers were not present; but a series of helically arranged scars can be seen on the surface. Kvaček in Bogner (2001) has suggested that these specimens are actually Eocene in age and the short shoots of *Nordenskiöldia borealis* Heer emend. Crane, Manchester et Dilcher, also found at the same locality. *Nordenskiöldia borealis*, a dicot from Trochodendraceae, was a widespread taxon in the Northern Hemisphere that probably grew by long-shoot/short-shoot growth (Crane et al. 1991). Specimens like these were linked to the characteristic fruits of *N. borealis* by anatomical similarities to the infructescence axes, the form and arrangement of the lenticels on the long shoots, and their co-occurrence at numerous localities (Crane et al. 1991).

Another potential acoralean, *Acoropsis eximia* (Goeppert et Menge) Bogner (Conwentz 1886; Bogner 1976) from the Eocene Baltic Amber, was reexamined by Bogner (1976). While the specimen is well preserved, Bogner (1976) and Mayo et al. (1997) regard this infructescence as an aroid, family Araceae, tribe Monstereae, because of its lack of tepals. So while this specimen is not acoralean, it may still be an early representative of the basal monocots.

The type specimen of *Aracaeites fritelii* Berry (1916) was reexamined by Crepet (1978). The specimen is incomplete, but shows little morphological similarity to *Acorus*. Like "*Acorus*" *brachystachys*, this specimen shows helically arranged diamond-shaped scars and may represent a short

shoot of some dicot like *Nordenskiöldia*. *Aracaeites parisiense* Fritel (1910), from the Paleocene of France, a taxon based on what was described as an incomplete inflorescence, is even more poorly preserved and its affinities remain in doubt (Mayo et al. 1997).

The only fossil material described to date, for which affinities to *Acorus* are accepted, are two small spadix specimens lacking a spathe from the Lower Eocene Wilcox flora of the southeastern USA. Originally described as *Acorus heeri* Berry (1930), *Acorites heeri* (Berry) Crepet, known from one inflorescence attached to a slender axis, was re-investigated by Crepet (1978). An additional partial specimen from the same locality, originally found by Dilcher (1971), shows cuticular preservation that could be closely compared to extant taxa. *Acorites heeri* shows helically arranged perfect flowers on an inflorescence axis with a trilobular ovary, bilocular anthers, and a small orbicular stigma (Crepet 1978). One specimen shows remains of perianth and paracytic stomata. Crepet (1978) suggests that these inflorescences are most closely comparable to *Acorus* based on morphology of the spadix, lack of a spathe, presence of a floral envelope, and structure of the epidermis. However, the presence of stomata on the perianth and a longer stalk on the inflorescence in the fossil indicate that some differences occur between this taxon and extant *Acorus*. Without whole plants, however, it is inadvisable to put these remains into the extant genus; and Crepet (1978) described them as *Acorites* rather than leaving them in *Acorus*. The acceptance of these fossils as representatives of Acoraceae (Mayo et al. 1997) make these the oldest known fossils of the family.

Fruits and seeds thought to belong to Acorales were listed by Nikitin (1976) from the *Quaternary Mamontovoj Gory Flora of Russia*. Katz et al. (1965: Plate 24, Fig. 3–7) illustrate these specimens showing an obovoid fruit that still shows some styler remains and an obovoid seed that shows small isodiametric cells in surface view. Mayo et al. (1997) accept this record of fruits and seeds because of similarities of this material to those of extant *Acorus* species.

To show the problems of interpretation for fossil compression remains of monocots, I illustrate structures that look like elongated spadices with four-parted flowers from the Paleocene Hanna Formation of Wyoming (Fig. 2, 3). Fossils like these are also known from the Paskapoo Formation (Paleocene) of Alberta and are found in the coarser sandstones, and in overly fine-grained mudstones containing leaves of *Zingiberopsis* Hickey et Peterson (Stockey pers. obs.). We have not been able to demonstrate the floral nature of these structures. In fact, the larger specimens (e.g., Fig. 3) have been thought to represent rooting structures of some kind (Brown 1962; D. R. Braman pers. comm., 2003). Only further extensive collecting at such sites will provide the data needed to interpret these fossil remains.

Recently, one specimen has been found of what appears to be a very large unisexual spadix bearing fruits (Fig. 4). Fruits are ovoid and slightly striated or ribbed showing what is probably an attenuate style tip. Where the fruits have abscised, there are densely packed scars (Fig. 4). Similar, but smaller, infructescences are known infrequently in the fossil record (e.g., Berry 1931). These fossils are most often found as isolated occurrences and the foliage to which they belong is unknown. Therefore, unless more specimens or well-pre-

