CARDSTONIA TOLMANII GEN. ET SP. NOV. (LIMNOCHARITACEAE) FROM THE UPPER CRETACEOUS OF ALBERTA, CANADA

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Several new broad-leaved monocots were identified in gray siltstones and fine-grained sandstones from the Upper Cretaceous (Campanian-Maastrichtian) St. Mary River Formation near Cardston, Alberta, Canada. Specimens are compression/impressions of long-petiolate aquatic plants that were probably buried *in situ*. Leaf blades are entire, ovate to elliptic, with deeply cordate bases; leaf blades are 5–12 cm long and 3.5–8.5 cm wide. Petioles are at least 4 mm wide with five to seven primary veins that enter the leaf blade. Venation is campylodromous, resulting in 23–27 primary veins with three medial veins that remain unbranched to the apex. Major and minor secondary veins (ABAB pattern) diverge at angles of 45°–65° near the midveins and 90° near the leaf margin. Tertiary veins are usually unbranched, but occasional dichotomies and anastomoses occur. No freely ending veinlets are visible. The Cardston specimens are compared with extant leaves of Alismatales and show closest similarities to those of *Limnocharis* L., *Hydrocleys* Rich., and *Butomopsis* Kunth. These leaves are also similar to fossil leaves of *Haemanthophyllum* Budantsev, in particular *H. cordatum* Golovneva from the Maastrichtian-Danian deposits of the Koryak Highlands, Russia. A reexamination of the genus *Haemanthophyllum*, the generitype (*H. kamtschaticum* Budantsev), the holotype for *H. cordatum*, and the Cardston specimens results in the description of a new genus, *Cardstonia tolmanii* gen. et sp. nov. (Limnocharitaceae). This study points to the need for reexamination of the remaining species in the genus *Haemanthophyllum*, which appear to represent a diverse assemblage of leaves of varying morphology that are probably not a natural group.

Keywords: Alismatales, *Aponogeton*, aquatic, *Butomopsis*, Cretaceous, *Echinodorus*, *Haemanthophyllum*, *Hydrocleys*, *Limnocharis*, monocot.

Introduction

The well-preserved fossil plants from the Upper Cretaceous Cardston Flora of southern Alberta have yielded 32 taxa of predominantly aquatic plants (Riley and Stockey 1999). These plants are compression/impressions that in some cases are nearly complete because of rapid burial in fine-grained sediments. Geologic data indicate that they were buried *in situ* in shallow oxbow lakes or ponds during a period of rapid sedimentation (Riley and Stockey 2000). Only two plants have been described in detail and reconstructed as whole plants: *Hydropteris pinnata* Rothwell and Stockey (1994), a heterosporous fern, and *Quereuxia angulata* (Newberry) Krysht. ex Baikovskaja (Stockey and Rothwell 1997), a floating, rosette-forming dicot.

The Cardston site is remarkable in its preservation of large-leaved monocots. Broad leaves of these herbaceous plants are usually rare in the fossil record (Herendeen and Crane 1995). At least six types of monocot leaves (in addition to those of a sabaloid palm) are present in sediments of the St. Mary River Formation at Cardston. One of these monocot leaf types has been compared with leaves described as *Haemanthophyllum* Budantsev (1983) from the Late

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Paleocene–Lower Eocene of western Kamchatka (Riley and Stockey 1998). This leaf type was originally assigned to the Amaryllidaceae, but further studies of leaf venation and comparisons to extant and fossil monocots have led several workers to suggest relationships to Alismataceae, Potamogetonaceae, and Aponogetonaceae (Heer 1868; Golovneva 1987, 1997; Boulter and Kvaček 1989). A number of leaves of differing morphology have been assigned to this genus (table 1), but their affinities remain in doubt (Golovneva 1997).

Several broad-leaved monocots generally conforming to *Haemanthophyllum* have been identified in the Cardston Flora (Riley and Stockey 1998). In this study we compare leaf morphology and detailed venation patterns of these Cretaceous leaves with fossils in the genus *Haemanthophyllum* and those of extant Aponogetonaceae, Alismataceae, Hydrocharitaceae, Stemonaceae, Potamogetonaceae, and Limnocharitaceae. We describe these remains as *Cardstonia tolmanii* Riley et Stockey gen. et sp. nov. and suggest that they have affinities to Limnocharitaceae.

Material and Methods

Fifty compression/impression specimens of these leaves have been collected from three sites on the banks of the St. Mary River below the reservoir and spillway (fig. 1).

Table 1

Comparative Morphology of *Haemanthophyllum* Budantsev Species

Species	Locality	Age	Length (cm)	Width (cm)	Blade	Base	Apex	NLV	NCV
Haemanthophyllum zhilinii (Pneva) Golovneva	Kazakhstan	Late Oligocene–Early Miocene	20–40	~11	Elliptical	Cuneate	Acuminate	11–13	10–20
Haemanthophyllum kamtschaticum Budantsev (Generitype)	Russia, Kamchatka Province	Late Paleocene/Eocene	?	7.5[a]	?	Cordate	?	~21	(**24–35**)
Haemanthophyllum kamtschaticum Budantsev (original description)	Russia, Kamchatka Province	Late Paleocene/Eocene	12–35	7–17	Broadly elliptical	Cordate	Attenuate to acuminate	17–21	9–13
Haemanthophyllum sp. 1	Russia, Amur Province	Paleocene	5	2	Elliptical	Cuneate	?	15	14–17 (**25**)
Haemanthophyllum sp. 2	Northern Ireland, County Antrim	Paleocene–Eocene boundary	?	2.2–2.8	Oblong	?	?	13 (**17**)	6–8
Haemanthophyllum nordenskioldii (Heer) Boulter et Kvaček	Norway, Spitsbergen	Early Paleocene/ Eocene	7–20	4–10	Elliptical to ovate	Cuneate to rounded	Rounded to attenuate	15–21	7–9 (**14**)
Haemanthophyllum sp. 3	United States, North Dakota, South Dakota	Paleocene	~30	~15	Broadly elliptical	?	Acuminate	25	9–12
Haemanthophyllum sp. 4	United States, Alaska	Paleocene	~11	~5	Ovate	Rounded to cuneate	Rounded	17–25	?
Haemanthophyllum sp. 5	Canada, Saskatchewan	Early Paleocene	~12	~7	?	?	Acuminate	27	15–17
Haemanthophyllum cordatum Golovneva	Russia, Koryak Highlands	Late Cretaceous–Early Paleocene	4–18	3–14	Ovate	Cordate	Rounded	(**13**)17–25	13–18 (**7–25**)
Cardston fossil	Canada, Alberta	Late Cretaceous	5–12	3.5–8.5	Ovate	Deeply cordate	Convex to rounded	23–27	10–40

Note. NLV = number of longitudinal veins (1° veins; does not include the fimbrial [marginal] vein); NCV = number of cross veins (2° veins) per centimeter; boldface = difference in observed number of veins; table modified from Golovneva (1997).

[a] Estimate of leaf width.
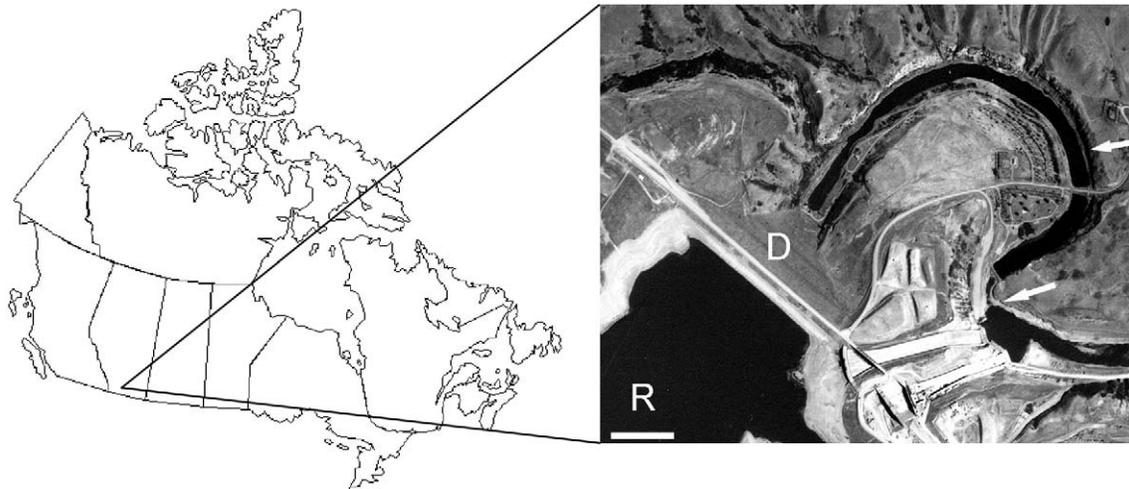
Fig. 1 Aerial photo of collecting locality in southern Alberta, Canada. Photo shows St. Mary Reservoir (*R*), associated dam (*D*), and both spillways. Locations of two fossil sites along banks of St. Mary River (arrows). Scale bar = 300 m.

Outcrops are part of the St. Mary River Formation, Upper Cretaceous, and are Late Campanian–Early Maastrichtian in age (Nadon 1988; Hamblin 1998; A. R. Sweet, personal communication, 2003).

Fossils come from alternating layers of siltstones and fine-grained sandstones that were deposited on the floodplains or the abandoned channels of an anastomosing river system (Nadon 1988, 1994). Most plants were preserved by rapid sedimentation in oxbow lakes or ponds. The best-preserved leaves are found in the siltstones. Specimens were prepared by degagement, photographed using a MicroLumina digital scanning camera (Leaf Systems), and processed using Adobe Photoshop 6.0.

All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA) and carry specimen numbers S50,939; S50,940; S50,947; S50,955–S50,958; S50,988; S50,989; S52,263–S52,283; S52,292–S52,295; S55,129–S55,135; S55,137–S55,150; S55,154.

Leaves of extant monocots from a large number of families (many previously suggested to have affinities to *Haemantho-phyllum* Golovneva 1997) were examined in the herbarium of the Missouri Botanical Garden; the Royal Botanic Gardens, Kew; the Munich Botanical Gardens; the University of Alberta Herbarium; and the published literature (Tomlinson 1982; van Bruggen 1990; Haynes and Holm-Nielsen 1992; Kassel-mann 1995, 2003; Cook 1996a, 1996b; Mayo et al. 1997; Kubitzki 1998) for similarities in morphology and growth habit to the fossils described here. Those of Alismataceae, Amaryllidaceae, Aponogetonaceae, Hydrocharitaceae, Lim-nocharitaceae, Potamogetonaceae, and Stemonaceae that showed the closest similarities were examined during this study from fresh and herbarium specimens from the Munich Botanical Gardens, Herbarium of the Northern Territory, Dar-win, Australia (DNA), and University of Alberta Vascular Plant Herbarium (ALTA) (table 2). Illustrations that appear in this article are only those leaves that showed the closest simi-larities to the fossils described here; however, additional taxa

appear in table 2. Photographs were taken using both trans-mitted and reflected light (figs. 5a–5h, 6a–6h).

Systematics

Order—Alismatales Lindley

Family—Limnocharitaceae Takhtajan

Genus—Cardstonia *Riley et Stockey gen. nov.*

Generic diagnosis. Leaves simple, ovate to elliptic, mar-gin entire; apex convex to rounded; base cordate. Venation campylodromous, primary veins originating at or near base, running in strongly recurved arches that converge apically, merging at or near apex; apical pore present. Prominent fim-brial vein present. Secondary veins diverging at low angles near midrib and higher angles near margin; alternating major and minor secondary veins, with ABAB pattern, occasionally anastomose and dichotomize. Tertiary (transverse) veins few, with straight to slightly curved courses, forming moderately developed (irregular shape, variable-sized) areolae.

Species. Cardstonia tolmanii Riley et Stockey sp. nov.

Holotype. UAPC-ALTA S55138 (fig. 2a).

Paratypes. UAPC-ALTA S50947, S52263, S52279, S52268, S52266, S52272, S50989.

