

THE AQUATIC ANGIOSPERM *TRAPAGO ANGULATA* FROM THE UPPER CRETACEOUS (MAASTRICHTIAN) ST. MARY RIVER FORMATION OF SOUTHERN ALBERTA

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A floating aquatic dicot with leaves assignable to *Trapago angulata* has been characterized from Upper Cretaceous (Maastrichtian) deposits of the St. Mary River Formation in southern Alberta, Canada. Reconstruction of the plant is based on nearly 500 specimens of various isolated and attached organs. Prominent floating rosettes of leaves were interconnected by submerged horizontal rhizomes with a distinct, crenulate surface and formed dense mats at the surfaces of small freshwater ponds. At least eight different leaf morphologies were produced. Rosettes bore opposite pairs of simple leaves and compound leaves with three, five, seven, nine, and possibly 11 leaflets. Highly dissected, submerged leaves of differing morphologies occur on rosette-bearing axes and rhizomes. Paired bud scales at the nodes of the crenulate rhizomes subtend both rhizome leaves and elongate, branched roots. Solitary flowers on long pedicels are attached in the axils of compound leaves. These remains are compared to those described as *Quereuxia angulata* (Newberry) Kryshstofovich from Russia, and extant *Trapa* L. Specimens from Russia, while showing leaves of morphology similar to that of *T. angulata*, differ in growth and branching pattern, supporting the interpretation that they are indeed different genera. Although *Trapago* has commonly been placed in the Trapaceae, the similarities between extant *Trapa* and *Trapago* could be attributed to convergence, and the familial affinities of the fossil remain uncertain.

Introduction

A remarkable fossil flora has been excavated near Cardston, Alberta, Canada. Five major herbaceous aquatic vascular plants dominate the various facies (Stockey and Stockey 1993). Among these taxa, which probably grew near the margins of an aquatic system, are whole plants that have been buried in growth position. The significance of the St. Mary River Spillway locality has been noted by Rothwell and Stockey (1994), who described *Hydropteris pinnata*, a species showing characters intermediate between the extant heterosporous marsileaceous and salviniaaceous ferns. These fossils enabled reconstruction of a phylogeny for the heterosporous ferns and documented monophyly of the group (i.e., Hydropteridales; Rothwell and Stockey 1994; Hasebe et al. 1995).

In this article we describe a second, reconstructed, whole plant from Cardston, *Trapago angulata* (Newberry) McIver and Basinger (1993), an aquatic angiosperm. Leaves like those of this plant have been described by various authors as *Neuropteris* Brongniart (Newberry 1861), *Trapa* L. (Lesquereux 1878; Dawson 1887; Ward 1887; Knowlton 1899, 1900; Hollick 1930; Berry 1935; Brown and Houldsworth 1939; Dorf 1942; Brown 1962), *Nymphaeites* Sternberg (Bell 1949), *Quereuxia* Kryshstofovich (1953; Samylina 1988; Golovneva 1991, 1994), and *Trapago* McIver and Basinger (1993). These leaves are common components of Upper Cretaceous and Paleocene floras in North America and Eurasia (Hickey 1977; McIver and Basinger 1993). In this article, we reconstruct one of the plants that bore this leaf type. We also distinguish the North American material both from modern *Trapa*

(Trapaceae) and from Russian fossil material that we suggest probably belonged to another extinct genus.

Material and methods

Specimens were collected from the east bank of the St. Mary River at the base of the reservoir spillway near Spring Coulee, 26 km northeast of the town of Cardston, Alberta (Rothwell and Stockey 1994). The fossiliferous beds lie within the fluvial portion of the St. Mary River Formation, which is characterized by channel sediments, crevasse splays, and overbank deposits (Nadon 1988). The St. Mary River Formation is Upper Cretaceous (Maastrichtian) and is roughly equivalent to the Whitemud Formation in southern Saskatchewan and the lower part of the Fox Hills Formation in Montana (fig. 1).

Fossils are preserved as compression/impressions, and most occur in a layer of gray siltstone about 20 cm thick. Large segments of relatively intact plant remains and fine-grained sediments of burial are both consistent with the interpretation that these fossils were deposited in a shallow pond during an overbank flood. Rhizomes, preserved in horizontal growth position near the base of the siltstone, are branched, with some branches penetrating vertically toward the top of the unit. Rosettes are usually preserved above horizontal rhizomes in the matrix. These features indicate that many of the plants were buried in place, apparently as the result of a sudden sedimentation event. Stems that attach emergent rosettes to apparently rooted rhizomes are relatively short (namely, <10 cm), suggesting that the environment of growth was at the shallow margin of a relatively quiet pond. This interpretation is also supported by consistent occurrence of the specimens immediately above *Hydropteris pinnata* (Rothwell and Stockey 1994), an amphibious heterosporous fern.