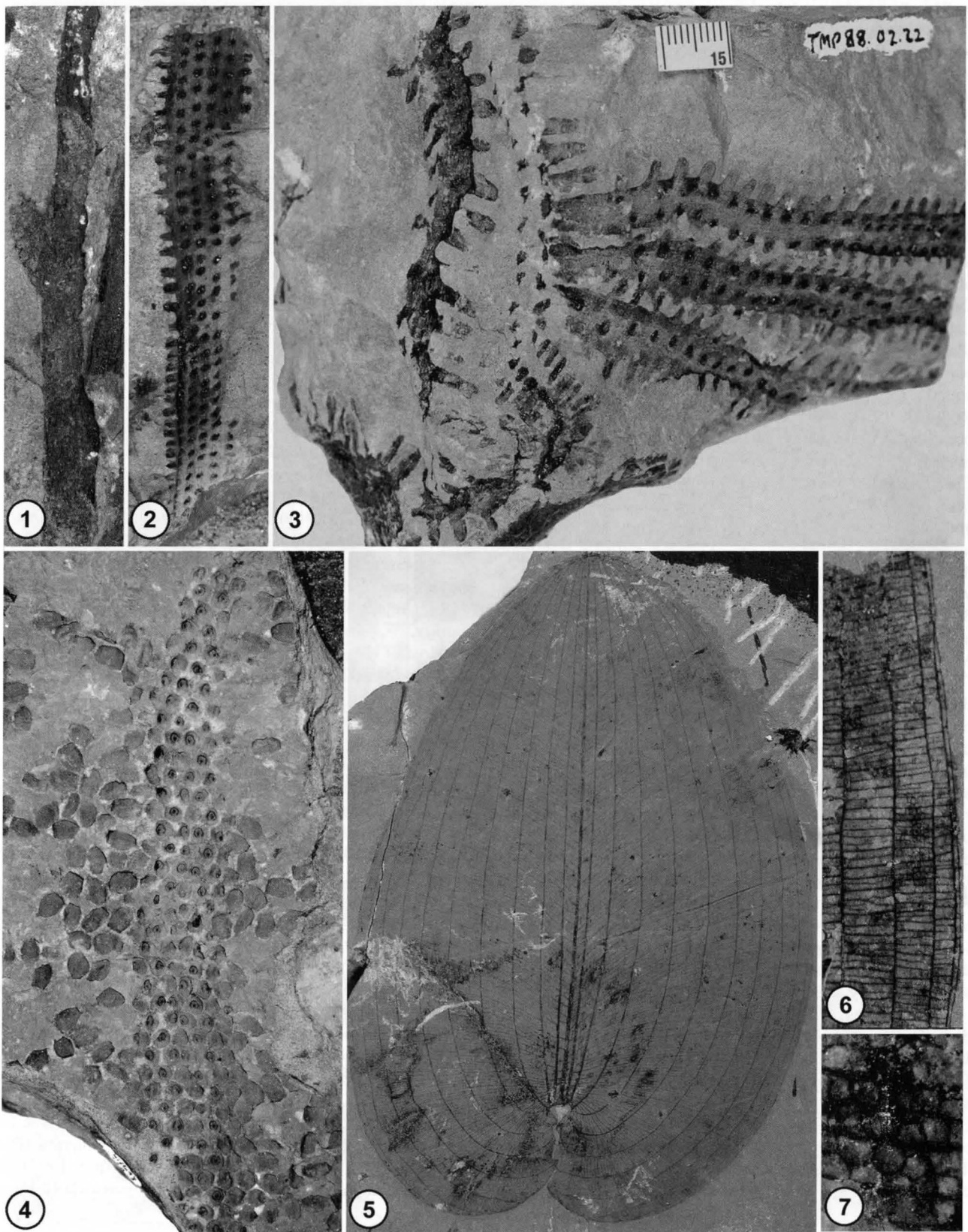


Fig. 1-7.—Fossil monocots and putative monocots.—1. "*Acorus*" *brachystachys* (SRM 50252) $\times 1.5$.—2. Spadix-like structure (DMNH 22479) $\times 0.8$.—3. Several axes, like that in Fig. 2, attached at right angles showing root-like nature (TMP 88.02.22) $\times 1.1$.—4. Spadix-like structure with dispersed seeds and seed scars on axis (DMNH 23219) $\times 0.7$.—5. *Cardstonia tolmanii* leaf (UAPC-ALTA S55138A) $\times 3.5$.—6. *Cardstonia tolmanii* leaf margin showing primary veins and secondary veins at right angles (UAPC-ALTA S52272) $\times 8$.—7. *Cardstonia tolmanii* leaf showing secondary veins and polygons of aerenchyma tissue overlapping veins (APC-ALTA S52263A) $\times 32$.

served specimens are found their affinities remain in doubt. Paleobotanists have decided to get at this problem in two ways. Firstly, to look for localities where monocot fossils are common. Secondly, we collect and study this material in a more systematic manner, trying whenever possible to reconstruct whole plants. This is the most difficult and time-consuming job.

Alismatales

Alismatales today contain aroids and alismatids (formerly Arales, Alismatales, Hydrocharitales, Aponogetonales, Scheuchzeriales, Potamogetonales, and Triuridales) and all of the taxa formerly regarded as *Helobiae* (Tomlinson 1982). One of our localities near Cardston, Alberta, Canada, in the Late Cretaceous (late Cenomanian to early Maastrichtian) St. Mary River Formation has yielded large numbers of aquatic plants, both dicots and monocots, as well as heterosporous aquatic ferns (Rothwell and Stockey 1993; Stockey and Rothwell 1997; Riley and Stockey 2004). Three types of broad-leaved monocots and leaves of sabaloid palms are present at the Cardston site. Over 50 specimens of leaves of *Cardstonia tolmanii* Riley et Stockey (2004) have recently been described (Fig. 5). Leaves range from 3.5–8.5 cm wide and 5–12 cm long with cordate bases. They are long petiolate and were buried in situ with the petioles extending downward into the sediment (Fig. 5, 8). Five to seven major veins enter the petiole, and the outermost branch to form 23–27 primary veins that converge just beneath the leaf apex at an apical pore (Fig. 5, 8, 9; Riley and Stockey 2004). Major and minor secondary veins in an ABAB pattern (Hickey and Peterson 1978) diverge at angles of 45–65° near the midvein and 90° near the leaf margin (Fig. 6, 8). Details of leaf venation were compared to several taxa of Alismatales that showed some similarity in form, including those in Alismataceae, Aponogetonaceae, Hydrocharitaceae, Limnocharitaceae, Potamogetonaceae (as well as those of Amaryllidaceae, and Stemonaceae). Compressions are preserved in such fine-grained sediments that the underlying structure of aerenchyma can be seen (Fig. 7). Riley and Stockey (2004) placed these leaves into a new genus *Cardstonia* Riley et Stockey of Limnocharitaceae with closest similarities to *Limnocharis* Bonpl. This study pointed out the need for a careful reexamination of leaves of extant alismatids and their venation patterns, which has so far not been done in a systematic way.

Fossil leaves similar to those of *Cardstonia* have been described by various authors in the genus *Haemanthophyllum* Budantsev. The type specimen of *Haemanthophyllum* (*H. kamtschaticum* Budantsev 1983) from Kamchatka and some of the described species, e.g., *H. cordatum* Golovneva (1987) from the Maastrichtian to Danian deposits of the Koryak Highlands, Russia, show most similarities to *Cardstonia*. The merging of the primary veins with the leaf margin (a character common in Alismataceae but not *Cardstonia*) dis-

tinguishes *Cardstonia* from fossil *Haemanthophyllum* leaves.

Further confusion over *Haemanthophyllum* has resulted in use of this name by various authors for leaves of differing morphology. Some of the described species have leaves more similar to those of *Aponogeton* L. f. (Golovneva 1997). Furthermore, if incomplete specimens are known (e.g., a portion of a cordate base with primary and secondary venation present), these pieces of fossil leaves might even belong to Stemonaceae or other widely divergent monocot families (Riley and Stockey 2004). It is, therefore, important to collect complete specimens and as much of a fossil plant as possible before taxonomic decisions are made as to affinities.

Leaves, previously assigned to Alismataceae that have been rejected due to incomplete preservation, include: *Alismacites primaevus* Saporta (1894), rejected by Teixeira (1948); *Alismaphyllum victormasonii* (Ward) Berry (1911), rejected by Doyle (1973), and Doyle and Hickey (1976); *Alismaphyllum cretaceum* Berry (1925), rejected by Daghljan (1981). *Alismaphyllites grandifolius* (Penhallow) Brown (1962) and fruits of *Sagittaria megaspermum* Brown (1962) from the Paleocene of North Dakota and Wyoming were tentatively assigned to the family by Daghljan (1981). However, in light of the studies of *Haemanthophyllum* and *Cardstonia* (discussed above), these remains need to be reinvestigated with well-preserved material. Haggard and Tiffney (1997) reject *Sagittaria megaspermum* as a member of the family.