Specific diagnosis. Leaves simple, ovate to elliptic, 5–12 cm long, 3.5–8.5 cm wide; l : w ratio 1.4 : 1; margin entire; apex convex to rounded; base cordate. Petiole 3–4 mm wide, at least 2 cm long, petiolar attachment marginal. Venation campylodromous, primary veins 23–27, with 3–5 medial veins originating at or near base; outer primaries running in strongly recurved arches that converge apically, merging at or near apex; apical pore present. Prominent fimbrial vein present. Secondary veins diverging at angles 45°–60° near midvein and 90° near margin; alternating major and minor secondary veins, with variable ABAB pattern, occasionally anastomose and dichotomize. Tertiary (transverse) veins few,

Table 2

Comparison of Morphological Characters of *Cardstonia tolmanii* with Selected Extant Taxa

Taxon	Family	Blade	Base	Apex	1° veins	1° veins merge w/fimbrial vein	1° veins merge w/ other 1° veins	2° veins per cm	Center	Margin	Major and minor 2° veins	2° veins anastomose	2° veins dichotomize	3° veins present
Cardstonia tolmanii Riley et Stockey		Ovate to elliptic	Cordate	Convex to rounded	23–27	N	Y	10–40	45–60	90	Y	Y	Y	Y
Alisma subcordatum Raf.	Alismataceae[a]	Obovate to elliptic	Decurrent	Convex	9	Y	N	5–12	35–45	70–90	N	N	Y	Y
Caldesia Parl. sp.	Alismataceae[a]	Ovate	Cordate	Acuminate	13–15	Y	N	30	60	90	Y	Y	Y	N
Echinodorus glaucus Rataj	Alismataceae[a]	Ovate to oblong	Cordate	Convex to rounded	11–12	Y	N	6–10	70–80	90	Y	Y	Y	Y[b]
Echinodorus grandiflorus (Chamisso et Schlechtendal) Micheli	Alismataceae[a]	Ovate	Cordate	Convex	15	Y	N	8–11	60	90	Y	Y	Y	Y[b]
Echinodorus subalatus (Mart.) Griseb.	Alismataceae[a]	Ovate	Convex	Straight to convex	9	Y	N	8–9	50–55	50–55	Y	Y	Y	Y[b]
Aponogeton madagascariensis L. f.	Aponogetonaceae[a]	Oblong	Decurrent	Emarginate	13	N	Y	5–6	80–90	80–90	N	N	N	N
Ottelia ulvifolia (Planch.) Walp.	Hydrocharitaceae[a]	Oblong	Cuneate	Straight	7–19	Y	N	3–4	60–90	60–90	Y	Y[c]	Y[c]	Y[b]
Butomopsis latifolia (D. Don) Kunth	Limnocharitaceae[a]	Elliptical	Cuneate	Straight to acuminate	7–9	N	Y	10–12	40–50	80–85	Y	Y	Y	Y
Hydrocleys martii Seubert	Limnocharitaceae[a]	Elliptical	Cordate	Rounded	11	N	Y[c]	6–20	70	90	Y	Y	Y	Y
Limnocharis flava (L.) Buchenau	Limnocharitaceae[a]	Elliptical	Cordate	Rounded	11–13	N	Y	11–13	60–80	90	Y	Y	Y	Y
Limnocharis laforestii Duchessaing	Limnocharitaceae[a]	Oblong	Cuneate	Acuminate	11–13	N	Y	8–11	65–75	75–90	Y	Y	Y	Y[b]
Potamogeton lucens L.	Potamogetonaceae[a]	Elliptic	Decurrent	Acuminate to convex	9	N	Y	6–10	40–60	60–80	N	Y	Y	Y
Haemanthus katherinae Baker	Amaryllidaceae[d]	Oblong	Cuneate	Acuminate	21	N	Y	11–23	60	80	Y[c]	Y	Y	Y[c]
Stemona tuberosa Lour.	Stemonaceae[e]	Ovate	Cordate	Acuminate	11	N[f]	N	28–30	90	90	Y	Y	Y	N

Note.   1° veins = number of primary veins in total (not including fimbrial); 2° veins per cm = number of secondary veins (both major and minor) per centimeter.
[a] Order Alismatales (APG 1998).
[b] Fourth-order venation.
[c] Rare occurrence.
[d] Order Asparagales (APG 1998).
[e] Order Pandanales (APG 1998).
[f] No fimbrial vein present.

with straight to slightly curved courses, forming moderately developed (irregular shape, variable-sized) areolae.

Etymology. The genus is named after the nearby town of Cardston, Alberta. The specific epithet is proposed in honor of Shayne Tolman of Cardston, Alberta, who brought the locality to our attention and spent many hours working with us in the field.

Locality. The locality is 26 km NE of the town of Cardston, Alberta (T5 R254 S12 SE 1/4 W4M; 49°22′10″N, 113°06′10″W; UTM Grid 12: 5470600N, 347300E).

Stratigraphic occurrence. St. Mary River Formation.

Age. Late Campanian–Early Maastrichtian, Upper Cretaceous.

Observations

Of the 50 specimens of this leaf type available, five are complete or nearly complete, and Morphotype Quality Index = 2 (Leaf Architecture Working Group 1999). Leaves are simple and ovate to elliptic with an entire margin (figs. 2a–2c). Several leaves have attached petioles that are up to 2 cm long (dictated by the size of the collected block). Petioles show five to seven longitudinal vascular bundles that lack transverse septa (fig. 2d). Petiolar attachment is basal, i.e., "marginal" (Leaf Architecture Working Group 1999) and the petioles are always bent down sharply into the siltstone matrix (figs. 2a–2d, 3e). The leaves were probably emergent and likely had long petioles with blades borne at right angles, or nearly so, to the petiole. Leaf blades are 5–12 cm long and 3.5–8.5 cm wide with a length/width ratio of 1.4:1 (table 2). Leaf apices are convex to rounded and the bases are deeply cordate (fig. 2a–2d; fig. 3a, 3b).

Venation is campylodromous, with 23–27 primary veins (fig. 2a, 2b). Five to seven primary veins enter the base of the leaf, the outermost primaries branching to give rise to the most basal primary veins (figs. 2d, 3e). The three medial primary veins are more or less parallel to one another for the entire length of the leaf (fig. 2a, 2b; fig. 3c). The outermost primary vein becomes the fimbrial (marginal) vein that dichotomizes several times in the cordate base and gives rise to additional primaries (fig. 2d; fig. 3d, 3e). The additional veins anastomose just beneath the apex of the leaf (figs. 2a, 3b). All of the remaining primary veins converge around an apical pore (fig. 3b).

Secondary veins ("cross" veins of Golovneva 1997) diverge from the closely spaced medial veins at angles of 40°–45° in most of the leaf blade to 90° near the leaf base (fig. 3c, 3e). Toward the leaf margin, secondary veins typically arise at angles of 90° or nearly so. There are from 10 to 40 of these secondary veins per cm, but 30–35 are common in most of the lamina. Their density is greatest near the leaf margin (fig. 2d; fig. 3c, 3d); there are fewer secondary veins near the midrib. In some of the best-preserved leaves there appear to be alternating major and minor (thick and thin) secondary veins (fig. 3f–3h) in an ABAB pattern (Hickey and Peterson 1978). This pattern is not always regular, however, and occasionally two thin veins occur between two thick veins (fig. 3f), ABABBAB. Or thin veins may be absent, ABAAAB (fig. 3d). Secondary veins occasionally dichotomize (fig. 3d, 3f) or anastomose (fig. 3f–3h).

Very few of what might be termed tertiary veins (using the terminology of the Leaf Architecture Working Group 1999 or transverse veins of Hickey and Peterson 1978) are seen in the fossil leaves. These are distinctly thinner veins that occur at right angles or nearly so to the secondary veins (fig. 3f, 3g). These veins typically run a straight or slightly curved course and terminate in the adjacent secondary vein.

In some of the best-preserved leaves there are polygonal patterns preserved on the surface of the fossils that have split between the two leaf surfaces (fig. 3i). While these polygonal patterns may represent tertiary venation, when examined closely, these hexagonal patterns overlap with the secondary veins and appear to be superimposed on them (fig. 3i). In some parts of the leaf they are preserved in sediment between the two leaf surfaces. It is probable that these patterns are the outlines of underlying aerenchyma due to their shape and position and not veins. The thickness of the dark material that outlines the polygonal pattern is about 50 μm in diameter, about the size of parenchyma cells.

Russian Fossil *Haemanthophyllum* Leaves

Haemanthophyllum kamtschaticum *Budantsev*

Budantsev first described the genus *Haemanthophyllum* in 1983 from the Paleocene–Eocene of western Kamchatka. The holotype of *Haemanthophyllum kamtschaticum* Budantsev (generitype) was reexamined here (fig. 4a, 4b; table 1). In addition to the type specimen, two other specimens were examined from the same locality (fig. 4c–4e). The specimen in figure 4c is illustrated by Budantsev (1983) in the original article. The other specimen (fig. 4d, 4e) is from the same locality but is not illustrated by Budantsev (1983). In addition to the specimens illustrated here, two other specimens (Budantsev 1983, pl. 63, figs. 1, 4) were not available for examination. In table 1 we show two rows of data for *H. kamtschaticum*; the first is from the original holotype, the second is Budantsev's (1983) concept of the species as shown in Golovneva's table (1997). This is necessary because there is only one holotype, but workers have often used a species concept derived from several fragments that, in our opinion, probably do not represent the same taxon.

The holotype of *H. kamtschaticum* is a leaf fragment with entire margin, cordate base, fimbrial vein, up to nine recurved primary veins, and 24–35 secondary veins per centimeter (table 1; fig. 4a). Note that the number of secondary veins per centimeter counted by us is markedly higher than the nine to 13 originally reported by Budantsev (1983) in the generic description. Secondary veins remain unbranched or dichotomize and/or anastomose between adjacent primary veins (fig. 4b). There are certain areas on the holotype where secondary veins show several closely spaced anastomosing dichotomies between the adjacent primaries (fig. 4b). Three closely spaced medial veins are not visible (fig. 4a). The second specimen Budantsev illustrated has a long, thickened petiole (>7 cm in length) with multiple veins that continue as a thickened costa into the blade (fig. 4c). The primary veins branch into the lamina from the midvein, with the most basal veins recurving into a cordate base that is slightly concave-convex (fig. 4c). Three closely spaced medial veins are not visible (fig. 4c). The third leaf fragment studied here (not illustrated by Budantsev) shows a fimbrial vein, dense
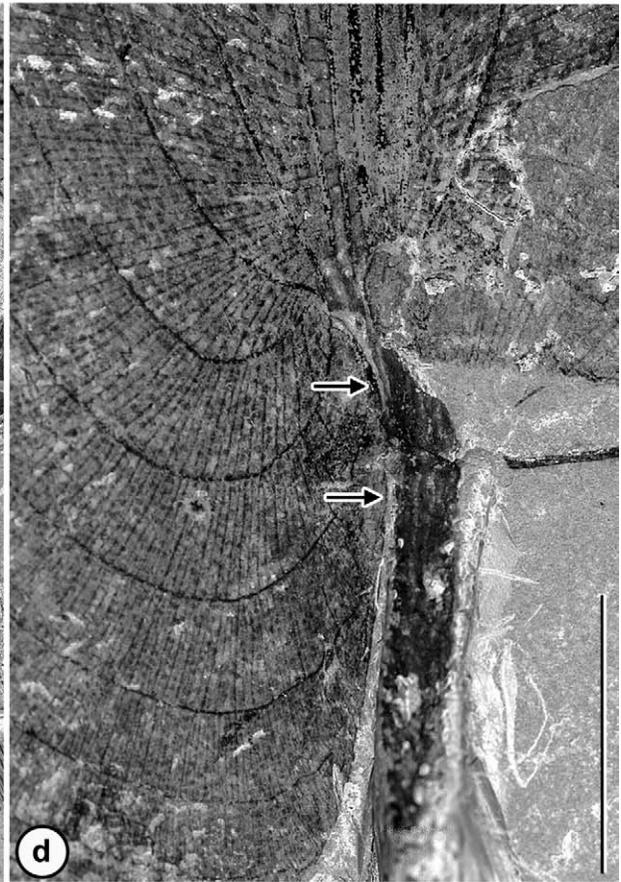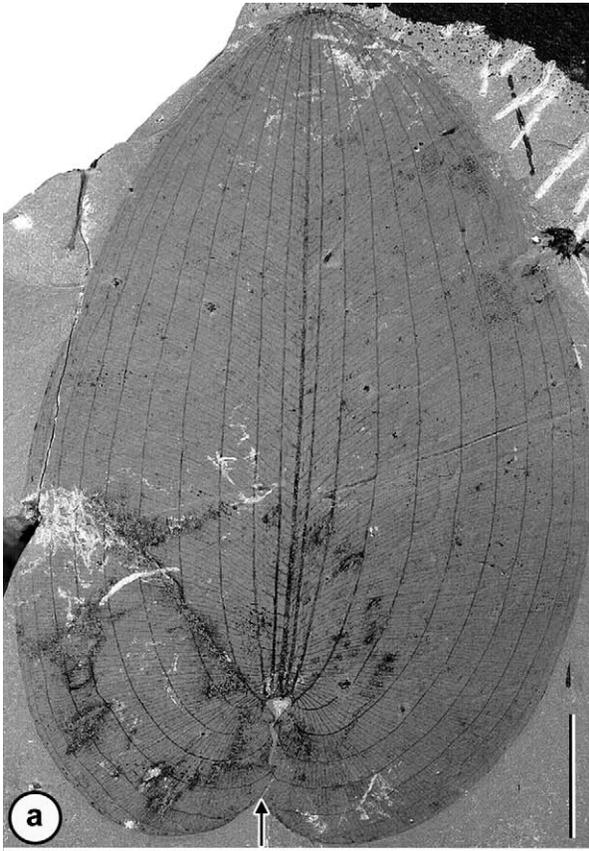
secondary veins (fig. 4*d*), and possible polygonal aerenchyma between secondary veins (fig. 4*e*).