The flora is low in diversity, with only four other major taxa of vascular plants present: *H. pinnata* Rothwell and Stockey (1994), an amphibious heterosporous fern; *Fortuna marsilioides* McIver and Basinger (1993); an unknown herbaceous dicot with clasping petioles, crenate leaf margins, and chloranthoid teeth; and a coryphoid or sabaloid palm (Stockey and Stockey 1993). In addition to these taxa, leafy shoots of a taxodiaceous conifer appear in the sediments but

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SYSTEM	SERIES	SOUTHERN ALBERTA	SOUTHERN SASKATCHEWAN	MONTANA
TERTIARY	Eocene			
		Paleocene	Porcupine Hills	Ravenscrag
	Willow Creek			
			Frenchman	Hell Creek
	Cretaceous	Maast	St. Mary River	Battle
			Whitemud	
			Eastend	
Camp		Blood Reserve	Bearpaw	Pierre
		Bearpaw		
	Oldman	Judith River		

Fig. 1 Stratigraphic column showing relative positions of Upper Cretaceous and lower Tertiary formations of Alberta, Saskatchewan, and Montana. Star indicates the approximate level of the fossil bearing sediments within the St. Mary River Formation. *Maast*, Maastichtian; *Camp*, Campanian.

are rare and occur as small broken fragments indicating that they probably were washed in from elsewhere.

Nearly 500 specimens of *Trapago angulata* were collected from benches approximately 1 m wide that were uncovered and allowed to weather for 1 yr prior to removal. This provided the best preserved and most easily retrievable specimens. Because of the three-dimensionality of the plants buried at this locality, unweathered material does not split well to reveal large fragments of plant fossils. Specimens were degassed as needed and studied and photographed with reflected light. Cleared leaves of extant *Trapa* were photographed using transmitted light. All specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA) and bear specimen numbers S38292–S38500, S38515–S38786, S38938–S38943.

Results

ROSETTES OF LEAVES

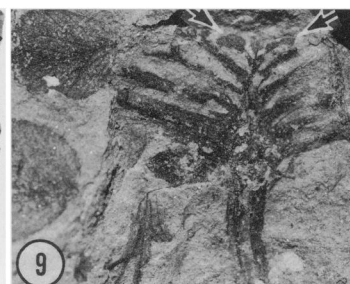
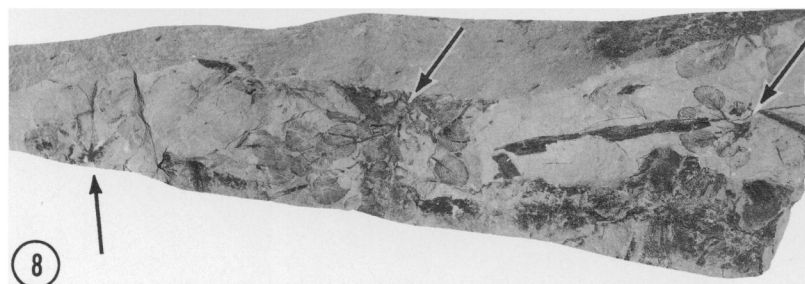
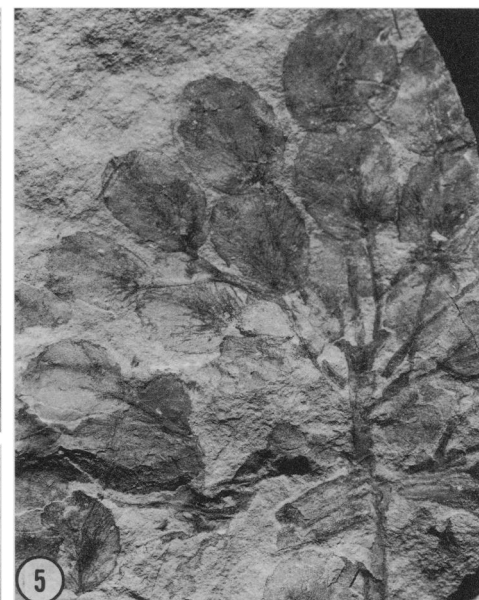
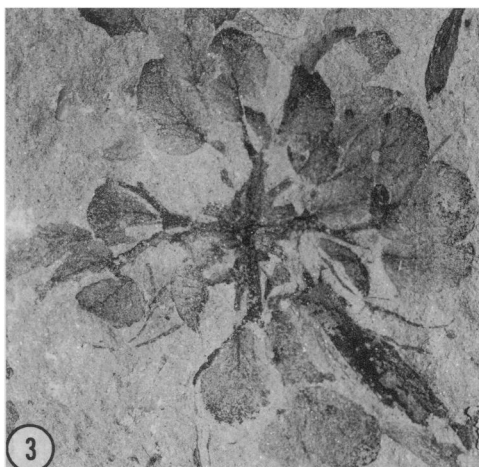
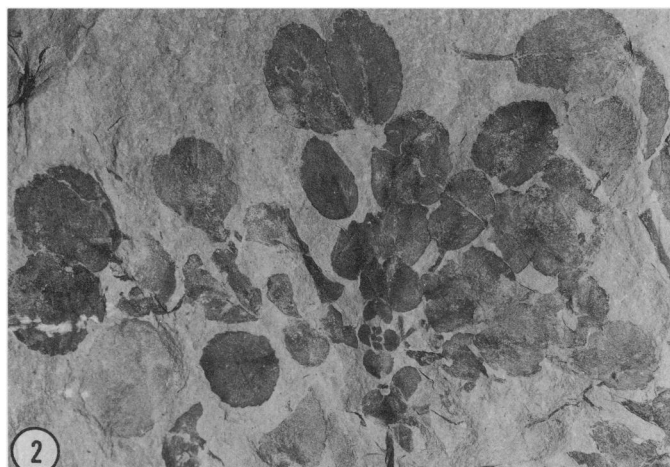
Leaves of *Trapago angulata* are heteromorphic and of at least eight different morphologies. The most