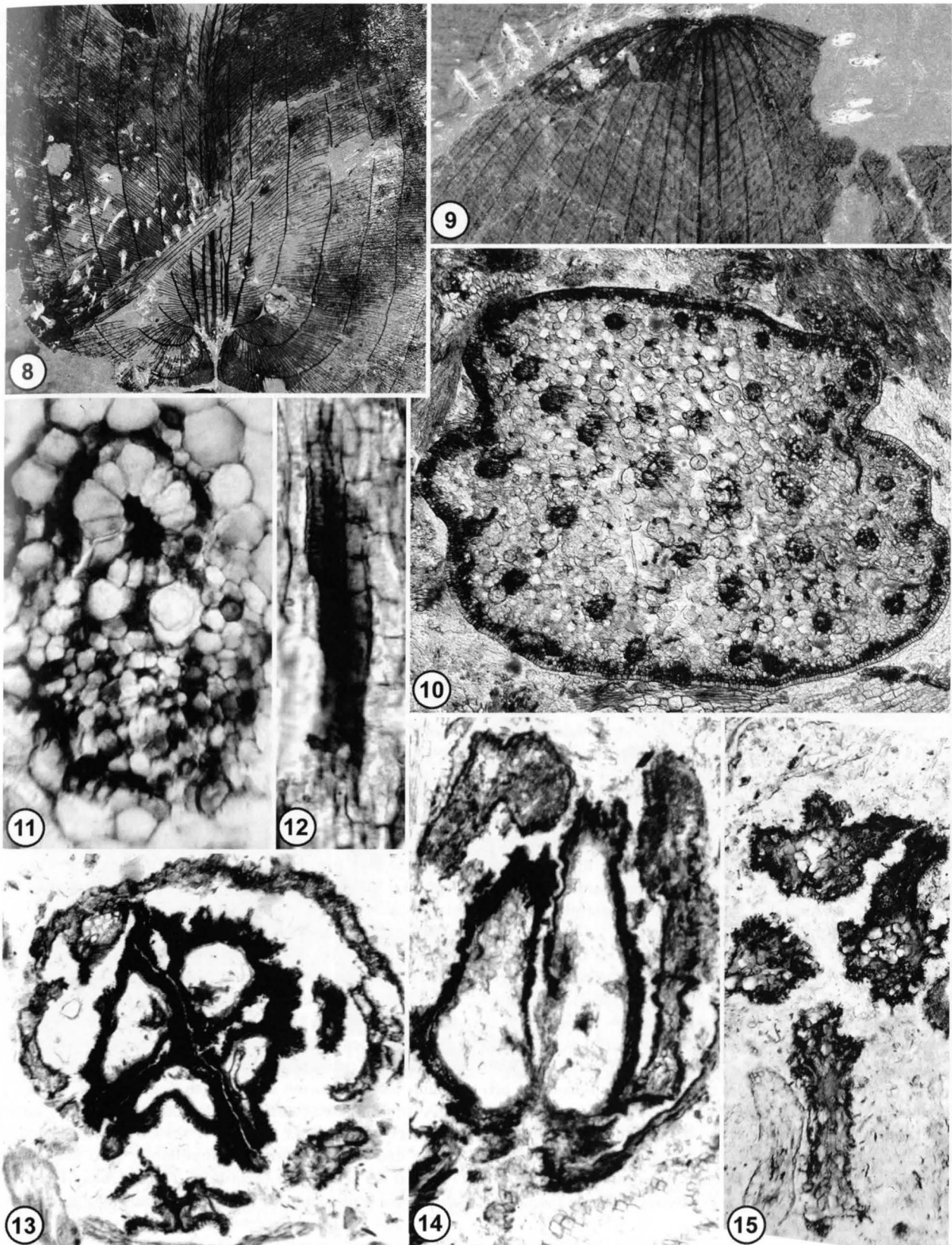
Most of the fossil pollen record of Alismataceae, like that of megafossils, is dubious (Erwin and Stockey 1989). All of the described pollen listed in Muller (1981) is regarded as pending further documentation.

The fossil record of fruits of Alismataceae was reviewed by Haggard and Tiffney (1997). Seven extant genera so far have been recorded in the Miocene and Pliocene of Europe and Siberia (Haggard and Tiffney 1997). Fruits of *Alisma* L. have been reported from the Oligocene of England (Chandler 1964) and the Miocene of Russia (Katz et al. 1965). These seem to be well documented and well preserved. *Alisma*-like fruits and seeds are also known from the Oligocene of Russia and have been included in the genera *Sagisma* Nikitin and *Caldesia* Parl. (Dorofeev 1963; Tahkajan et al. 1963; Daghljan 1981). Fruits included in the genera *Alisma* and *Butomus* L. by Mai (1985, 2000) are known from the Miocene and Oligocene of Europe from several localities.

The fossil record of *Caldesia* was extensively reviewed by Haggard and Tiffney (1997), with a leaf record reported from the Miocene Clarkia Flora of Idaho (Smiley and Rember 1985). Fruits of *Caldesia* are known from the Oligocene through the Pleistocene (Dorofeev 1977; Haggard and Tiffney 1997; Mai 2000) and occur in North America in the Miocene Brandon Lignite (Haggard and Tiffney 1997). The study of Haggard and Tiffney (1997) is particularly impor-

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Fig. 8–15.—Basal monocots.—8. *Cardstonia tolmanii* showing cordate leaf base and petiole dipping into matrix (UAPC-ALTA S50947A) × 7.5.—9. *Cardstonia tolmanii* leaf showing primary veins converging at apical pore (UAPC-ALTA S52295) × 4.—10. *Heleophyton helobiaeoides* petiole cross section showing five series of vascular bundles (UAPC-ALTA P2313 B top #1) × 50.—11. *Heleophyton helobiaeoides* vascular bundle showing protoxylem lacuna (dark) and two large thin-walled tracheary elements beneath (UAPC-ALTA



P2313 B top #0) $\times 465$.—12. *Heleophyton helobiaeoides* longitudinal section of protoxylem lacuna showing cells with thickened inner walls and scalariform thickenings on thin-walled xylem (UAPC-ALTA P2313 B side #0) $\times 415$.—13. Small flower in cross section showing four carpels, two tepals, bract, and remains of stamens (UAPC-ALTA P5831 B bottom #8) $\times 70$.—14. Longitudinal section of flower showing apocarpus gynoecium and two stamens (UAPC-ALTA P1631 B top a #15) $\times 75$.—15. Oblique transverse section of flower showing carpels with styles that extend out laterally (UAPC-ALTA B bottom b #42) $\times 75$.

tant because these authors not only describe new material, but study seeds of extant *Caldesia* using scanning electron microscopy of sections as well as external surfaces. This type of anatomical study and/or sectioning of alismatid plant material are needed to help paleobotanists interpret the isolated organs found in many deposits.

One locality that preserves fossil alismatids in anatomical detail is the Princeton chert of British Columbia, Canada. The first of the described taxa was *Heleophyton helobiaeoides* Erwin et Stockey (1989), based on a petiole of an aquatic alismatid. The *H. helobiaeoides* petiole is rectangular in section with 36 circular-to-oval vascular bundles in five series (Fig. 10), similar to those described for *Sagittaria* L. and *Echinodorus* Rich. ex Engelm. (Meyer 1932, 1935). Individual vascular bundles are most similar to those described for *Butomus* L. (Cheadle and Uhl 1948), with a protoxylem lacuna that is surrounded by a ring of cells with a thickened inner wall, thin-walled xylem with annular, helical-to-scalariform secondary wall thickenings, and a well-developed phloem strand (Fig. 11, 12). Several types of monocot stem remains are also present in the chert and we are trying to reconstruct the *Heleophyton* Erwin et Stockey plant.