Haemanthophyllum cordatum *Golovneva*

The holotype of *Haemanthophyllum cordatum* Golovneva (1987) from the late Maastrichtian-Danian sediments (Rarytkin Series) of the Koryak Highlands in Russia was reexamined but was difficult to study because the specimen is preserved as a black impression on a black matrix (fig. 4*f*–4*h*). The leaf has an entire margin, convex to rounded apex, cordate base, and a "triple midvein" (three closely spaced medial veins). The number of primary veins appears to be 25, with a fimbrial vein visible in some marginal areas. The margin was not preserved or was slightly degaged away in parts of the specimen, making it difficult to trace the path of the outermost veins. Golovneva (1987, pl. I, 1) originally illustrated the outermost primary veins merging with the fimbrial vein; however, we cannot observe the actual leaf margin with certainty in many areas of the specimen. It appears that several of the primary veins do merge together at the apex of the leaf. Golovneva reports 18 secondary veins per centimeter in this species; we count seven to 25 secondaries.

Extant Monocot Leaves

Leaves of *Alisma subcordata* Raf. (Alismataceae) are obovate to elliptical with decurrent bases and convex to acuminate apices (table 2). Some leaves show an emarginate apex with an acuminate leaf tip. There are nine primary veins, the outer two of which merge with the fimbrial vein midway up the leaf. The primary veins do not merge beneath the leaf apex but extend into the tip itself. There are five to 12 secondary veins per centimeter that do not anastomose but sometimes dichotomize (table 2). Secondary veins, all of more or less equal thickness, diverge at angles of 35°–45° near the midvein and 70°–90° near the leaf margin (table 2). Tertiary veins are present and occasionally dichotomize, and they have a wavy or sinuous course in the lamina, often arising at right angles. Golovneva (1994) illustrates similar secondary venation in *Alisma plantago-aquatica* L. These veins form the irregular, rectangular areoles.

Caldesia Parl. (Alismataceae) leaves (ALTA 49675) were examined from a plant growing at the Technische Hochschule Zürich (fig. 5*c*, 5*d*). They are ovate with cordate bases and acuminate apices, with 13–15 primary veins (fig. 5*c*; table 2). (Note: *Caldesia parnassifolia* [Bassi ex L.] Parl. [MO 2326418] examined at the Missouri Botanical Garden Her-

barium had 17 primary veins.) All of the primary veins merge with the fimbrial vein (fig. 5*c*, arrows) except the medial vein, which enters the leaf tip. There are 30 secondary veins per centimeter that arise at angles of 60°–70° near the midvein and 90° near the leaf margin. There are major and minor secondary veins that anastomose and dichotomize (fig. 5*d*). Tertiary veins appear to be absent (fig. 5*d*).

We examined eight different species of *Echinodorus* Rich. ex Engelm. (Alismataceae). Of these, *Echinodorus inpai* Rataj, *Echinodorus osiris* Rataj, *Echinodorus longiscapus* Arech., *Echinodorus decumbens* Kasselmann, and *Echinodorus uruguayensis* Arech. were not put in table 2 as they greatly differ from the fossil leaves in being narrow, oblong leaves with very few primary veins. *Echinodorus glaucus* Rataj (Alismataceae) leaves are ovate to oblong with cordate bases and convex to rounded apices (fig. 5*a*; table 2). There are 11–13 primary veins, the outermost of which merge with the fimbrial vein (fig. 5*a*, arrows), while the inner three veins enter the leaf tip. There are six to 10 secondary veins per centimeter diverging at 70°–80° near the center of the leaf and 80°–90° near the margin (table 2). Secondary veins have a curving course, and some appear straight or slightly sinusoidal. Major and minor (thick and thin) secondary veins occur, show a very irregular course, and can anastomose and dichotomize (table 2). Tertiary veins are present, and tertiary and possible quaternary veins form irregular, polygonal areolae.

Leaves of *Echinodorus grandiflorus* (Chamisso et Schlechtendal) Micheli (Alismataceae) are ovate with cordate bases and convex apices (table 2). They have 15–17 primary veins, the outermost of which merge with the fimbrial vein, whereas the inner three extend into the leaf apex (table 2). The most basal primary veins are very weak in this taxon but run the same course as the stronger primary veins. There are eight to 11 secondary veins per centimeter diverging at angles of 60° near the midvein and 80°–90° near the leaf margin (table 2). Secondary veins have a slightly curving course, and some are straight or sinusoidal. Major (fig. 5*b*, at *x*) and minor (fig. 5*b*, at *o*) secondary veins are present. The minor secondary veins often show a sinuous course, while the stronger secondary veins have a straighter course (fig. 5*b*). Tertiary veins usually arise perpendicular to secondary veins, often dichotomize, and produce irregular areoles (fig. 5*b*). Quaternary veins do occur but are rare (table 2).

Echinodorus subalatus (Mart.) Griseb. (Alismataceae) leaves are ovate with convex bases and straight to slightly convex apices (table 2). There are nine primary veins, the outer three on each side merge with the margin. There are eight or nine secondary veins per centimeter, which diverge at 50°–55°

Fig. 2 *Cardstonia tolmanii* Riley et Stockey leaves. Scale bar = 0.5 cm. *a*, Holotype showing entire margin, rounded apex, cordate base, and three closely spaced medial veins. All primary veins appear to diminish in thickness toward apex. Note primary veins recurved in base and continuing to apex without merging with marginal vein. Overlapping lobes of the lamina (arrow) are probably an artifact of deposition. Holotype S55138A. *b*, Large lamina showing entire margin, cordate base with single lobe, and three closely spaced medial veins. Note steep angle of divergence of secondary veins near midvein and marginal vein dichotomizing in base (arrow) giving rise to additional primary veins; possible herbivory (*). S52263A. *c*, Large lamina showing petiole/lamina interface descending into matrix between cordate lobes. Note basally thickened primary veins on each side of three closely spaced medial veins; arrow indicates dichotomy of primary medial vein. S50947A. *d*, Cordate base showing petiole descending into matrix at 30°, recurved primary veins radiating near petiole/lamina interface, and large number of secondary veins per centimeter. Note marginal vein dichotomizing and giving rise to primary veins (arrows). S52279A.
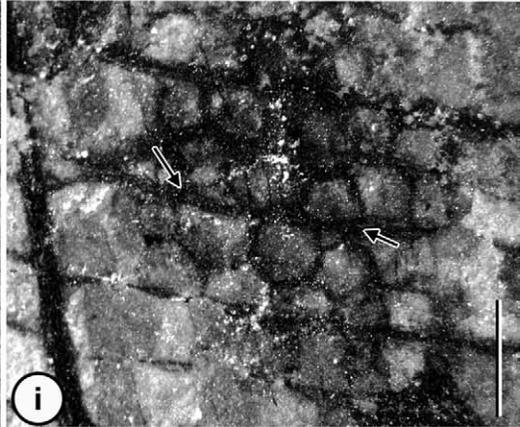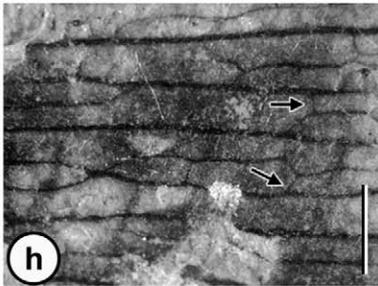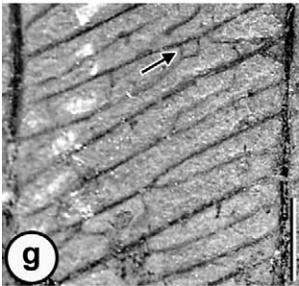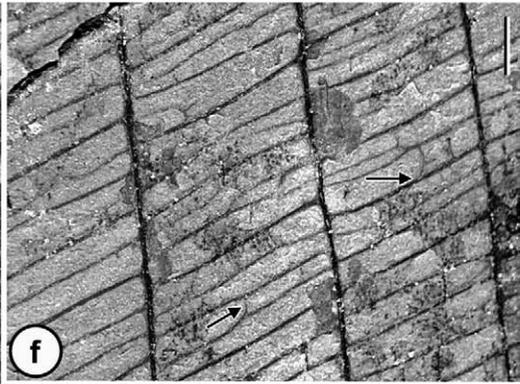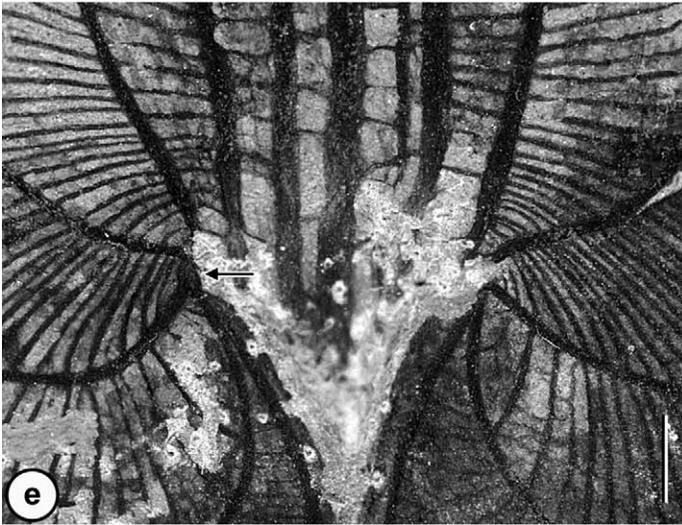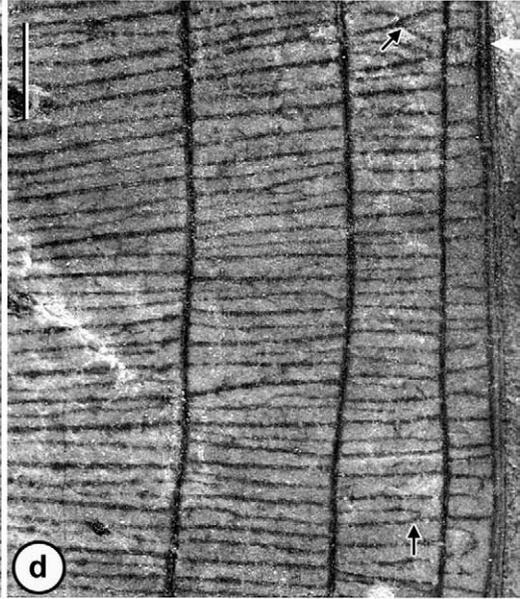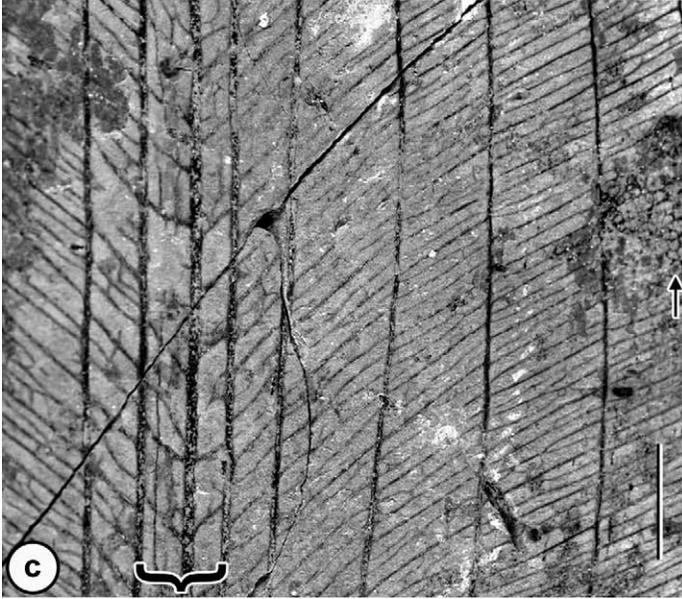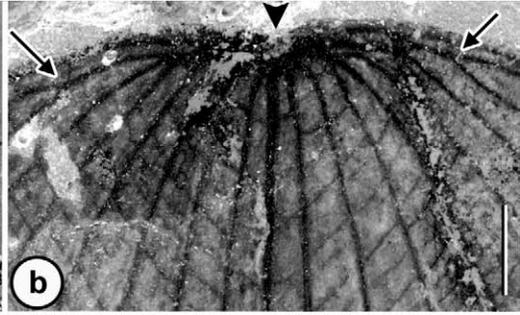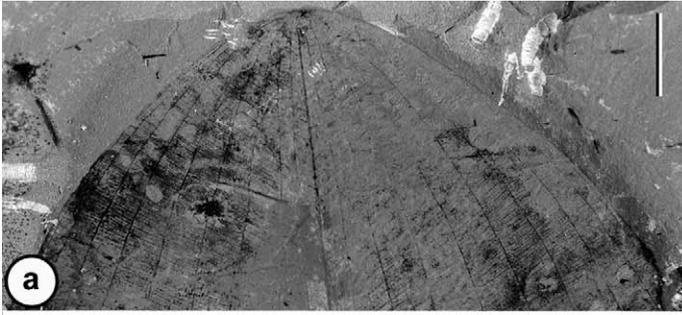
near the center and margins of the leaf. These secondaries are often not straight but run a sinusoidal course in the leaf lamina. Major and minor secondary veins are present, dichotomize frequently, and anastomose occasionally. Minor secondary veins occur irregularly and frequently curve apically, terminating in the above major secondary before reaching the adjacent primary. Tertiary veins are perpendicular, or nearly so, to the secondaries. They have a straight to sinuous course and dichotomize toward the midvein. Fourth-order veins are present (table 2) and form irregular, rectangular to rarely triangular areolae.