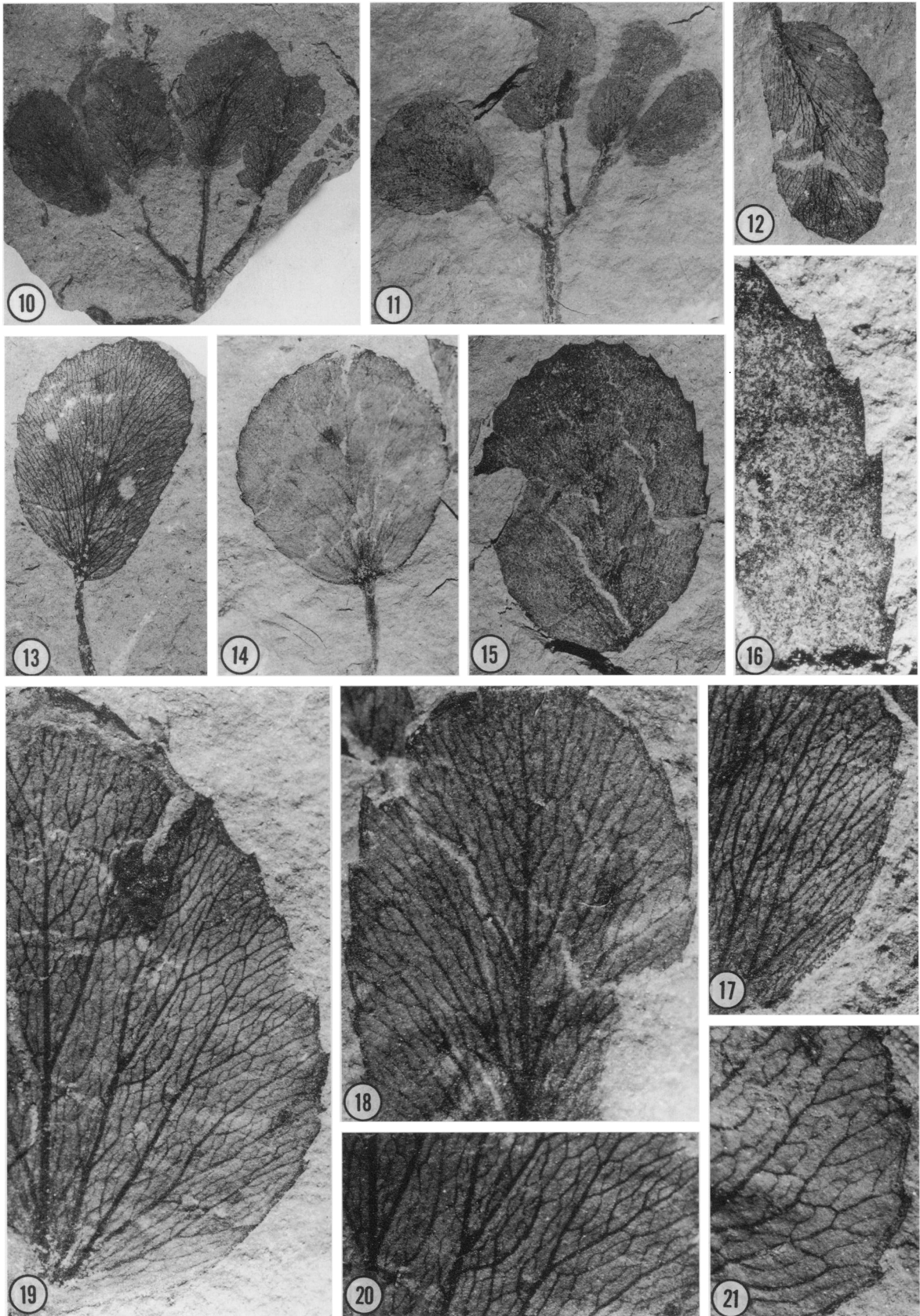
commonly encountered of these occur in an opposite, decussate arrangement, forming floating rosettes (figs. 2–7) on branches that attach to a rhizome system (fig. 8). At the apex of these floating shoots, leaves are simple for the first four nodes (fig. 2). At the fifth node, compound leaves are produced (fig. 3). Progressing proximally, the next two pairs of leaves have three leaflets. These are followed by two pairs with five leaflets, and then seven, and then nine, and possibly up to 11 leaflets per leaf (figs. 4, 5, 10, 11). The number of leaflets per leaf were determined by counting the number of opposite pairs and comparing these to the number of attached petioles in longitudinally preserved rosettes and by examining detached leaf fragments. This heteroblastic series of leaves is consistent among the specimens studied and documents a determinate pattern of growth. Because we consistently find four pairs of simple leaves at the apex of the rosettes and because it is highly unlikely that the more or less mature simple leaves could ever have become compound later, these rosettes clearly had reached the end of their growth potential.