One possible alismataceous floral type has also been identified in the Princeton chert (Fig. 13–15). Large numbers of these flowers are found scattered throughout the chert matrix. The small flowers (0.8 mm in diameter) are apocarpous, with four carpels, four stamens, two tepals, and a bract or prophyll. While the anthers are filled with gold contents, the structures inside are only 6–8 μm in diameter and were described by Currah and Stockey (1991) as the spores of smut fungi, the first evidence of Ustilaginales in the fossil record. The structure of these flowers is similar to those of Aponogetonaceae, however, the presence of four rather than six stamens precludes their assignment to this family. The position of stamens relative to carpels precludes assignment in Potamogetonaceae. Further study of these flowers and a reconstruction of their morphology is underway (Smith and Stockey 2004), as well as a developmental sequence of the laterally flattened fruits (Fig. 16) produced by these flowers. Large numbers of vegetative remains occur along with the flowers and fruits and it is hoped that a whole plant reconstruction will be possible.

Leaves assigned to Aponogetonaceae were described by Zhilin (1974a, b, 1989) and Pneva (1988) from the Oligocene of Kazakhstan. However, Golovneva (1997) has treated some of this material in *Haemanthophyllum*. Much of it is known from small fragments and more material is needed to describe these taxa in detail. Boulter and Kvaček's (1989) material of narrow, oblong leaves with parallelodromous primary venation, from the late Paleocene/early Eocene of Ireland, resembles *Aponogeton tertiaris* Zhilin (1974b), but more material is needed to confirm the affinities of this and other fossil leaf fragments assigned by some to *Haemanthophyllum*, Aponogetonaceae, or Potamogetonaceae (see Riley and Stockey 2004 for a review).

Potamogetonaceae are well represented in the fossil record of the Tertiary at some localities (Mai 2000). Exceptionally well-preserved *Potamogeton* L. leaves have been reported from the late Miocene Styrian Basin at Wörth near Kirchberg/Raab in Austria that show epidermal cell outlines (Kovar-Eder and Krainer 1990; Kovar-Eder 1992). The fruit rec-

ord of Potamogetonaceae was reviewed by Collinson (1982) in which she emends Reid and Chandler's (1926) diagnosis of the extinct genus *Limnocarpus* Reid and describes five new fossil taxa: *Selseycarpus*, *Eulimnocarpus*, *Limnocarpella*, *Medardus*, and *Palaeoruppia*. These five genera contain taxa formerly treated in *Limnocarpus* by Chandler (1961), Dorofeev (1968), and Bůžek and Holý (1981). Collinson (1982) describes a new genus based on fruits, *Midravalva* Collinson from Saudi Arabia that shows affinities to modern *Ruppia* L. The genus *Limnocarpus* is now restricted to bicarpellate, laterally flattened fossil fruits with a triangular germination valve. Collinson (1982) provides a table of comparison of these taxa and the results of a morphological cladistic analysis using 15 fruit characters. In light of recent cladistic analyses (Les et al. 1997), *Ruppia* is considered to be in its own family and its inclusion in Hydrocharitaceae makes the family biphyletic (Judd et al. 2002). Clearly, whole plant data for many of the fruits and seeds known in the Tertiary would be invaluable in our understanding of these taxa.

Hydrocharitaceae are represented by seeds of *Hydrocharis* L. (Mai 1999, 2000) from the Miocene of Lausitz and *Stratiotes* L. beginning from the Late Paleocene of England (Collinson 1986, 1990; Collinson et al. 1993), Eocene and Upper Oligocene to Upper Miocene in Europe (Mai 2000; Kvaček 2003). Mai (1999) provides a key to the Eocene seeds. Mai and Walther (1978, 1985) recognize *Ottelia* Pers., *Hydrilla* Rich., *Vallisneria* Scop., *Hydrocharis*, and *Stratiotes* based on seeds from the Upper Eocene Weißelster-Becken near Leipzig, Germany. *Stratiotes* by far has the best fossil record with 15 extinct species described (Cook and Urmi-König 1983). Leaves similar to *Thalassia* Banks and their crystals were described by Brack-Hanes and Greco (1988) from the Eocene of Florida and the seagrass community by Ivany et al. (1990). Wilde (1989) described leaves similar to *Hydrocharis* based on venation and well-preserved cuticle with anomocytic stomata in the freshwater deposits from the Eocene of Messel, Germany. Leaves of *Hydrochariphyllum buzekii* Kvaček (2003) have been described from the Miocene Most Formation of north Bohemia, Czech Republic.

Najadaceae seeds are common in the Oligocene of Europe (Friis 1985; Mai 1985; Collinson 1988; Collinson et al. 1993). These resemble extant *Najas* L. and about 17 species have been described from the Tertiary (Friis 1985), most of these from Russia (Dorofeev 1963, 1966, 1969, 1978).

Cymodoceaceae, a family of five marine genera, Posidoniaceae with one genus, and Zosteraceae with three genera, which live in marine or brackish water (Cook 1990), have very problematic fossil records. Daghljan (1981) and Kuo and McComb (1998a, b, c) have reviewed these records and agree that most of them are unreliable. Kuo and McComb (1998a) do accept the records of *Thassocharis* Debey from the Upper Cretaceous of The Netherlands (Voigt and Domke 1955) and *Thalassodendron* den Hartog from the Eocene of Florida (Lumbert et al. 1984). These authors did not review the records of *Posidocea frickingeri* Gregor (1991) from the Paleocene of Italy or the newly described *Posidonia* König fossils from the Eocene near Hallthurm (Gregor 2003) that are believed to be reliable (J. Bogner pers. comm., 2004).