Leaves of *Aponogeton madagascariensis* L. f. (Aponogetonaceae) are oblong to slightly obovate with asymmetrical decurrent bases and emarginate apices (table 2). The leaves examined here were submerged and have a fenestrate lamina. There are 13 primary veins, all of which merge with other primary veins from the outside in, but not with the marginal vein. This anastomosing sequence starts with the outermost primaries merging with adjacent primaries just below the apex continuing admedially. There are three closely spaced medial veins that run the entire length of the lamina. The number of secondary veins per centimeter is five or six (table 2). Secondary veins are of uniform thickness, do not anastomose or dichotomize, and diverge at 80°–90° near the midvein and the margins. There are no tertiary veins in this species.

Ottelia ulvifolia (Planch.) Walp. (Hydrocharitaceae) have leaves that are oblong, somewhat linear, with cuneate bases and straight apices (table 2). All the leaves of this species that we examined were growing submerged. There are seven to 19 primary veins, the outermost of which merge with the fimbrial vein. The inner primary veins continue to the apex and join in the leaf tip. There are only three or four secondary veins per centimeter (table 2). The angle of divergence of secondary veins is 60°–90° in the center of the leaf and 60°–90° near leaf margins. There are major and minor secondary veins; however, secondary veins rarely anastomose or dichotomize. Third- and possible fourth-order veins make up rectangular to elongate polygonal areoles, especially near the midvein. Areoles are larger near the midvein and decrease in size toward the leaf margin.

Leaves of *Butomopsis latifolia* (D. Don) Kunth (Limnocharitaceae) are elliptical with cuneate bases and straight to acuminate apices (table 2; fig. 6e, 6g). There are seven to nine primary veins, the outermost of which merge with the adjacent primary vein near the leaf apex (fig. 6g). There are

10–12 secondary veins per centimeter that diverge at angles of 40°–50° near the midvein and 80°–85° near the margin (table 2; fig. 6f–6h). Major and minor secondary veins are present (fig. 6g). Major secondary veins run a fairly straight course, dichotomize occasionally, and anastomose rarely. Minor secondary veins appear irregularly between major secondary veins and run a weak sinusoidal course (fig. 6h); these commonly dichotomize and anastomose, with branches occasionally curving toward the leaf apex and terminating in the adjacent secondary. Tertiary veins form well-developed four to many-sided polygonal areoles (fig. 6f, 6h). Areoles are vertically elongate near the center of the leaf (fig. 6f) and horizontally elongate near the leaf margins (fig. 6h). *Butomopsis* leaves, like those of *Limnocharis* (below) are fleshy, especially near the center.

Hydrocleys martii Seubert (Limnocharitaceae) leaves are elliptic with cordate bases and rounded apices (table 2; fig. 5e). There are 11 primary veins that continue to the apex but do not merge with adjacent primaries or the fimbrial vein (fig. 5e; table 2). Leaves show three closely spaced medial veins (fig. 5f). The two adjacent primaries thin toward the leaf apex and do not reach the apex. One leaf showed two primaries anastomosing beneath the apex (fig. 5e, arrow). The primary veins merge at the apex, forming an apical ring (fig. 5e). There are six to 20 secondary veins per centimeter (far fewer secondary veins near the midrib) that arise at angles of 70° near the midvein and 90° at the margin (table 2). Major and minor secondary veins are present (table 2), and both are more or less straight. Tertiary veins are mostly perpendicular to the secondary veins and form regular, polygonal areoles that are elongated vertically near the midrib (fig. 5f) and horizontally near the leaf margins. There are no quaternary veins.

Leaves of *Limnocharis flava* (L.) Buchenau (Limnocharitaceae) are elliptical with cordate bases and rounded apices (fig. 5g, 5h). There are 11–13 primary veins, 10–12 of which merge with adjacent primaries near the apex (normally within 1 mm of the apex). The midvein is the only primary vein that does not merge with other primaries. The primary veins do not merge with the fimbrial vein. There are 11–13 secondary veins per centimeter that diverge at angles of 60°–80° near the midline and 90° near the margin. Major and minor secondary veins are present and consistently alternate with each other in the ABAB pattern (Hickey and Peterson 1978). The major secondary veins run a straight course and occasionally dichotomize but do not appear to anastomose

Fig. 3 *Cardstonia tolmanii* Riley et Stockey leaves. *a*, Lamina showing convex to rounded leaf apex. Scale bar = 5 mm. S52268A. *b*, Apex showing primary veins converging at what appears to be dark apical gland. Note primary veins occasionally anastomosing with adjacent primary near apex (arrows), but absence of primary veins merging with marginal vein. Scale bar = 2 mm. S52266A. *c*, Middle laminar area showing three closely spaced medial veins (bracket), angle of divergence of secondary veins, and finely preserved internal tissue (arrow), possibly aerenchyma. Note increase in number of secondary veins per centimeter toward margin. Scale bar = 1 mm. S52263A. *d*, Leaf margin showing secondary veins that anastomose and dichotomize (arrows), that appear to alternate irregularly between major and minor veins, and that run perpendicular to the primary veins. Note marginal vein. Scale bar = 1 mm. S52272. *e*, Base of leaf (fig. 2c) showing three closely spaced medial veins and apparent palmate radiation of primary veins (arrow). Scale bar = 1 mm. S50947A. *f*, Venation from *c* showing alternation between major and minor secondary veins. Major veins can be either opposite or alternate between primaries. Note irregular branching pattern of tertiary veins (arrows). Scale bar = 1 mm. S52263A. *g*, Venation showing anastomosing and dichotomizing of major and minor veins. Note rare square-shaped areole (arrow). Scale bar = 1 mm. S52263A. *h*, Venation showing extensive anastomosing and dichotomizing of primarily minor veins. Note tertiary veins crossing between adjacent secondary veins (arrows). Scale bar = 1 mm. S50989. *i*, Possible aerenchyma. Note several lacunae appear to overlap secondary veins (arrows). Scale bar = 0.5 mm. S52263A.
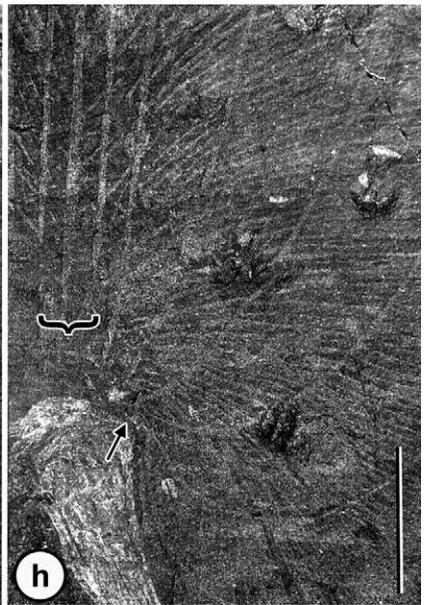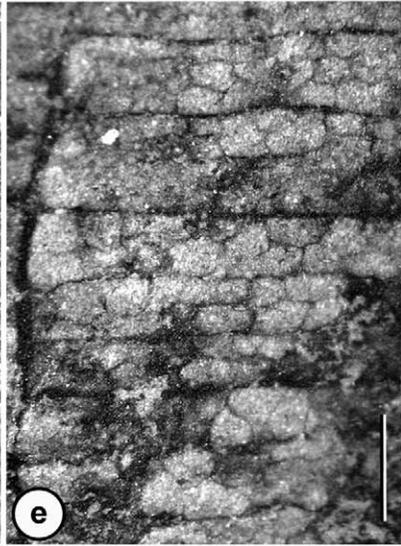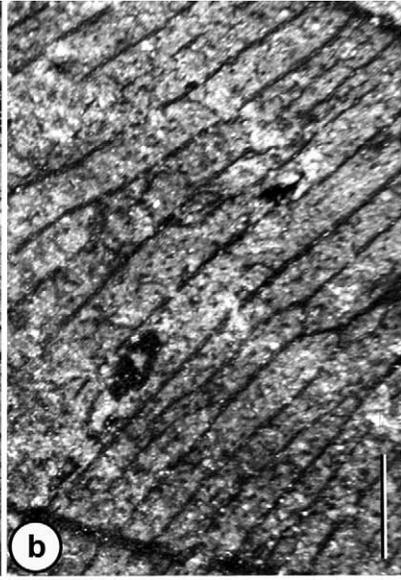
(fig. 5*h*). The minor secondary veins regularly dichotomize and anastomose, running a weak sinusoidal course (fig. 5*h*). Tertiary veins are present and frequently dichotomize and anastomose (fig. 5*h*), forming a network of polygonal areoles that appear to be concentrated on the adaxial side of the leaf lamina. Near the center of the leaf on the abaxial surface is another series of tertiary veins forming regular, polygonal, reticulate areolae. In herbarium specimens it is necessary to use both transmitted and reflected light of various intensities to see these vein patterns clearly. Leaves of *L. flava* are fleshy and full of aerenchyma, especially near the center.