The rosettes at Cardston are almost always preserved in growth position and may be fractured near the apex of the secondary axis (fig. 2), in the middle of the rosette (fig. 3), or near the base (fig. 4). Nodes are very short at the apex of these determinate secondary axes (fig. 9), and often most of a rosette can be seen on the split rock surface (figs. 2, 4). Submerged leaves are fused into a collar around the secondary axis beneath the compound leaves and are highly dissected and filiform at their tips (figs. 4, 29, 31). Rarely do we find material that fractures longitudinally (figs. 9, 22). However, such specimens are extremely informative because they reveal both the extremely short internodes at the shoot apex (fig. 9) and an extended proximal zone where the internodes are much longer (fig. 22).

Simple leaves and compound leaflets both have a similar, highly variable morphology ranging from symmetrical, obovate to elliptical to nearly ovate (figs. 12–15). Apices are rounded to obtuse and bases rounded or cuneate, sometimes asymmetrical (figs. 12–15). Margins are serrate, entire near the base of the leaflet, with simple mucronate, glandular teeth (figs. 16, 21). Venation is pinnate, craspedodromous (figs. 12, 13, 18) to nearly actinodromous near the leaflet base in some specimens (figs. 14, 19). Primary veins are typically thicker near the base and weaker near the apex, and

Figs. 2–9 *Trapago angulata* (Newberry) McIver and Basinger, rosettes of determinate growth in various views. Fig. 2, Upper surface of rosette showing alternately arranged simple leaves at apex, subtended by pairs of compound leaves. S38519; $\times 1.5$. Fig. 3, Rosette fractured through midlevel, showing opposite arrangement of compound leaves. S38524; $\times 3$. Fig. 4, Upper surface of rosette from which apical nodes have been removed. Note highly dissected, submerged, basal leaves at center. S38520; $\times 2$. Fig. 5, Cross section of rosette showing relatively complete compound leaves that bore five and seven leaflets. S38515A; $\times 2$. Fig. 6, Upper surface of rosette with missing apex, showing superimposed leaves of increasing complexity basally. S38547; $\times 2$. Fig. 7, Rosette showing position of attached flower or immature fruit (at arrow). S38523; $\times 1$. Fig. 8, Rock surface showing relative positions of rosettes (at arrows) that are attached at adjacent nodes on submerged rhizome. S38522; $\times 0.6$. Fig. 9, Rosette fractured in longitudinal view showing lengths of internodes and simple leaves (at arrows) attached at apex. S38545; $\times 3$.





usually show some deflections near the leaflet tip. Secondary veins branch dichotomously and thin toward the margin (figs. 17–19). The angle of divergence of secondary veins is 30–35 degrees. Occasional incurving intersecondaries are present in some specimens (fig. 19). Tertiary veins vary in size and have a random reticulate course. Quaternary veins form the irregular areolae; freely ending veinlets are rare or absent (figs. 17–21).

A prominent marginal or fimbrial vein is formed by the coalescence of second, third, and fourth order veins near the margin (figs. 17–19, 21). When these veins approach the margin near a tooth, each forks with one branch extending into the tooth and the other bending apically to merge with the marginal vein (fig. 21). Some specimens appear to have surface papillae or trichomes, but these structures have not been identified with certainty. Leaves were probably aerenchymatous and fleshy; therefore, the appearance of any one leaf depends on how it was fractured upon collecting and the variability of preservation. When split near the abaxial surface the venation is often distinct (figs. 12, 13, 17–21), but when split through the middle or near the adaxial surface venation is less distinct (figs. 14–16).