A preliminary report of two types of timorous staminate

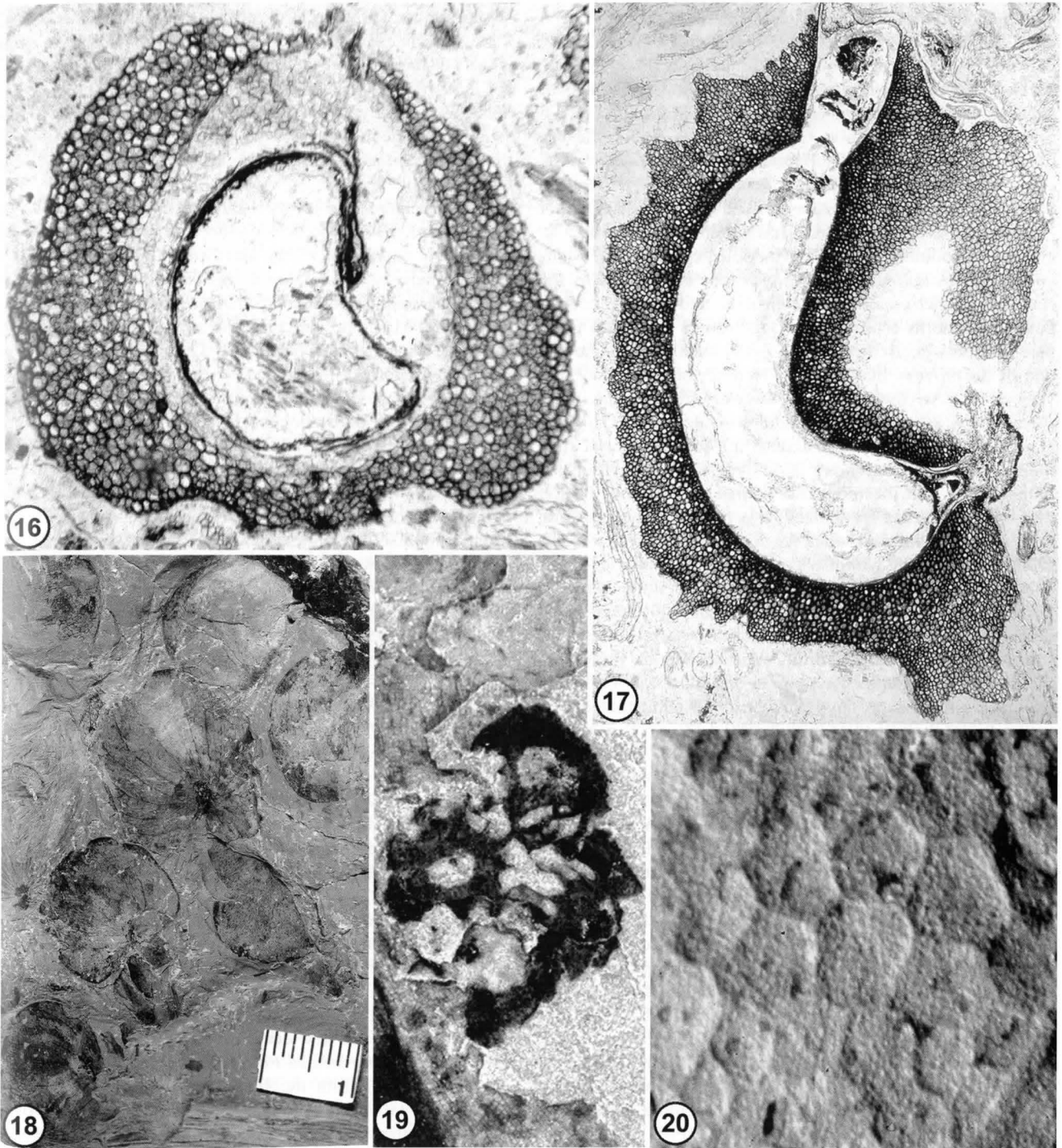


Fig. 16–20.—Basal monocots.—16. Longitudinal section of fruit showing uniform fruit wall and one seed (UAPC-ALTA P1631 C bottom #23) $\times 70$.—17. Longitudinal section of *Keratosperma allenbyense* seed showing micropyle with cover (at top), epistase, hypostase, and podium. Hollow area at right indicates position of the raphe (UAPC-ALTA P5836 E1 bottom #2b) $\times 40$.—18. *Linnobiophyllum scutatatum* group of four small rosettes attached by stolons (not visible) (UAPC-ALTA S37120A) $\times 1.5$.—19. Staminate flower of *Linnobiophyllum scutatatum* (UAPC-ALTA S37247) $\times 187$.—20. *Linnobiophyllum scutatatum* leaf surface showing small epidermal cells, trichomes (dark), and large polygons of underlying aerenchyma tissue (UAPC-ALTA S37267B) $\times 40$.

flowers similar to Triuridales appeared in the Allon Flora of the Late Cretaceous (Santonian) of Georgia, USA (Herendeen et al. 1999), but these flowers have not yet been formally described. Additional evidence of the family Triuridaceae was reported by Gandolfo et al. (2000) with well-

preserved, charcoaled flowers from the Old Crossman Clay Pit in New Jersey. These flowers from the Raritan Formation are Upper Cretaceous (Turonian) in age and are also the oldest known unequivocal monocot flowers (Gandolfo et al. 2002). Only small staminate flowers have so far been

identified but they are well preserved, with six tepals and three stamens containing prolate, monosulcate pollen. Gandolfo et al. (2002) describe these remains in three separate species: *Mabelia connatifila* Gandolfo, Nixon et Crepet, *M. archaia* Gandolfo, Nixon et Crepet, and *Nuhliantha nyanzaiana* Gandolfo, Nixon et Crepet. *Mabelia connatifila* has basally connate filaments, ornamented anthers, pores on the connective extensions, psilate pollen, and a flat glabrous receptacle, while *M. archaia* has sunken anthers, lacks anther ornamentation and pores, and has reticulate pollen and an elevated glandular receptacle (Gandolfo et al. 2002). *Nuhliantha nyanzaiana* has a central pistillode surrounded by the stamens, shorter connective extensions, and finely reticulate pollen (Gandolfo et al. 2002). Gandolfo et al. (2002) compare their flowers to those of the Allon locality and state that one of the flowers described by Herendeen et al. (1999) is very similar to their species *Mabelia archaia*; the other seems to be a new taxon (Gandolfo et al. 2002). Gandolfo et al. (2002) further suggest that this fossil material may indicate that the triurids are a very early branch within the monocots or that the monocots themselves are much older than was previously recognized. It is possible that this floral type is basal. Cladistic analyses using these floral remains found them nested within a completely saprophytic Triuridaceae (Gandolfo et al. 2002). With only floral remains, however, it is difficult to say what kind of habit these plants displayed. It is hoped that more localities, such as these two from the Cretaceous of North America, will be found and that vegetative remains may help in our understanding of the evolution of the saprophytic/mycotrophic habit that occurs in the extant monocots of this family.

Araceae

Araceae have been the subject of extensive review in the past few years (Mayo et al. 1997; Keating 2002). Mayo et al. (1997) devote a short chapter to the fossil record including leaves, spadices, fruits and seeds, and pollen. Fossils excluded from Araceae are also discussed by these authors. Additional reviews appear in Gregor and Bogner (1984, 1989) and Grayum (1990). Keating (2002) emphasized several interesting aspects of this record and added some recent data. Some of these taxa have been discussed above, e.g., the reproductive structures of *Acoropsis eximia*. I will only discuss the new or most significant records here.

The oldest Araceae fossils reported to date are mesofossils of *Mayoa portugallica* Friis, Pedersen et Crane from Torres Vedras in the Western Portuguese Basin (Friis et al. 2004). This species was described based on large masses of pollen attached to a cutinized structure. However, preservation is too poor to allow for the interpretation of inflorescences or flowers (Friis et al. 2004). Grains are inaperturate, elliptical with a striate surface, and are compared with pollen of subfamily Monsteroideae, tribe Spathiphyllae (Friis et al. 2004).

The oldest megafossil remains of Araceae may be those of an aroid infructescence from the Late Cretaceous (Campanian) of southern Alberta, Canada (Bogner et al. 2005). The specimen, although incomplete, is permineralized and represents what is interpreted as a spadix that probably had bisexual flowers with a trilocular gynoeceum and one ellip-

soidal, ribbed, anatropous seed per locule (Bogner et al. 2005). Fruits are surrounded by the remains of six tepals in whorls of three, and the carpels show attenuated styles. Bogner et al. (2005) believe that this fossil spadix shows affinities to subfamily Orontioideae, but that it probably represents a new genus with spadix and styler region similar to those of *Symplocarpus* Salisb. ex Nutt. (Orontioideae) (Bogner et al. 2005).