Limnocharis laforestii Duchessaing (Limnocharitaceae) leaves are oblong with cuneate bases and acuminate apices (fig. 6*a*, 6*c*; table 2). There are 11–13 primary veins, with the three adjacent primary veins on each side of the three medial veins merging near the apex (fig. 6*a*–6*c*). The primary veins do not merge with the margin. The two medial veins that run adjacent to the midvein are noticeably thinner (fig. 6*b*) and do not reach the apex (fig. 6*c*). There are eight to 11 secondary veins per centimeter that diverge at angles of 65°–75° near the midvein (fig. 6*c*) and 75°–90° near the margin (fig. 6*d*; table 2). Major and minor secondary veins regularly alternate and run straight to slightly sinusoidal courses while occasionally dichotomizing but rarely anastomosing (fig. 6*c*). Tertiary veins appear random reticulate; i.e., they anastomose with other tertiary or secondary veins at random angles (Leaf Architecture Working Group 1999), forming well-developed polygonal areolae (fig. 6*b*, 6*d*). As in *L. flava,* there is a second set of overlapping regular polygonal reticulate veins in the center of the leaf near the abaxial leaf surface (fig. 6*d*). These veins arise from the primary and secondary veins. Quaternary veins are present, forming freely ending veinlets that appear unbranched and one-branched (fig. 6*d*).

Leaves of *Potamogeton lucens* L. (Potamogetonaceae) are elliptical with decurrent bases and acuminate to convex apices (table 1). There are nine primary veins that merge with adjacent primaries near the leaf apex. There is a single midvein, and the adjacent primaries are widely spaced from this medial vein. This species shows minute serrations at the leaf margin and a distinct fimbrial vein. Other species have been described with clearly serrate margins (e.g., *Potamogeton crispus* L.) or what appear to be entire margins with serrations that are not visible to the naked eye (e.g., *Potamogeton perfoliatus* L.) (Cook 1996*a*). Primary veins do not merge with the fimbrial vein (table 1). The number of secondary veins per centimeter is only six to 10, and the angles of divergence of the secondaries are 40°–60° near the midvein and 60°–80° near the leaf margin (table 1). There are no major and minor secondary veins. Secondary veins often anastomose and dichotomize, and distinct tertiary veins occur at right angles to the secondary veins. They often show a sinuous course in between secondary veins but always arise perpendicular to the adjacent secondary vein. Tertiary veins also rarely dichotomize.

Haemanthus katherinae Baker (Amaryllidaceae) leaves are generally oblong with cuneate bases and acuminate tips (table 1). There are 21 primary veins that do not merge with the fimbrial vein, and many of the primary veins merge near the leaf apex. There are 11–23 secondary veins per centimeter with an angle of divergence of 60° near the center increasing to 80° near the margin. Secondary veins often dichotomize and sometimes anastomose. There is a common occurrence of what could be termed "intersecondary veins" (Leaf Architecture Working Group 1999) that do not reach the adjacent primary or the margin. These are slightly thinner than the normal secondary veins, and they usually end blindly. *Haemanthus* leaves also do not show a regular alternation of thin and thick secondary veins (an ABAB pattern). Occasional slightly thinner veins continue between the adjacent primary veins, but these are rare. Regular tertiary veins occur rarely (table 1).

Stemona tuberosa Lour. (Stemonaceae) have ovate leaves with cordate bases and acuminate tips (table 1). There are 11 primary veins; the outer three on each side merge with the leaf margin. These primary veins continue along the margin and then end in the margin. The outer primaries do not merge with each other at the margin but disappear prior to reaching the leaf apex. There is a single medial primary vein, and the adjacent primaries are widely spaced from this medial vein. These four adjacent primaries continue to the apex of the leaf and enter the acuminate tip without merging. The number of secondary veins per centimeter is 28–30, and the angles of divergence of secondary veins are 90° both in the center of the leaf and near the leaf margin (table 1). There appear to be major and minor secondary veins in regular alternation between adjacent primaries. These secondary veins can dichotomize and anastomose. No tertiary veins were observed (table 1).

Discussion

Comparison with Fossil Leaves

An entire margin, parallel petiolar veins, and campylodromous primary venation (Leaf Architecture Working Group

Fig. 4   *Haemanthophyllum kamtschaticum* Budantsev (*a–e*) and *Haemanthophyllum cordatum* Golovneva (*f–h*) leaves. *a*, *H. kamtschaticum*, generitype, leaf fragment showing cordate base, recurved primary veins, dense secondary veins, and marginal vein (arrow). Scale bar = 0.5 cm. 960-1/2091 BIN RAS. *b*, *Haemanthophyllum kamtschaticum*, generitype, enlarged lamina from *a* showing secondary veins dichotomizing and anastomosing. Scale bar = 1 mm. 960-1/2091 BIN RAS. *c*, "*Haemanthophyllum kamtschaticum*" leaf fragment showing long thickened petiole, cordate base, and large laminar size. Scale bar = 3 cm. 960-1/2092 BIN RAS. *d*, *Haemanthophyllum kamtschaticum*, generitype, lamina from *a* enlarged to show secondary vein density and marginal vein. Scale bar = 2 mm. 960-2/2091 BIN RAS. *e*, *Haemanthophyllum* sp. (from type locality) lamina showing areolae. Scale bar = 1 mm. 960-1/3017 BIN RAS. *f*, *Haemanthophyllum cordatum*, holotype, lamina showing rounded apex and single lobe of cordate base. Scale bar = 2 cm. 967A/101 BIN RAS. *g*, *Haemanthophyllum cordatum* leaf apex from *f*. Scale bar = 0.5 cm. 967A/101 BIN RAS. *h*, *Haemanthophyllum cordatum* leaf base from *f* showing three closely spaced medial veins (bracket), recurved primary veins, and angle of divergence of secondary veins. Note radiating primary veins near petiole attachment (arrow). Scale bar = 0.5 cm. 967A/101 BIN RAS.
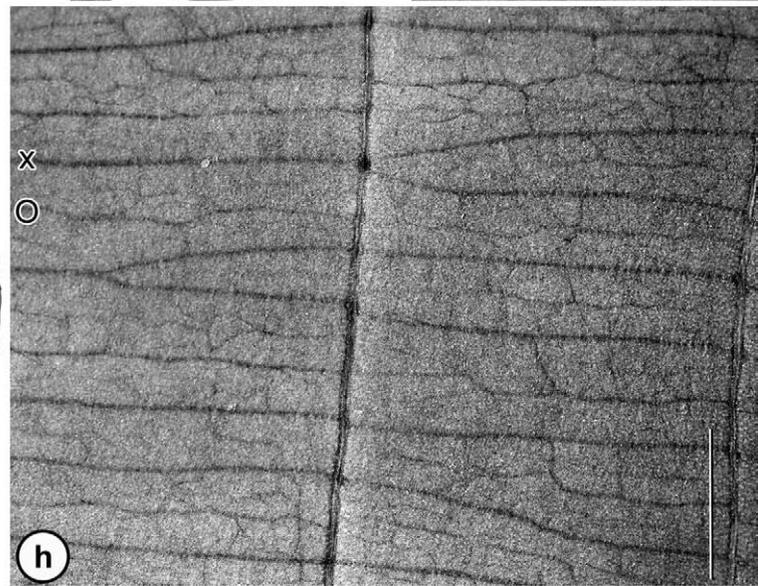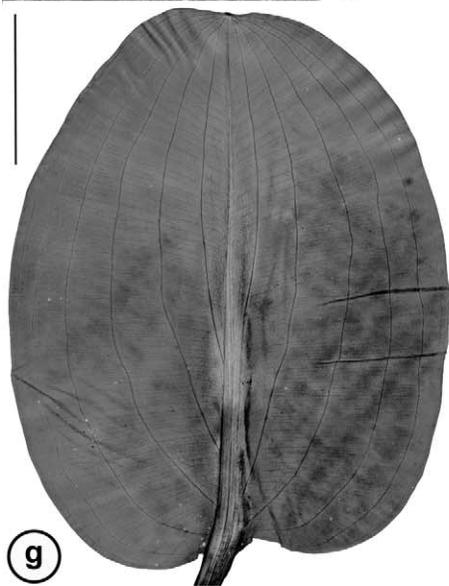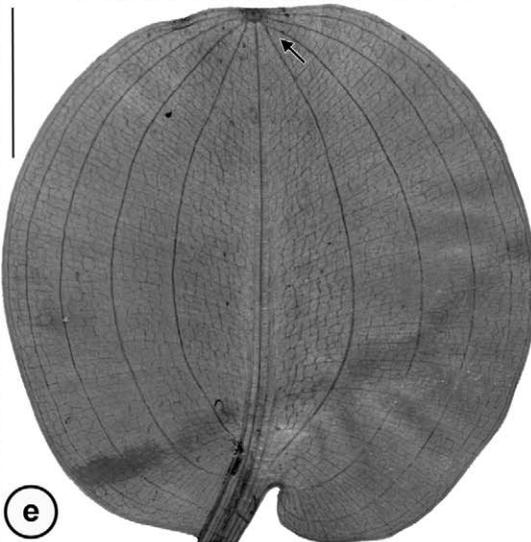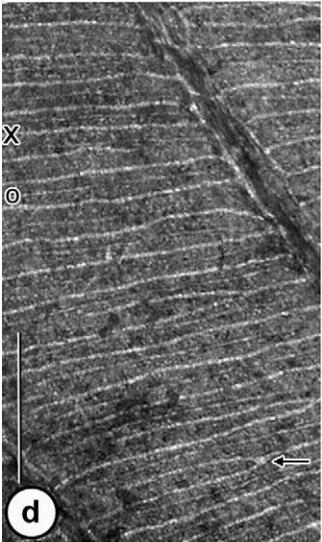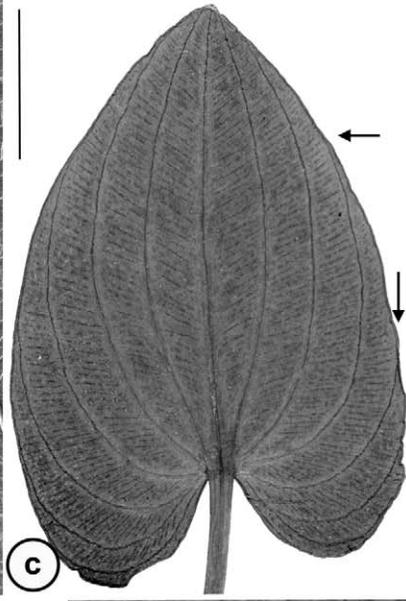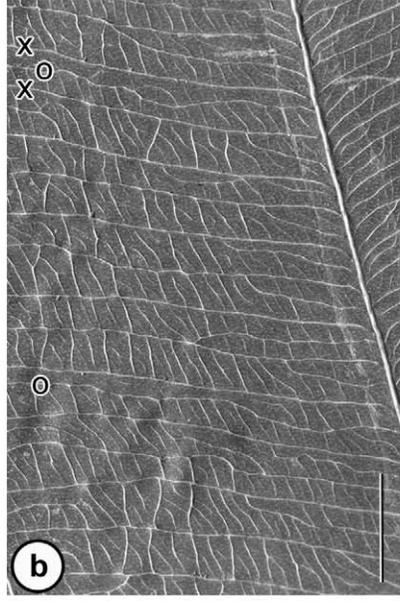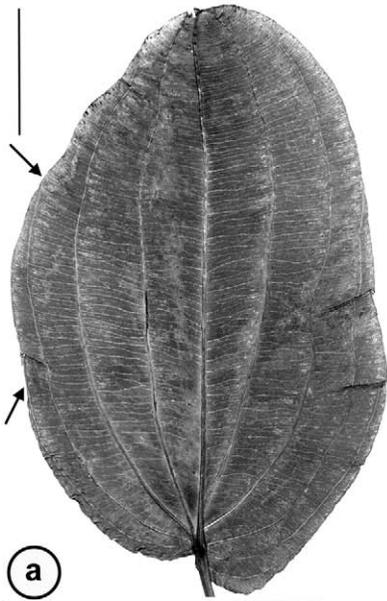
1999) of the fossil leaves from Cardston indicate that this plant is a monocotyledon. The ovate blade with a large number of primary veins originating at or near the leaf base and converging at or near the apex, dense secondary veins, and thin, higher-order veins forming polygonal areolae (Golovneva 1997) are similar to those in leaves described as *Haemanthophyllum* Budantsev (1983). Budantsev (1983) erected *Haemanthophyllum* based on 20 fossil leaves collected from several localities in Kamchatka, Russia. These localities range in age from Late Paleocene/Early Eocene (Anadyrka Formation) to Middle to Late Eocene (Tkaprorayam Formation). The specimens Budantsev illustrated, and the one that we studied that he did not illustrate, were incomplete fragments. From these fragments of apices, bases, and margins of different ages, Budantsev (1983) constructed the concept of the genus *Haemanthophyllum*. Subsequent authors placed other species of varying geologic ages and localities in this genus due to morphological similarities (table 1). This resulted in a diverse array of taxa being assigned to *Haemanthophyllum* based on this questionable association of leaf parts.