Stems that terminate in the rosettes are relatively smooth in proximal regions and show no prominent surface features (figs. 9, 22). They are 1.5–2.0 mm wide and at least 4.5 cm long. Internally they show two parallel, darkened bands that probably represent internal vascular strands (figs. 9, 22). These stems were probably circular in cross section (fig. 31) except near the apex where they are typically tetragonal (fig. 32). Internally, they show a four-angled center that probably represents an impression of the stele and four peripheral areas that may be large cortical lacunae (fig. 31). These stems are borne on horizontal rhizomes.

RHIZOMES

Leaves that are identical in branching morphology to the largest leaves on the rosettes, but that are more highly branched and lack leaflets or blade surface, are attached to large rhizome systems associated with rosettes in the matrix (figs. 23, 27, 30, 35). Arrangement of the petiolules on these submerged leaves is equivalent to what is seen in large rosette leaves when they are compressed from the side (cf. figs. 5, 27). The fimbriate nature of these rhizome leaves (fig. 27) further indicates that they grew submerged. This func-

tional, morphological adaptation occurs in many unrelated aquatic taxa (Cook 1978).

Rhizomes that bear these bladeless compound leaves have a crenulate surface ornamentation that is very characteristic of this taxon at the Cardston locality (figs. 25, 26, 30). This rhizome surface is not seen on other plants from the locality (all of which have shown leaf attachment) and serves as a marker for parts of the same plant. Extrapolating from the surface features on rhizomes of known affinity with *Trapago* has allowed an understanding of its growth habit and other attached organs.

Rhizomes from 3–8 mm in diameter have been found with up to four nodes present (figs. 23–28, 30). The longest complete specimen is 11 cm long (fig. 28). In addition to compound rhizome leaves, buds or branches with elliptical bud scales and branching roots occur at the nodes (figs. 23–26, 28, 30). Nodes on the rhizome are thickened and distinct (figs. 23–28), and the rhizome is often deflected at the node when branching occurs (e.g., fig. 24). The distance between nodes varies from 1.0 to 7.5 cm. Rhizomes appear to have been connected in a fairly extensive network below the water surface. Because of the three-dimensionality of the preservation of these rhizomes, the entire system is difficult to reconstruct, but the branching of rhizomes is common in our material (figs. 23, 25, 26).