The best-known aroid fossils are those of fruits and seeds (Mayo et al. 1997). These have been reviewed in detail by Madison and Tiffney (1976), and Gregor and Bogner (1984, 1989). There is a good fossil record of subfamilies Monsteroideae and Lasioideae from European brown coals of Oligocene, Miocene, and Pliocene age (Mayo et al. 1997). Three fossil genera: *Epipremnites* Gregor et Bogner, *Scindapsites* Gregor et Bogner, and *Urospathites* Gregor et Bogner are known from Europe (Gregor and Bogner 1984, 1989). The best known of the fossil aroid seeds is *Keratosperra allenbyense* Cevallos-Ferriz et Stockey (1988) from the Middle Eocene Princeton chert of British Columbia, Canada (Fig. 17; Smith and Stockey 2003). Seeds are anacampylotropous with a warty seed coat (containing scattered, round idioblasts), a single dorsal ridge, and two lateral ridges (Smith and Stockey 2003). There is a thin micropylar cover, an epistase or nucellar cap (Fig. 17), and evidence of mucilage in the space below the micropyle. Seeds have a prominent hypostase and podium at the chalazal end. Endosperm and a monocotyledonous embryo were reported in some seeds (Cevallos-Ferriz and Stockey 1988). These seeds were compared in detail anatomically to those of extant aroids (Seubert 1993, 1997) and represent the oldest evidence of the lasioid clade (subfamily Lasioideae) (Smith and Stockey 2003).

The fossil leaf record, like that of alismatids, is problematic, but some good examples are known in North America, and some of these are from aroid groups that, according to molecular phylogenetic analyses, are derived (Mayo et al. 1997). Hickey (1977) described large leaves of the genus *Peltandra* Raf. from the early Eocene Camel's Butte Member in the Golden Valley Flora. These large leaves have from 8–10 parallel veins running along the margin and show the distinct pattern of *Peltandra*. *Peltandra primaeva* Hickey differs from extant species in having a greater number of marginal veins and a wider marginal zone (Hickey 1977). Large leaves described as *Philodendron limnestis* Dilcher et Daghljan (1977) from the Eocene Claiborne Formation of Tennessee, with well-preserved upper and lower epidermis, show prominent vein patterns typical of some Araceae. Dilcher and Daghljan (1977) originally classified these remains in *Philodendron* Schott subgen. *Meconostigma* Schott. In a later monograph of this subgenus by Mayo (1991), it was suggested that these leaves are probably more similar to the genus *Typhonodorum* Schott. *Typhonodorum* and *Peltandra* today are classified in the subfamily Aroideae, tribe Peltandreae (Mayo et al. 1997) that seems to have been common during the Eocene in North America.

Nitophyllites zaizanica Iljinsk., from the Paleocene of Kazakhstan, was originally thought to represent an alga, but was later included in Podostemaceae (Iljinskaya 1963). In 1975 Fedotov placed this material in Araceae. He compared this taxon to *Alocasia* G. Don and *Colocasia* Schott, but

these leaves are fragments and better material is needed for a full description (Dilcher and Daghljan 1977). They differ from "*Philodendron*" *limnestis* in having numerous anastomoses of the marginal veins, stomata rarely found on the adaxial surface, and lack of epidermal papillae (Dilcher and Daghljan 1977).

Other tribes of Araceae, subfamily Aroideae, are represented by leaves. The best known of these are *Caladiosoma miocenicum* Berry from the Miocene of Trinidad (Berry 1925) that may represent tribe Caladieae Schott. This leaf is generally accepted as aroid and similar to *Caladium* Ventenat or *Xanthosoma* Schott (Mayo et al. 1997).

Araceophyllum Kräusel (1929) leaves were described from the Miocene and Pliocene of Sumatra. Mayo et al. (1997) distinguish two types of leaves: *Araceophyllum engleri* Kräusel that they include in subfamily Pothoideae Engl. and *Araceophyllum tobleri* Kräusel in subfamily Monsteroideae, tribe Monstereae Engl. Clearly this genus needs to be recircumscribed and the two species described in separate genera. Other species assigned to *Araceophyllum*, *A. striatum* Weyland (1957) and *A. tarnocense* Rásky (1964), are regarded as too incomplete to even be included in the family.

Araciphyllites austriacus J. Kvaček et Herman nom. inval. (2004) is a species recently described from the Cretaceous (Campanian) of Grünbach, Austria. Unfortunately, this species is based on a type ("*Araciphyllites tertarius* (Engelh.) Wilde, Z. Kvaček et Bogner 2003") that has not been published and the genus is, therefore, nomen nudum. Kvaček and Herman (2004) describe this genus as showing a venation pattern similar to *Lysichiton* Schott and *Orontium* L. (Araceae, subfamily Orontioideae Mayo, Bogner et Boyce) with an incomplete, wide, multi-stranded midrib. Lateral veins in *A. austriacus* arise at steep angles from the midrib and parallel venation of three weakly differentiated subsets of veins are arranged in a BdCdB pattern (Kvaček and Herman 2004). Transverse veins are oriented obliquely or perpendicularly and areoles are elongate and polygonal-quadrangular (Kvaček and Herman 2004).

All the taxa of Araceae described above are based on isolated organs, but whole plants are known from compression fossils described as *Limnobiophyllum scutatatum* (Dawson) Krassilov emend. Z. Kvaček (1995). These plants were originally allied with Lemnaceae, in particular the genus *Spirodela* Schleid., because of their large size, and a relationship to the genus *Pistia* L. was suggested (see McIver and Basinger 1993 and Kvaček 1995 for a complete discussion of the nomenclatural problems for these plants). A similar plant, *Limnobiophyllum expansum* (Heer) Kvaček (1995), was described from the Miocene of Europe and differs from *L. scutatatum* in having a vascular strand in the stolons, smaller rosettes of leaves that may lack an apical notch (Stockey et al. 1997). Large numbers of specimens of *Limnobiophyllum scutatatum* from lacustrine sediments at the Paleocene Joffre Bridge locality in central Alberta, Canada, (Fig. 18–20) were studied by Stockey et al. (1997). Whole plants were preserved, including stems with attached leaves (Fig. 18) with well-preserved epidermis and some internal tissues (Fig. 20), stolons, roots, and flowers (Fig. 19), including anthers with in situ pollen. Whole plants were reconstructed and phylogenetic relationships among *Limnobiophyllum*, living genera of Lemnaceae, *Pistia*, and other genera of Ara-

ceae were tested with cladistic analysis using the morphological characters of fossils as well as extant plants (Stockey et al. 1997).