Five species of *Haemanthophyllum* are currently recognized by Golovneva (1997): *Haemanthophyllum kamtschaticum* Budantsev, *Haemanthophyllum zhilinii* (Pneva) Golovneva, *Haemanthophyllum nordenskioldii* (Heer) Boulter et Kvaček, *Haemanthophyllum cordatum* Golovneva, and *Haemanthophyllum* sp. from Ireland (table 1). The remaining species assigned to *Haemanthophyllum* resemble *H. kamtschaticum* (table 1, *Haemanthophyllum* sp. 3, 5) or *H. nordenskioldii* (table 1, *Haemanthophyllum* sp. 1, 4) (Golovneva 2000).

The holotype for *H. kamtschaticum* (the generitype) is a fragment of one lobe of a cordate base from the Anadyrka Formation of the Late Paleocene/Early Eocene (fig. 4*a*, 4*b*, 4*d*). The thickness, branching pattern, and density of the primary and secondary veins are similar to our leaves; however, without an attached apex, midrib, or petiole, it is difficult to compare *H. kamtschaticum* with our leaves morphologically. And as our study shows, widely disparate monocot families may show similar venation patterns if only portions of one leaf are examined. The second fragmentary base with a petiole from the same locality, assigned to *H. kamtschaticum* (Budantsev 1983), is also without an apex and most of the lamina (fig. 4*c*). The primary veins are barely visible, but they appear to be fewer in number, and the angle at which they recurve is shallower than in the holotype specimen. Although a drawing of the secondary veins of this specimen appears in

Golovneva (1997, fig. 2*a*), we were unable to observe the secondary veins in the actual specimen. Because of the state of preservation, it is not possible to determine whether the holotype and this second specimen belong to the same taxon.

The remaining leaf fragments illustrated by Budantsev (1983, pl. 63, figs. 1, 4) and Golovneva (1997, fig. 2*b*–2*d*) are from localities within the Tkaprovayam Formation that are younger (Middle to Late Eocene) than the previously discussed specimens from the Anadyrka Formation. These specimens are also unconnected leaf fragments of varying shape with a fimbrial vein and numerous primary and secondary veins (Budantsev 1983; Golovneva 1997). The fragmentary nature of the specimens, and the locality and age differences preclude the assignment of these specimens to *H. kamtschaticum*. It appears to us that there may be several types of monocot leaves present in these localities and better specimens are needed to assess their affinities.

Leaf fragments from three different localities (Ashutas Mountain, Zhayremsk Quarry, and Kinyak) of comparable ages (Late Oligocene to Early Miocene) from Kazakhstan have been suggested to represent a single species, *H. zhilinii* (Golovneva 1997). Previous workers have assigned fragmentary specimens from Ashutas Mountain to *Alisma macrophylla* Heer (Kryshtofovich et al. 1956) and *Aponogeton zhilinii* Pneva (1988). Zhilin (1974) described a small laminar fragment from Kinyak as *Aponogeton*, which Pneva sp. (1988) later included in *A. zhilinii*. All of the illustrated fossils show some similarities in primary and secondary venation and density to *Haemanthophyllum*, and certain specimens appear similar to *H. kamtschaticum* (Golovneva 1997, fig. 5*a*, 5*c*). However, the fragmentary nature of the material and lack of clear morphological characters (i.e., laminar characters, base and apex shape, and overall leaf size) leave their taxonomic affinities in doubt.

Golovneva, after reexamining Heer's specimens in Stockholm, suggests that leaf specimens from the early Paleocene Barentsburg Formation and the Eocene Skilvika Formation of Spitsbergen be assigned to *H. nordenskioldii* (Heer) Boulter et Kvaček (Golovneva 1997; our table 1). Heer (1868) originally assigned fragmentary specimens from the Barentsberg Formation (Heer 1868, pl. 30, figs. 1*b*, 5*b*, 6*a*, 7; Golovneva 1997, fig. 1*b*) and several fragmentary specimens from the Skilvika Formation (Heer 1876, pl. 27, figs. 1, 2, 3*a*) to *Potamogeton nordenskioldii* based on small laminae (relative to *Alisma macrophylla*) and convex (blunt) apices.

Fig. 5 Selected extant taxa of Alismatales. *a*, *Echinodorus glaucus* Rataj leaf showing round apex, cordate base, recurved primary veins in base, and secondary veins nearly perpendicular at center. Note outer primary veins merge with margin before reaching apex (arrows). Scale bar = 3 cm. *b*, *Echinodorus grandiflorus*, abaxial surface, lamina showing many linear secondary veins (*x*'s) and fewer irregular sinusoidal secondary veins (*o*'s). Note numerous linear and branched tertiary veins running perpendicular to and terminating in adjacent secondary veins. Scale bar = 5 mm. *c*, *Caldesia* sp., leaf showing convex apex, deeply cordate base, recurved primary veins. Note outer primary veins merging with marginal vein subapically (arrows). Scale bar = 1 cm. *d*, *Caldesia* sp., leaf showing major (*x*) and minor (*0*) secondary veins. Note dichotomizing of major secondary veins (arrows). Scale bar = 1 mm. *e*, *Hydrocleys martii* Seubert, leaf showing rounded apex, cordate base, and recurved primary veins terminating in an apical gland. Note adjacent primary veins anastomosing (arrow); primary veins do not merge with marginal vein. Scale bar = 5 mm. *f*, *Hydrocleys martii*, abaxial surface of leaf base showing three closely spaced medial veins and angle of divergence of secondary veins. Note numerous tertiary veins forming distinct areoles. Scale bar = 2 mm. *g*, *Limnocharis flava* (L.) Buchenau, abaxial surface of leaf showing rounded apex, cordate base, and recurved primary veins terminating in an apical gland. Note three closely spaced medial veins in base of leaf. Scale bar = 4 cm. *h*, *Limnocharis flava*, abaxial surface, lamina showing major (*x*) and minor (*o*) secondary veins branching and irregular branching of tertiary veins. Scale bar = 3 mm.
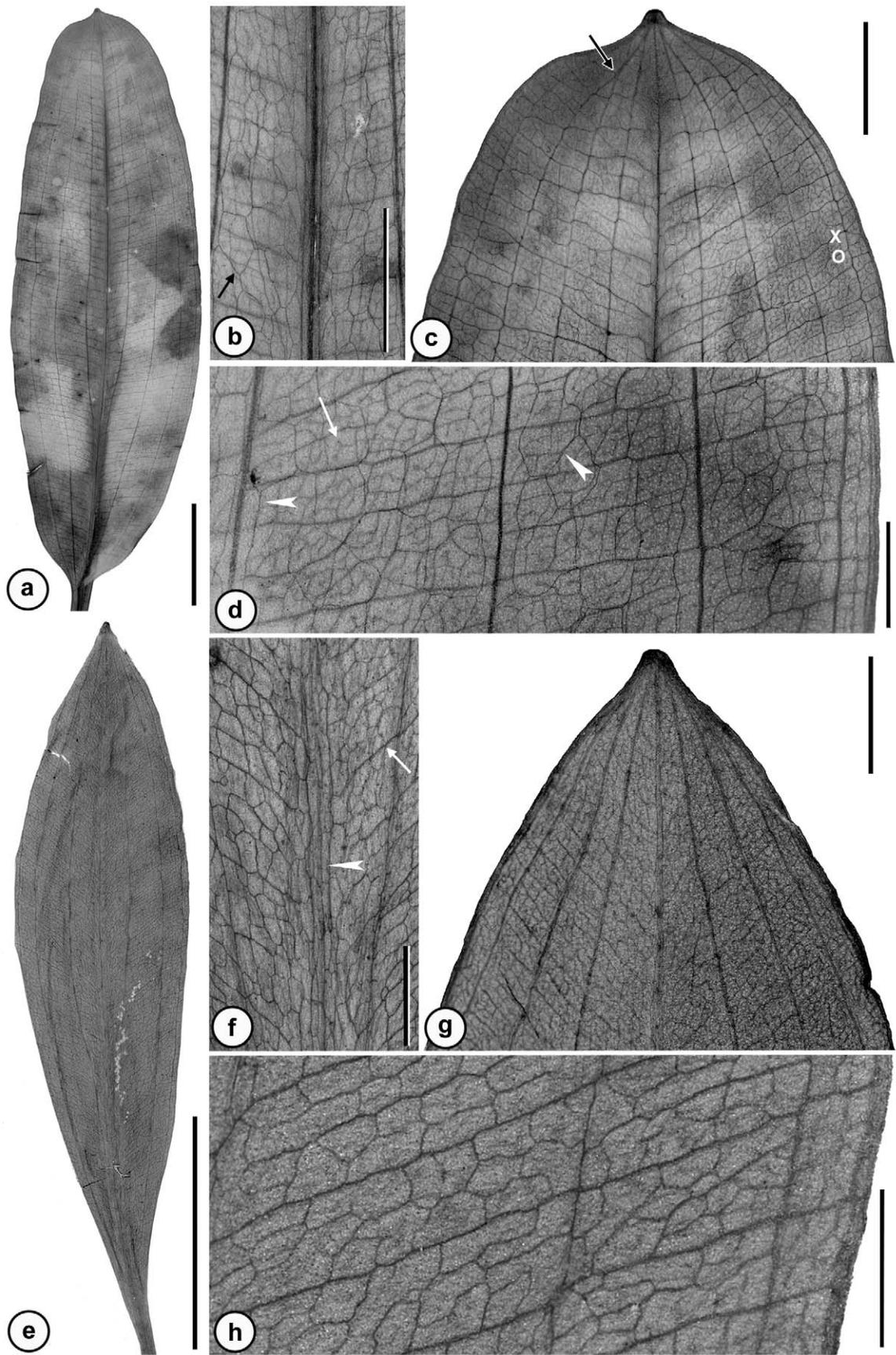
He assigned the remaining specimens from the Skilvika Formation to *A. macrophylla* based on large laminae and acuminate leaf tips (Heer 1876, pl. 26, figs. 1–6; pl. 27, figs. 3*b*, 3*c*, 4–7; Golovneva 1997, fig. 1*a*, 1*c*). Golovneva (1997) suggested that both leaf types belong to the same species of *Haemanthophyllum* [now called *H. nordenskioldii* (Heer) Boulter et Kvaček]. However, the assignment of these fragmentary plant remains of varying morphology and age to *Haemanthophyllum* is tenuous. In addition, the leaves from Spitsbergen, unlike our leaves, have larger laminae, cuneate bases, attenuate to convex apices, lack three closely spaced medial veins in the leaf base, and have only seven to nine cross veins per centimeter (table 1).

Boulter and Kvaček (1989, fig. 22D, 22E; table 1, *Haemanthophyllum* sp. 2) originally assigned fragmentary specimens with narrow oblong leaves and parallelodromous primary venation from the Late Paleocene/Early Eocene of Ireland to *H. nordenskioldii*. Golovneva (1997) concluded that the leaf characters were sufficiently different from the Spitsbergen material and recommend that they be removed from *H. nordenskioldii* but recognized that they may represent a new species of *Haemanthophyllum* (Golovneva 1997; L. B. Golovneva, personal communication, 1999). Again, without an apex or base it is difficult to classify the Irish material. The Irish leaves differ in morphology from the Cardston leaves but resemble fragmentary remains described by Zhilin (1974) as *Aponogeton tertiarius* Zhil. These leaves may show affinities to extant Aponogetonaceae or Potamogetonaceae.