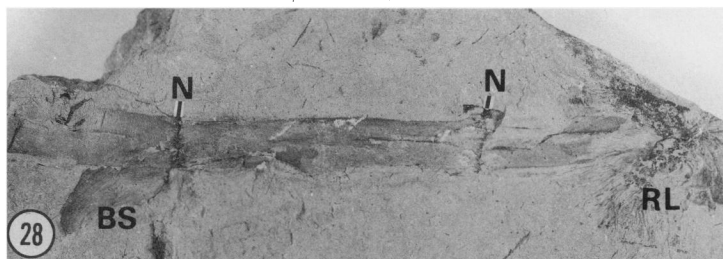
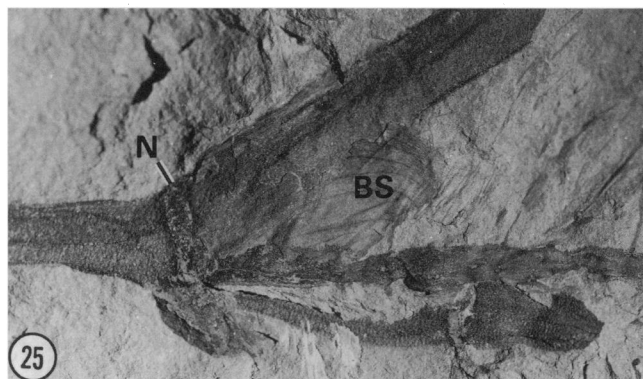
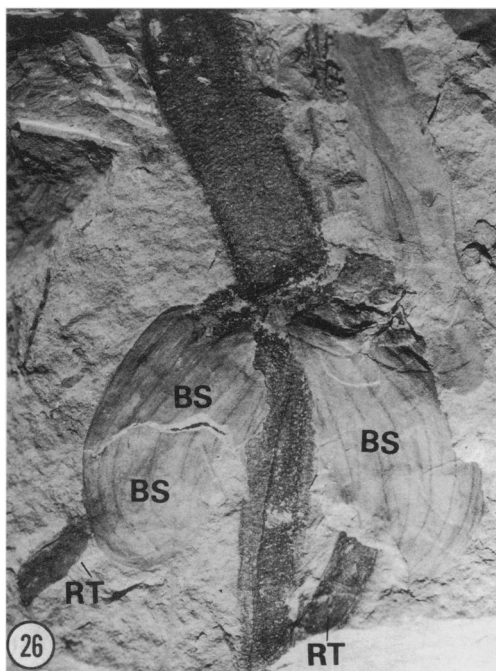
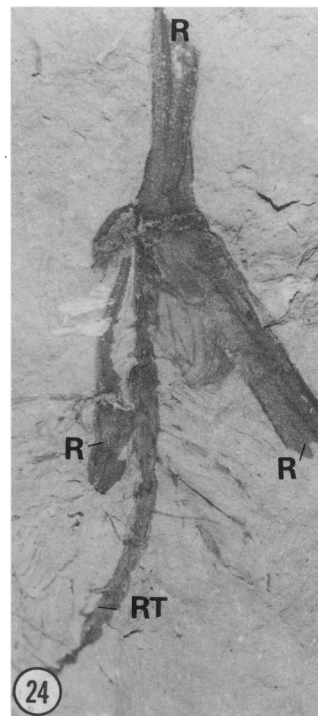
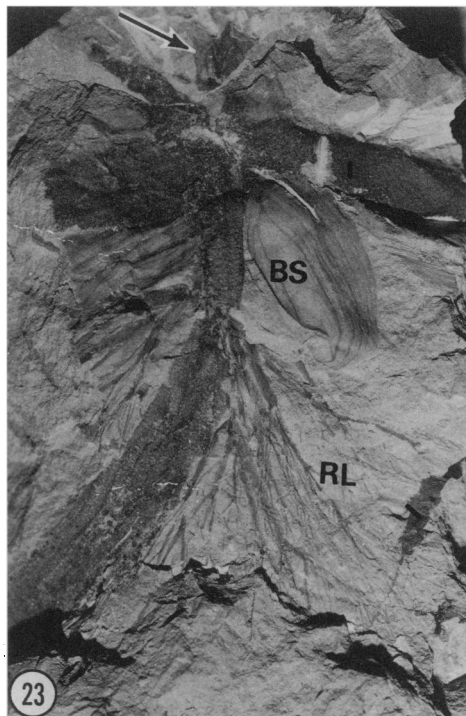
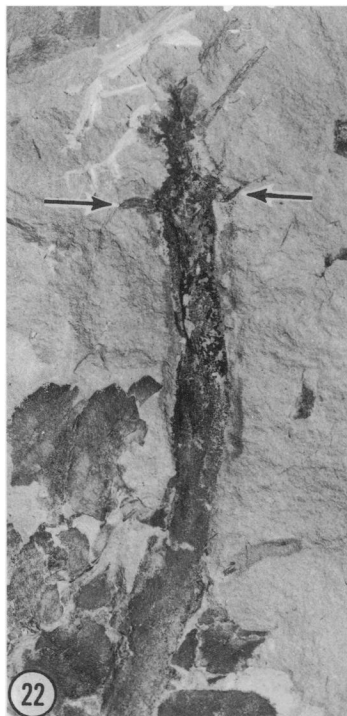
Many of the buds are intact, but in other specimens a rhizome and a branching root extend from between the paired bud scales (fig. 26). Bud scales are 1.2–2.0 cm long and show a series of more or less parallel veins that converge toward the apex (figs. 23–26). In one specimen, a smooth stem of comparable diameter to the base of the rosette stems appears to diverge from between the paired bud scales (fig. 23, at arrow). Specimens of this type provide crucial data for documenting the overall morphology of this plant.

ROOTS

Roots are elongate, up to at least 4 cm long, and branch at right angles to produce elongate, filiform laterals (figs. 24–26). These roots were probably attached to the substrate where the water was shallow, but in deeper parts of the pond were probably suspended in the water column, as in many other aquatic plants (e.g., *Pistia*, *Spirodela*, and *Limnobiophyllum*; Cook 1990; Stockey et al. 1996). One specimen (fig. 26) shows

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Figs. 10–21 *Trapago angulata* (Newberry) McIver and Basinger, leaves and leaflets. Fig. 10, Compound leaf with five leaflets. Note arrangement of petiolules. S38529; × 3. Fig. 11, Compound leaf showing five leaflets and branching arrangement of petiolules. S38530; × 3. Figs. 12–15, Leaflets from compound leaves showing range of variation in size and shape. Fig. 12, S38538a, × 3; fig. 13, S38538b, × 3; fig. 14, S38535, × 3; fig. 15, S38525, × 4. Fig. 16, Mucronate teeth at leaflet margin. S38525; × 10. Fig. 17, Fine venation near margin. Note size and shape of areolae and marginal vein. S38534; × 10. Fig. 18, Pinnate craspedodromous pattern of major venation. Note marginal vein and dichotomizing secondary veins at left. S38537; × 10. Fig. 19, Overall pattern of venation, with veins diminishing in thickness toward apex. Note that some secondary veins terminate in mucronate teeth, while others appear to terminate at marginal vein in sinus distal to tooth. S38536; × 8. Fig. 20, Dichotomizing secondary veins with curving intertertiary vein (near center); tertiary and quaternary veins forming irregular areolae. S38536; × 10. Fig. 21, Venation near margin of compound leaflet. Note prominent marginal vein. S38532; × 11.



two roots borne at a node, while others appear to have been borne singly (fig. 25). While it is difficult to tell rhizome branches from roots arising at some nodes, the rhizome surface is crenulate, and small lateral root scars are usually visible on the roots. Such features have been useful in these determinations.