Traditional morphological studies have indicated a close relationship between the floating aroid *Pistia* and Lemnaceae (Rothwell et al. 2004). A single origin of a floating aquatic habit is supported by molecular analyses using the chloroplast gene *rbcl* (Duvall et al. 1993a; Les et al. 1997) and the morphological analysis by Stockey et al. (1997) using a combination of fossil and living species. However, other analyses using chloroplast restriction site data remove *Pistia* and Lemnaceae to distantly related clades and embed both within Araceae (e.g., French et al. 1995; Mayo et al. 1997; Renner and Weerasooriya 2002). Conflicting morphological data (Grayum 1990, 1992; Tarasevich 1990) also indicates that this might be the case. Some of the discrepancies between relationship and phylogenetic position of Lemnaceae within the aroids may have been due to low sampling of aroid and lemnooid genera in molecular analyses and the inclusion of too few taxa to overcome exemplar effects (Rothwell et al. 2004). To help distinguish between the competing hypotheses of affinities and phylogenetic position of Lemnaceae, a broad range of samples using chloroplast DNA sequences of the *trnL-trnF* intergenic spacer region were used in a study by Rothwell et al. (2004). These data agree with the results of French et al. (1995), Renner and Weerasooriya (2002), Cabrera et al. (2003), and Renner and Zhang (2004) that there were probably at least two independent origins of a floating aquatic habit in extant aroids (including Lemnoideae, formerly Lemnaceae).

Recent work on Cretaceous fossils from western North America, Russia, and now China (Johnson et al. 1999; K. Johnson pers. comm., 2003) on the plant known as "*Pistia*" *corrugata* Lesq. (Fig. 21–24) indicates that there may be at least three or more independent origins of this floating, aquatic growth habit. "*Pistia*" *corrugata* (Lesquereux 1878) has been reported now from numerous sites ranging in age from Campanian to Late Maastrichtian (Johnson et al. 1999). Recently, over 70 whole plants have been uncovered at Dinosaur Park (Campanian, Dinosaur Park Formation) near Brooks, Alberta, that show as many as six plantlets attached by stolons on one rock slab (Fig. 21). These small rosettes have stems with attached roots and leaves with a basal "pouch" that was probably filled with aerenchyma in life (Fig. 22). Several vascular bundles enter the leaf base on the abaxial side and some of these branch to supply the venation on the adaxial leaf surface (Fig. 23). Leaves were trumpet-shaped with a large aerenchymatous base and a blade that probably floated on the surface of the water. There is a sub-marginal collective vein and at least two marginal veins with branching veins that form a fringe or rim around the leaf. Examination of compressed leaves from the abaxial surface shows that the aerenchymatous tissue did not extend into this leaf margin, but was centered under the main circular area within the margins. Leaves have a prominent apical notch and their surfaces are covered with trichomes. The apical notch and several veins entering the leaf blade are similar to those seen in *Pistia*, but details of venation are markedly different. Venation in the lateral rim is similar to that described by Mayo et al. (1997) in *Carlephyton* Jum. or *Arophyton* Jum. (Araceae, subfamily Aroideae, tribe Ar-

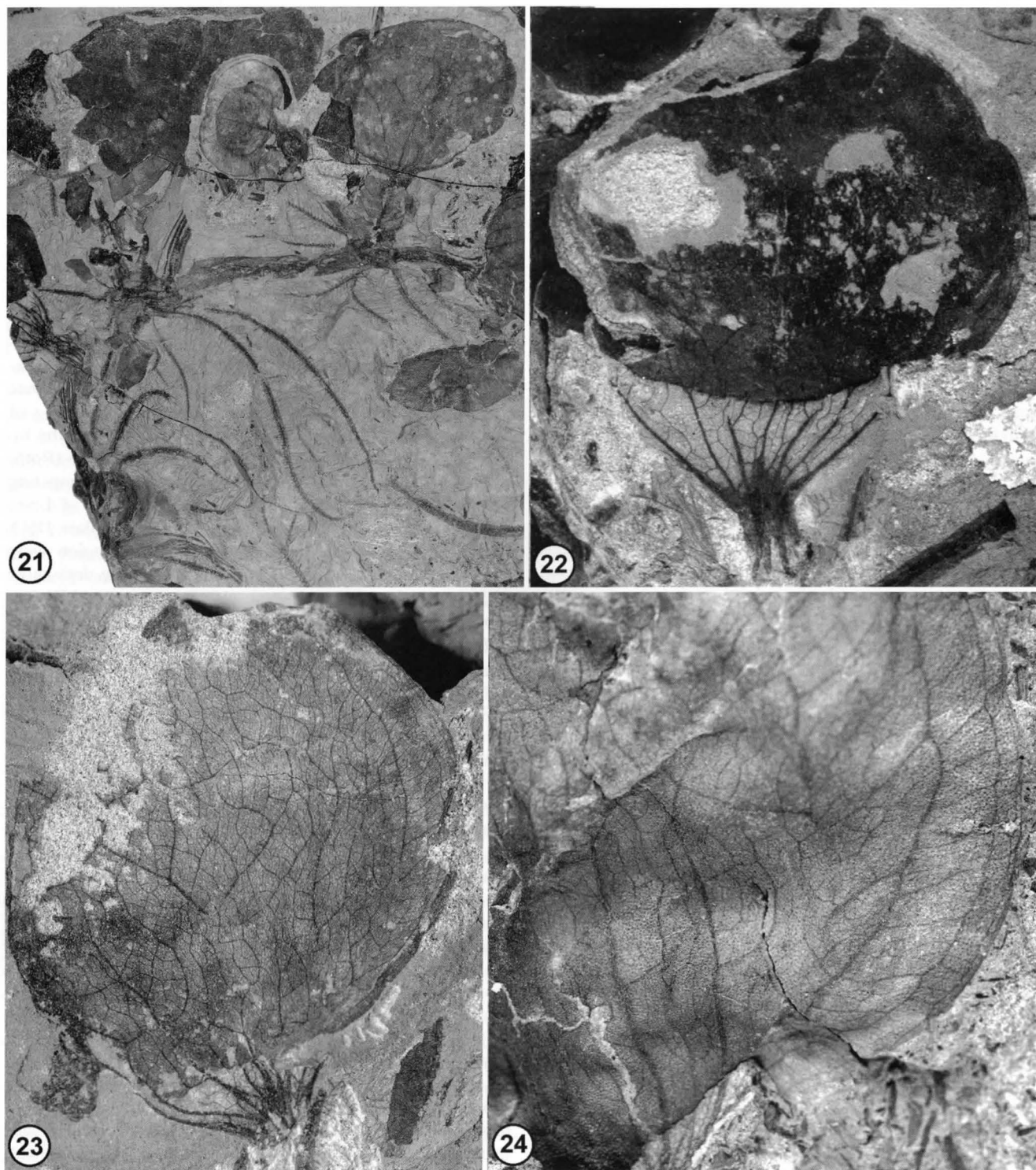


Fig. 21–24.—“*Pistia*” *corrugata*.—21. Several plants attached by stolons and showing branched aquatic roots (TMP 95.98.29A) \times 7.5.—22. Leaf showing basal “pouch” and major abaxial venation (DMNH 10383) \times 15.—23. Leaf showing adaxial venation and lateral rim (DMNH 10376) \times 16.—24. Leaf showing venation on adaxial surface and in rim (DMNH 8658) \times 25.

ophyteae) that form a submarginal collective vein and one to two marginal veins. These taxa differ considerably in leaf shape, however, from “*Pistia*” *corrugata* and are not floating aquatics. While these fossil plants known as “*Pistia*” *corrugata* resemble *Pistia* in growth habit, they are clearly

very different morphologically and are being described in a new genus.