Other leaf fragments sometimes assigned to *Haemanthophyllum* include a specimen with a strong "triple midvein," representing the middle to basal part of a leaf from the Early Paleocene of the Tsagajan Formation in the Amur Region of Russia. This leaf appears similar to specimens described as *H. nordenskioldii* (Krassilov 1976, pl. 11, figs. 3, 4; table 1, *Haemanthophyllum* sp. 1). The specimen is fragmentary, lacking an apex and base (Golovneva 1997 suggests the base is cuneate). The secondary veins appear to be as numerous as 25 per centimeter, slightly greater than the 14–17 reported by Golovneva (1997), and diverge at nearly 90° near the midvein. The difference in the angle of divergence of secondary veins and the lack of a cordate base with recurved primary veins distinguish these specimens from the Cardston leaves.

There are several known occurrences of *Haemanthophyllum*-like leaves from North America (table 1). Brown (1962, pl. 15, figs. 1, 4, 6) described fragmentary specimens of monocot leaves with large blades from the Paleocene Fort Union Formation in North and South Dakota as *Alismaphyllites grandifolius* (Penhallow) Brown. These leaves from two different localities were combined by Golovneva (1997, table) and described as *Haemanthophyllum* sp. 3. An acuminate leaf apex, described as an unidentified monocot by McIver and Basinger (1993) from the Paleocene Ravenscrag Formation of Saskatchewan, Canada, has been referred to as *Haemanthophyllum* sp. 5 by Golovneva (1997; our table 1). Two leaf fragments also similar to *Haemanthophyllum* have been described from the Paleocene Sagavanirktok Formation of northern Alaska (Spicer et al. 1994). One is a fragmentary cuneate leaf base (Spicer et al. 1994, fig. 3.2); the other is a fragment of a rounded apex (Spicer et al. 1994, fig. 3.3). These specimens are referred to as *Haemanthophyllum* sp. 4 (Golovneva 1997; our table 1). It is quite possible that these are fragments of two different taxa. All of the specimens are too poorly known to assign them with certainty to *Haemanthophyllum* or the fossil leaves described in this article, and are in need of reinvestigation once more specimens are found.

The Cardston fossil leaves are most similar to *H. cordatum* (Golovneva 1987). The overall shape, size, number of primary veins, merging of several primary veins below the apex, and angles of divergence of secondary veins are similar; however, there are several notable differences. Golovneva (1987, fig. 1) illustrates the outermost primary veins merging with the margin. In the Cardston leaves the primary veins continue to the apex without merging with the margin. This is a key character that distinguishes the Russian specimens from our fossils. An apical pore is present in the Cardston leaves, but because of poor preservation, its presence or absence is unknown in the Russian material. A larger number of secondary veins per centimeter is seen in the Cardston leaves (up to 40) than in *H. cordatum* (13–18). Even considering variability in preservation and our counts of seven to 25 veins per centimeter on the holotype specimen of *H. cordatum*, it appears that the secondary veins have a greater density in the Cardston leaves (table 1). In addition to these morphological differences, the Cardston leaves are older than those of *H. cordatum* by at least 5 m.yr., based on Russian stratigraphy (table 1).

Comparison with Extant Monocots

Budantsev (1983) based the name *Haemanthophyllum* on similarities of the fossil leaves to leaves of *Haemanthus* L. (Amaryllidaceae). Several workers concluded that these leaves were more closely related to *Aponogeton* (Zhilin 1974; Golovneva 1987, 1997; Pneva 1988; Boulter and Kvaček 1989) or *Potamogeton* (Heer 1868, 1876; Krassilov 1976; Boulter and Kvaček 1989). Heer (1876), Krystofovich et al.

Fig. 6 Leaves of Alismatales. *a*, *Limnocharis laforestii* Duchessaing, whole leaf. Scale bar = 2 cm. *b*, *Limnocharis laforestii*, adaxial surface of leaf base showing three closely spaced medial veins and random reticulate tertiary veins (arrow). Scale bar = 5 mm. *c*, *Limnocharis laforestii*, leaf apex showing primary veins merging near apex (arrow) and major (*x*) and minor (*o*) secondary veins. Scale bar = 1 cm. *d*, *Limnocharis laforestii*, abaxial leaf surface showing abaxial tertiary veins (arrowheads) that are slightly darker than abaxial tertiary veins. Note freely ending veinlets (4° veins) on adaxial side (arrow) and marginal vein. Scale bar = 2 mm. *e*, *Butomopsis latifolia* (D. Don) Kunth, whole leaf. Scale bar = 3 cm. DNA 1759. *f*, *Butomopsis latifolia*, adaxial leaf surface showing secondary veins (arrow) and tertiary veins with vertical elongate areoles over midvein (arrowhead). Scale bar = 3 mm. DNA 23463. *g*, *Butomopsis latifolia*, adaxial leaf apex showing primary and secondary vein patterns. Scale bar = 5 mm. DNA 23463. *h*, *Butomopsis latifolia*, leaf margin showing major and minor secondary veins and tertiary veins with horizontally elongate areoles. Note marginal vein. Scale bar = 2 mm. DNA 23463.

(1956), Brown (1962), and Golovneva (1997) also compared fossil leaf fragments with those of Alismataceae. Our comparisons further include Hydrocharitaceae, Limnocharitaceae, and Stemonaceae (table 2).

Fossil leaves from Cardston differ from those of *Haemanthus* in general leaf shape. *Haemanthus* leaves are oblong with cuneate bases and acuminate tips, whereas the fossils are ovate with cordate bases and convex to rounded apices. A number of characters are, however, shared by these two taxa, including the number of primary veins and primary veins that merge near the leaf apex and not with the margin. The number of secondary veins per centimeter overlap between these two taxa, but the fossil leaves have greater numbers of secondary veins per centimeter, especially near the margin. The angles of divergence of the secondary veins are similar; however, angles near the center in the fossil leaves can be more acute (table 2). The fossil leaves show regular major and minor secondary veins. Minor secondary veins in *Haemanthus* are rare. The midvein is undulating in *Haemanthus*, unlike that seen in the fossil leaves. Secondary veins in *Haemanthus* may dichotomize and anastomose as in the fossil leaves, but common intersecondary veins occur in this genus. These do not occur in the fossil leaves. Tertiary veins are very rare in *Haemanthus* leaves but are relatively more common in the fossil leaves from Cardston.

Leaves of *Stemona* are ovate with cordate bases like those of the fossils, but with acuminate apices rather than convex to rounded, as in the fossils (table 2). The number of primary veins is small (11) compared to the 23–27 veins seen in the fossil leaves. The primary veins in *Stemona* reach the margin and extend partway up the leaf in the margin (becoming what might be considered a fimbrial vein). However, in *Stemona* the primary veins never merge in the margin. The lowermost primary disappears just as the inner adjacent primary vein approaches the margin and continues toward the apex as a fimbrial vein. The number of secondary veins per centimeter is comparable between *Stemona* and *Cardstonia*, and their angles of divergence near the margin are both 90°. However, leaves of *Stemona* show angles of 90° throughout the leaf, even near the midvein, while those of the fossil leaves are 45°–60° near the center of the leaf. The secondary veins are similar to those of *Cardstonia* with regular alternation of major and minor secondaries that dichotomize and anastomose. Tertiary veins, however, were not observed in leaves of *S. tuberosa*.

Leaves of *Potamogeton lucens* are elliptic with decurrent bases and acuminate to convex tips. Leaf shape in the family Potamogetonaceae is highly variable and often heteromorphic, with floating leaves that are broad and petiolate and submerged leaves that are very thin to lanceolate or elliptic (Cook 1996*b*). There are about 80–90 species of *Potamogeton*, some of which show minute teeth and serrated margins (Cook 1996*a*). The number of primary veins, however, is much smaller than in the fossil leaves described here (table 2). The primaries, like those in *Cardstonia* leaves, do not merge with the fimbrial vein but continue to the leaf apex. The number of secondary veins per centimeter in *P. lucens* is very small, and there are no minor secondary veins. In addition, the tertiary veins in *P. lucens* diverge at right angles and show a sinuous course between secondary veins, and they rarely dichotomize.

Van Bruggen (1990) studied *Aponogeton* leaves in some detail. We closely examined *Aponogeton madagascariensis* (table 1) and *Aponogeton ulvaceous* in this study. *Aponogeton* leaves are more oblong (linear) than those of the Cardston fossil taxon. While *A. madagascariensis* has a decurrent base, the shape can vary in *Aponogeton* with some species (e.g., *Aponogeton cordatus* Jumelle) developing a shallow cordate base (van Bruggen 1990). The fossil leaves have deeply cordate bases with lobes that extend for some distance below the point of petiolar attachment, unlike any extant species of *Aponogeton*. The leaf apex shape in *Aponogeton* can be straight, convex, rounded, or emarginate (van Bruggen 1990). The fossil leaves show convex to rounded apices that are similar to some *Aponogeton* species, e.g., *Aponogeton jacobsenii* van Bruggen (van Bruggen 1990).

The 13 primary veins in *A. madagascariensis* are significantly fewer than the 23–27 observed in the fossil leaves. This is also consistent with the typical 11–15 primary veins reported by Tomlinson (1982) for the genus *Aponogeton*. The primary veins do not merge with the fimbrial vein but do merge with adjacent primaries in *Aponogeton* and *Cardstonia*. In *Aponogeton*, the first veins to merge near the apex are the outermost pair of primary veins, each of which merges with an adjacent primary. This pattern continues until most of the primaries join at the leaf apex. Although adjacent primaries do occasionally merge in the fossil leaves, there does not appear to be a successive admedial pattern of merger as seen in *Aponogeton*. The number of secondary veins per centimeter is five to six in *A. madagascariensis*, while the Cardston fossil leaves show a much greater density (10–40). Secondary veins diverge at angles of 80°–90° in *A. madagascariensis* at the center and margins of the leaf, while those in *Cardstonia* leaves diverge at angles of 45°–60° in the center and 90° at the margins. *Aponogeton* leaves lack major and minor secondary veins, whereas there is a consistent alternation of major and minor veins in the fossil leaves. Although secondary veins are not seen dichotomizing or anastomosing in *A. madagascariensis* var. *madagascariensis*, they do dichotomize or anastomose occasionally in *A. madagascariensis* var. *henkelianus* (van Bruggen 1990). Third-order veins are normally absent in submerged leaves of *Aponogeton* (Tomlinson 1982) but can form well-developed regular areolae in emergent leaves, e.g., *Aponogeton junceus* Lehm. (=*Aponogeton spathaceum* E. Meyer). Third-order veins in the Cardston fossil leaves are few in number and form irregular areolae, unlike those of *Aponogeton*. An apical pore, as in the Cardston fossil leaves, has been reported in old leaves of *Aponogeton* (Tomlinson 1982).

Leaves of *Ottelia ulvifolia* (Hydrocharitaceae) differ in shape from the ovate leaves from Cardston (with cordate bases and convex to rounded apices) in being oblong to linear with cuneate bases and straight apices. The genus *Ottelia* Pers. contains about 21 species (Cook 1996*b*), however, and cordate bases have been reported in some taxa (Tomlinson 1982). There are fewer primary veins (seven to 19) than in *Cardstonia*. The outer veins in *O. ulvifolia* merge with the margin, unlike those in *Cardstonia*, which continue to the apex. There are fewer secondary veins per centimeter (three or four) than the 10–40 seen in the Cardston leaves. Angles of divergence of secondary veins in *Ottelia* are 60°–90° and

45°–60° in *Cardstonia* in the center of the leaf and 60°–90° and 90° near the margins, respectively. Major and minor secondary veins occur in both (table 2); however, secondary veins rarely anastomose or dichotomize as they do in the Cardston fossil leaves. The rectangular to elongate polygonal areoles that are formed by third- and fourth-order veins in *O. ulvifolia* are absent in the Cardston leaves.