FLOWERS AND FRUITS

Although several putative floral organs and fruits have been associated with *Trapago* specimens at other localities, the consistency of association is not very reliable. Only one of the previously described "fruits" (fig. 2 of Brown and Houldsworth 1939; Brown 1962, pl. 58, fig. 2) appears to be convincingly attached (Brown and Houldsworth 1939; Brown 1962), but our reexamination of the specimen reveals a discontinuity between the pedicel and the base of the putative fruit that demonstrates a lack of organic attachment. McIver and Basinger (1993) also examined this specimen and the one illustrated in figure 1 of Brown and Houldsworth (1939; Brown 1962, pl. 58, fig. 1) and stated that the specimen in figure 1 (a morphologically different fruit) was not attached. We also reexamined this specimen and agree that it is not attached and may have nothing to do with the *Trapago* leaves in question.

Among our specimens, we have found one flower or immature fruit 3 mm wide and 5 mm long attached by a long pedicel in the axil of one of the compound leaves of a rosette (figs. 7, 36). It is similar in overall structure, size, and mode and position of pedicel attachment (fig. 7, at arrow) to the specimen figured by Brown and Houldsworth (1939, fig. 2) and Brown (1962, pl. 58, fig. 2). Our specimen appears to have a fused corolla, three lobes of which are visible in the compression (fig. 36, at arrows). The ovary area shows several vertically overlapping structures that may represent ovules (fig. 36).

Another possible flower (fig. 37) has been found isolated in the rock matrix. This structure is comparable in size to the attached specimen and also shows what appears to be a fused floral cup surrounding a slightly swollen ovary (fig. 37, at *O*). More distally the specimen exhibits several lobes that are interpreted to represent perianth parts. One isolated spiny structure, 7 × 7 mm, resembling a fruit of *Trapa* also has been found in the matrix (figs. 33, 34). We wish to stress that the latter two structures are not in attach-

ment and may have nothing to do with the plant in question. It is hoped that with further investigation of *Trapago* at this and other sites, a clearer understanding of the floral morphology will be possible. However, the obvious prolific vegetative propagation of *Trapago angulata* suggests that flowering may have been rare.