Use of taxa such as “*Pistia*” *corrugata* or other fossils to date the nodes of phylogenetic trees is currently being done by some authors. Bremer (2000) followed this approach for

the early Cretaceous monocot lineages. These dates, however, are only as good as the fossil evidence. Descriptions of fossils of basal monocots such as Tofieldiaceae (at the base of the Alismatales clade, in Graham et al. 2006), based on *Dicolpopollis* pollen that is listed as pending (Muller 1981), are tentative at best. Clearly the fossil record of *Pistia* (only parts of which are described above) is misinterpreted. Many supposed “*Pistia*”-like plants have been described (McIver and Basinger 1993; Stockey et al. 1997), but some of these are so badly preserved that their affinities are very doubtful. All of these taxa need to be reexamined and in many cases better fossil material discovered. Many similar looking aquatics are often lumped into genera with which they have nothing in common.

The genus *Porosia* Hickey (1977) was a name given to round, suborbiculate, or reniform bodies that are permeated with tubules oriented at right angles to the surface. *Porosia verrucosa* (Lesq.) Hickey has been confused with *Limnobiophyllum scutatum*, *L. expansum*, *Pistia*, and maybe other taxa as well (Hickey 1977; Serbet 1997; Manchester 2002). Krassilov (1973) placed them in Araceae and they have been treated as aerenchymatous leaves. Some of the specimens actually may be leaves, but others appear to be seeds or fruits (Hoffman 1995; Serbet 1997). Serbet (1997) sectioned one such “*Porosia*”-like structure from the Cretaceous near Drumheller, Alberta, and found that these were actually seed-like bodies rather than leaves. The seed-like bodies are also present in the Paleocene Joffre Bridge Flora (Hoffman 1995), but their preservation does not allow for detailed study using sections. The external ornamentation varies from that illustrated by Hickey (1977), and it is obvious that several types of things are being confused because of their similar size, shape, and sometimes ornamentation.

DISCUSSION

While the fossil record of basal monocots is very incomplete, there do seem to be well-preserved and well-identified taxa. Prior to the 1970s much of what was described must be taken with extreme caution. Rigorous paleobotanical study in the past 30 years has resulted in more carefully described and interpreted fossil remains. The lack of anatomical and morphological study in extant basal monocots (in fact, most angiosperms) has made the paleobotanist's job difficult, and often forces us to supply that data as well. While most paleobotanists have realized that isolated plant organs do not constitute a whole plant, neobotanists often do not understand this concept of morphotaxon.

It has been known for some time that isolated organs of very different plants can appear similar or identical in the fossil record. This is not only due to the vagaries of preservation, but is the real result of different rates of evolutionary change in morphological characters in different parts of the plant. In the dicots a good example of this phenomenon would be the extinct taxa included in Cercidiphyllaceae. The extinct genera *Trochodendrocarpus* Kryst., *Nyssidium* Iljinsk., and *Joffrea* Crane et Stockey all have leaves similar to those of extant *Cercidiphyllum* Sieb. et Zucc. (Crane and Stockey 1986). Fruits are follicles with several winged seeds and a similar morphology in all taxa. However, when these fossil plants are reconstructed, important differences emerge.

Cercidiphyllum and *Joffrea* grow by long-shoot/short-shoot growth, while *Nyssidium* and *Trochodendrocarpus* have only been demonstrated to have long-shoot growth. Infructescences of *Cercidiphyllum* are small with only 2–8 follicles per infructescence, while those of the fossil taxa can reach 15–40 and are borne on elongate racemes (Crane and Stockey 1986). Phyllotaxy varies when attached leaves and leaf scars are examined (see Crane and Stockey 1986 for a complete comparison). Thus, if one isolated organ such as a leaf or fruit is found, or even an entire infructescence, we do not know which of these taxa is present.

For other types of fossil plants, we know that roots are conservative organs and that a root alone is often not enough to determine the parent plant (Stewart and Rothwell 1993). It is very difficult to tell, with our current state of knowledge about fossil monocots, whether these types of problems are significant, and caution is advised. While most monocots are herbaceous and the interpretation of growth habits of plants that are represented by leaves is probably somewhat reliable, the differences in rates of evolution of reproductive structures and vegetative organs, and the combinations of characters present in certain taxa, can only be determined when whole plants are reconstructed. An inflorescence similar to a particular aroid genus, may indicate that this genus is present in the fossil record. However, it may only truly indicate that this type of inflorescence is present in the fossil record and a level of character evolution for this plant part is known. What the whole plant looked like that produced the inflorescence is still unknown. Knowing what we know about fossil dicots should cause us to question our interpretations based on a single organ and the use of these organs in other types of analyses.

The floating aquatic habit of the plant known as “*Pistia*” *corrugata* has caused early workers to place this taxon into Araceae and the genus *Pistia* (Lesquereux 1878; McIver and Basinger 1993). However, we now know that this and other taxa such as *Limnobiophyllum scutatum* (Stockey et al. 1997) have been completely misidentified.

Evidence of this type of problem from fossil monocots is seen in the plant *Limnobiophyllum*. Isolated pollen was identified as belonging to Pandanaceae (Elsik 1968; Jarzen 1983; Fleming 1990). Even detailed morphological and ultrastructural characters seemed to indicate a close relationship of this pollen (*Pandaniidites* Elsik [1968]) to extant Pandanaceae (Hotton et al. 1994). However, the discovery of this pollen type in the anthers of the flowers of *Limnobiophyllum*, a plant more closely related to Araceae, subfamily Lemnoideae, changed our perspective of these as whole plants and reinforced the similarities of this pollen type to that described for extant duckweeds (Stockey et al. 1997). This finding explains the conflicting climatic data suggested by the presence of Pandanaceae (primarily tropical) vs. Lemnaceae (geographically widespread) in Paleocene sediments (e.g., Sweet 1986).

Cladistic analysis and molecular phylogenies have suggested relationships between taxa that have previously been difficult to place in a taxonomic framework based on morphology alone. In some cases, conflicts between morphology and molecular phylogenies remain unresolved. This is where the fossil record has become increasingly important in our understanding of the evolution of flowering plants. Further

work on basal monocots, using well-preserved and reconstructed whole plants, promises to provide evidence of many of the important character changes that have resulted in the combinations of characters that we see in extant basal monocots and will help to determine the mode and tempo of evolution for these groups.

ACKNOWLEDGMENTS

The author would like to thank Dr. Else-Marie Friis, Swedish Museum of Natural History, Dr. Kirk R. Johnson, Denver Museum of Science and Nature, and Dr. Dennis Braman, Royal Tyrrell Museum of Palaeontology, for the loan of specimens, and Dr. Josef Bogner, Munich Botanical Garden, for helpful discussion, a critical review, and specimens of extant aroids. This work was supported in part by NSERC (Natural Sciences and Engineering Research Council of Canada) grant A-6908.

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