The Cardston fossil leaves are more similar to those of Alismataceae and Limnocharitaceae than to leaves of any of the other families examined here. Ovate leaf shapes with cordate bases occur in Alismataceae, as in *Cardstonia* (table 2; Meyer 1935*b*). Leaves of *Alisma* differ in leaf base shape, lack of major and minor secondary veins, and the secondary veins do not anastomose (table 2; Golovneva 1994). Those of *Caldesia* have more acuminate tips and lack tertiary veins (table 2; Mayr 1943). Similar to the fossil leaves, apices can be convex to rounded in *Alisma* and some *Echinodorus* species. There are fewer primary veins in Alismataceae (nine to 15) than in the fossils that show (23–27). In all the Alismataceae examined, the outer primary veins merge with the fimbrial vein. In the fossil leaves, all primary veins continue to the leaf apex before fusing. The number of secondary veins per centimeter is far fewer in most taxa of Alismataceae, but *Echinodorus* species and *Alisma* can reach the lower limits seen in the fossils. Secondary venation in *Caldesia* is very similar to that in the fossil leaves. Secondary veins in *Echinodorus* have a more curved course in the leaf than those seen in the fossils. The species of *Echinodorus* that we examined have fourth-order veins, and the areoles (formed by tertiary and sometimes quaternary veins) are vertically elongate, unlike the horizontally elongate areoles in the fossil leaves. "Weakly developed" apical pores have been reported in older leaves of *Echinodorus* (Tomlinson 1982) but were not observed by us in any of the leaves that we examined. Internal aerenchyma tissues have been described in this family by Meyer (1934, 1935*a*) and Stant (1964), and large lacunae are present in the leaf midrib with much smaller air spaces in the lateral laminae.

The fossil leaves from Cardston show the greatest similarities to those of Limnocharitaceae. *Hydrocleys* has leaves that are nearly ovate to suborbicular (Stant 1967; Cook 1996*b*). In "dicot" leaf terminology (Leaf Architecture Working Group 1999), the leaf illustrated in figure 5*e* is classed as elliptic. Bases are cordate as in the fossil leaves (Stant 1967). The number of primary veins is only 11 in *Hydrocleys* compared to 23–27 in *Cardstonia*. The primary veins do not merge with the fimbrial vein but do merge with other primary veins near the leaf apex as in *Cardstonia*. These leaves show three closely spaced medial veins as in *Cardstonia*, but the two veins on either side of the midvein do not reach the leaf apex. The number of secondary veins per centimeter overlaps that seen in the Cardston leaves but never reaches the 40 per centimeter maximum seen in the fossils. Angles of divergence of secondary veins are similar to those in the Cardston leaves but generally greater near the center of the leaf. Major and minor secondary veins are present that anastomose and dichotomize as in the fossils, and the secondary veins also have a more or less straight course. The tertiary veins in *Hydrocleys* arise at nearly right angles from the secondary veins, and there is much more regular areolation than

in the fossils. There is an apical pore in *Hydrocleys*, as in *Cardstonia* (Stant 1967).

Leaves of *Butomopsis* are elliptical with cuneate bases, straight to acuminate apices, and are markedly different in shape than leaves from Cardston (table 2; fig. 6*e*). The number of primary veins in *Butomopsis latifolia* is only seven to nine, the lowest count for the family and more similar to some Alismataceae than the fossil leaves. The primary veins, like those in the fossils and other Limnocharitaceae, do not merge with the margin but merge at or near the apex. Angles of divergence of secondary veins are very similar to those of the fossil leaves. Major and minor secondary veins with a more or less straight course that dichotomize and anastomose (although rarely) are similar to the Cardston leaves. Tertiary veins form somewhat irregular but well-developed polygonal areoles. As in *Hydrocleys*, the areoles are more elongate toward the center of the leaf than the margins.

Limnocharis laforestii leaves are oblong with cuneate bases and acuminate apices and therefore differ in general shape from the Cardston leaves (table 2). As in *Hydrocleys*, there are 11–13 primary veins that do not merge with the margin, and three closely spaced medial veins are seen near the leaf base, but the two veins on either side do not reach the leaf apex. The number of secondary veins per centimeter (eight to 11) overlaps the minimal number seen in the fossil leaves (table 2). Angles of divergence of secondary veins are similar to those seen in the fossil leaves but generally greater near the center of the leaf. Major and minor secondary veins that run nearly straight are similar to those seen in the Cardston leaves. These leaves, however, have randomly reticulate tertiary veins with well-developed polygonal areoles, unlike the irregular areolation seen in *Cardstonia*. Quaternary veins also occur in this species. These form freely ending veinlets, like those reported in "dicot" leaves (Leaf Architecture Working Group 1999) and unlike those seen in any of the other monocot taxa observed by us.

Leaves of *Limnocharis flava* show the closest similarities to the Cardston fossil leaves in many characters. The general leaf shape with a cordate base and rounded apex are similar between the two. While the number of primary veins is only 11–13 in *L. flava*, the primary veins do not merge with the fimbrial vein but do merge with other primary veins beneath the apex, and an apical pore is present (Stant 1967). The angles of divergence of the secondary veins are very similar, while slightly higher in the center of the leaf than in the Cardston fossils (table 2). The number of secondary veins per centimeter in *L. flava* is at the low end for *Cardstonia*. Tertiary veins are very similar to those in the Cardston leaves, and they frequently dichotomize and anastomose. Irregular polygonal areolae are present in *L. flava* on the adaxial surface, similar to those seen in *Cardstonia*.

We observed internal patterns of aerenchyma in all leaves of Limnocharitaceae that we examined. These leaves are especially fleshy near the leaf center, whereas the fossil leaves seem to be fleshy throughout. In all extant Limnocharitaceae, there appears to be a set of tertiary veins that form larger areoles on the abaxial surface of the leaf. These veins are not seen in reflected light when adaxial leaf surfaces are examined. They are best seen with a combination of transmitted and reflected light on a dissecting microscope. Illustrations of venation of

Butomopsis (fig. 6*h*), *L. laforestii* (fig. 6*d*), *Hydrocleys* (fig. 5*h*) are photographed in this type of light. It is difficult to see through the paper on herbarium sheets, and this type of examination of leaf venation is best done on pressed leaves that are not mounted on sheets. The photograph of *L. flava* (fig. 5*h*) was taken with a predominance of reflected light. In all of these leaves there is an abaxial set of tertiary veins that can be seen to connect to the secondary veins in several places. If these leaves were found as fossils, the predominant pattern seen would depend on how the specimen was cracked open and how close the fracture is to each surface. We illustrate a similar tertiary vein pattern (fig. 4*e*) in the *Haemanthophyllum* sp. fragment from the type locality (one of the specimens collected by Budantsev).

It should be noted that some authors might be observing internal aerenchyma patterns as well as a second set of tertiary veins in fossil leaves. Observations of the leaves of "*Haemanthophyllum*" in the fossil record have had various interpretations of tertiary venation. Golovneva (1997, pl. 9, fig. 8) illustrates small polygonal areolae in *H. kamtschaticum*, and we show similar features in the Cardston leaves (fig 3*i*). We are interpreting these polygons that can overlap veins in compressions (fig 3*i*, arrows) as underlying aerenchyma. In some fossil specimens it may be extremely difficult to tell whether the patterns observed are underlying aerenchyma or tertiary venation patterns or both. The regularity of the nearly hexagonal aerenchyma, if preserved, and its overlap with overlying veins are seen when there is good fossil preservation. Furthermore, the size ranges of the cells surrounding the lacunae are about 50 μm, a reasonable size for parenchyma cells.

While the fossil leaves from Cardston described here have similar numbers of primary veins to those of the genus *Haemanthus*, their venation details and presence of an apical pore where the veins converge are most like leaves in Alismataceae and Limnocharitaceae. The merging of primary veins with the fimbrial vein in most Alismataceae is a major difference in leaf architecture. Thus, the fossil leaves are most similar to those of Limnocharitaceae in overall vein patterns and the presence of an apical pore where the primary veins converge and unite (Sauvageau 1891, 1893; Stant 1967). Within Limnocharitaceae, *L. flava* shows the closest venation pattern, even to the order of tertiary veins, to the leaves from Cardston.

The Cardston leaves have a unique combination of characters, including the large number of primary veins, the three to five closely spaced medial veins that are continuous to the leaf apex, and the irregular areolae formed by tertiary veins. There are few secondary veins in the midrib region, while the number dramatically increases toward the leaf margin. Thus, the Cardston leaves are described as *Cardstonia tolmanii* sp. nov., Limnocharitaceae, as they show many of the characters of leaves in this family. They are most similar to those of *L. flava* differing only in the amount of aerenchyma present in the leaf and the number of primary veins.

Limnocharitaceae have often been included in Butomaceae, but a number of characters have suggested a relationship to Alismataceae (Cronquist 1981). In cladistic analyses, Limnocharitaceae and Alismataceae form a clade, with Butomaceae either as the sister group or as the basal member of the sister

group (Haynes and Holm-Nielsen 1992; Les and Haynes 1995; Les et al. 1997; Soros and Les 2001, 2002). Morphological cladistic analyses (Haynes and Holm-Nielsen 1992) indicate that Limnocharitaceae and Alismataceae may be sister groups, or that Alismataceae are nested within Limnocharitaceae (Haynes and Holm-Nielsen 1992). In molecular studies using *rbc*L, Limnocharitaceae is embedded within Alismataceae, indicating that Alismataceae may be paraphyletic (Les et al. 1997). Data from the internal transcribed spacers (ITS-1; ITS-2) of the nuclear ribosomal region, *rbc*L, the flanking introns and coding region of chloroplast *matK*, and morphology all indicate a sister relationship between Alismataceae and Limnocharitaceae (Soros and Les 2001, 2002).

Our reinvestigation of the genus *Haemanthophyllum* suggests that this genus should probably be restricted to leaf fragments that show cordate bases with similar venation patterns to the generitype. Budantsev's (1983) holotype specimen is incomplete. We show in this study that if only leaf base fragments are known (i.e., the cordate lobes), leaves of this type might be mistaken for those of *Stemona* or *Caldesia*, which show similar secondary vein characteristics. However, when whole leaves are found, these may prove to have other affinities. The suggestion that some leaves that have been described as *Haemanthophyllum* are more similar to *Aponogeton* is a valid one (Golovneva 1997), but the Cardston material is clearly different from Aponogetonaceae in several characters. It becomes evident that most of the previously described species of *Haemanthophyllum* should be reexamined, and larger numbers of more complete specimens are needed from each particular locality before descriptions are made and family assignments suggested. At the Cardston locality we have a second monocot with broad leaves that are elliptic with rounded bases and a distinctly different tertiary venation pattern from that seen in *Cardstonia* that will be the subject of another study.

This study also points out the need for a comprehensive monocot leaf venation terminology. The *Manual of Leaf Architecture* (Leaf Architecture Working Group 1999) covers "dicotyledonous" leaves and net-veined monocotyledonous angiosperms. However, we ran into several problems in using these terms for the monocot leaves described in this article. While primary vein terminology will work with these leaves, terminology for secondary and tertiary vein patterns is more problematical. We have tried to describe these patterns in several ways and to use the dicot terminology when possible. However, the distinctions between different leaf venation patterns are not always seen in table format using these "dicot" terms, even though we can distinguish the leaves qualitatively.

The preservation of fossil monocot leaves (other than those of palms) is rare (Herendeen and Crane 1995). Hickey and Peterson (1978) discussed the problems in the identification of fossil monocot leaf remains and proposed a terminology that they used for zingiberalean monocots. Boyd (1992) suggested additional vein patterns in several families of Zingiberales. However, in some species of Alismataceae, venation is much more complex. We found differing abaxial and adaxial vein patterns; and we were only able to use this "bar code" terminology to a limited degree in our study for the veins

near the adaxial surface. The abaxial patterns are less like those of zingiberalean monocots with anastomosing veins that lack the ABAB pattern.

The St. Mary River Reservoir locality near Cardston, Alberta, has yielded a large number of extremely well-preserved broad-leaved monocots in fine-grained sediments. This remarkable preservation has provided detailed data on the leaf architecture of many taxa, including aerenchyma patterns and internal anatomy in some rhizomes. Many plants are also buried *in situ*, providing insights into the ancient habitats and environments of the fossil taxa at the time of deposition. Further work at this site will provide a better understanding of the diversity of these ancient aquatic communities and their paleoenvironment.

Acknowledgments

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