Discussion

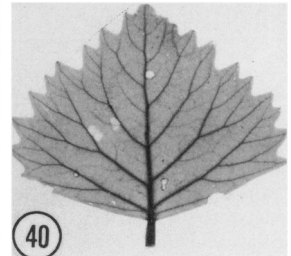
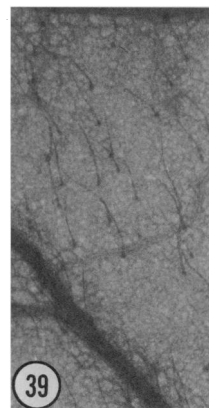
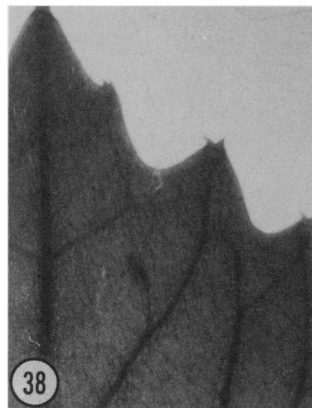
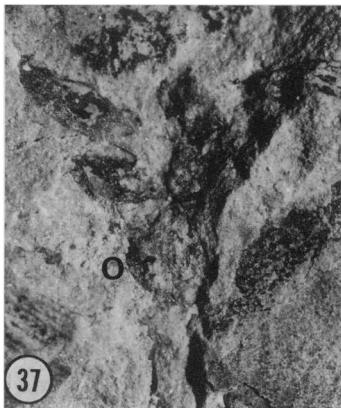
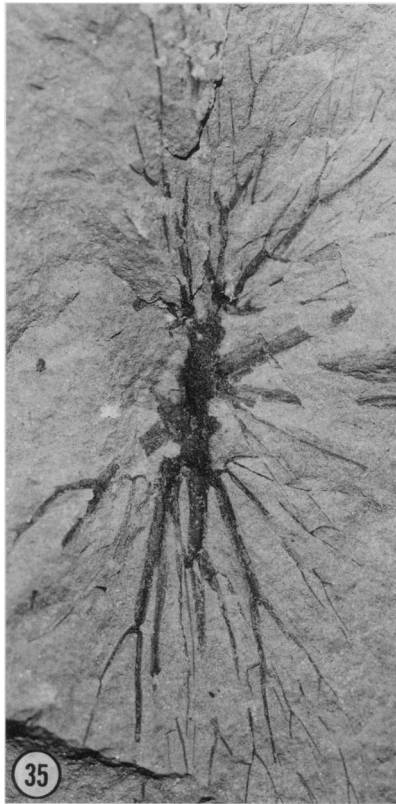
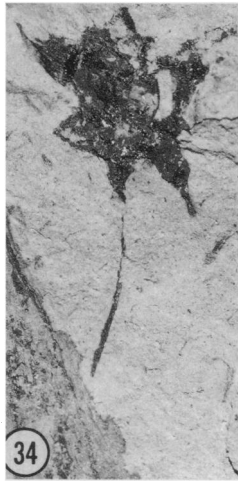
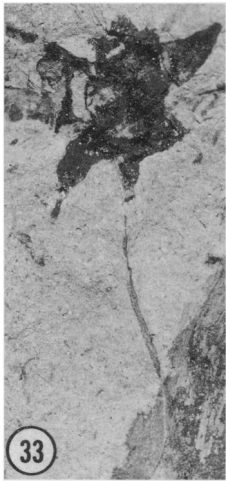
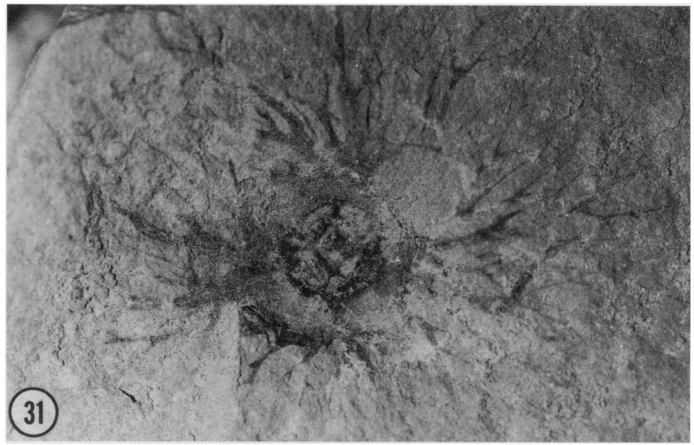
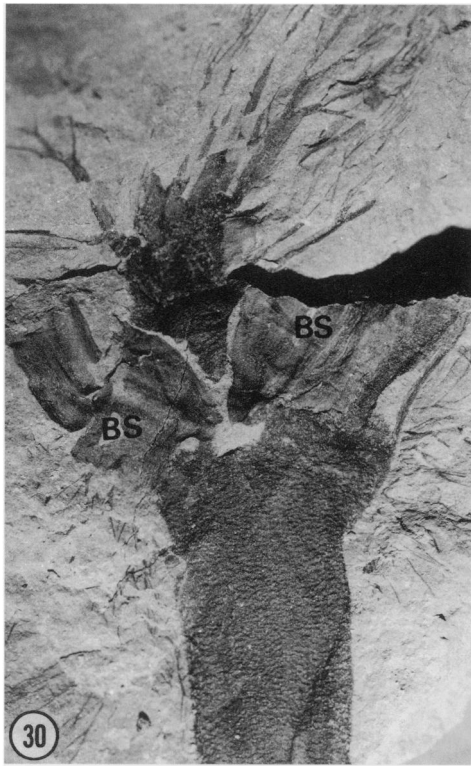
Among the numerous North American occurrences of leaves assignable to *Trapago angulata*, plants that produced the Cardston specimens are the most completely known. These plants were aquatic dicots with prominent, floating rosettes of leaves. The rosette branches arose from a submerged rhizome system that probably grew in shallow areas and near the margins of freshwater ponds in the back swamps of a meandering river system. *Trapago* rhizomes branched repeatedly, and the floating rosettes probably formed large mats on the water surface (fig. 41). In addition to the branches bearing rosettes, rhizomes bore one to two elongated branched roots, paired bud scales, and bladeless submerged rhizome leaves at the nodes (fig. 41).

At least eight different leaf morphologies were present on these aquatic plants. The rosettes show determinate growth and bear, at closely spaced nodes, both simple leaves and compound leaves of three, five, seven, nine, and possibly 11 leaflets. Submerged, highly dissected leaves are borne at a node directly beneath the floating rosettes (fig. 41). Bladeless rhizome leaves are identical in branching pattern to the compound leaves of the floating rosettes but lack any lamina. Bud scales show a series of parallel veins and are common at nodes. Crenulate surface patterns of rhizomes that bear the rhizome leaves are an important character used in linking the above and below water sections as parts of the same taxon.

Although several authors in the past have reported fruits in association with *Trapago* or *Trapago*-like plants (Berry 1935; Brown and Houldsworth 1939; Kryshstofovich 1953; Brown 1962; Samylina 1988; Golovneva 1991, 1994), reinvestigations of these by McIver and Basinger (1993) and by us (discussed above) indicate that the previously described putative fruits are not attached. As indicated by our attached specimen (figs. 7, 36), these plants probably bore solitary flowers on a long pedicel that arose in the axil of the compound leaves. While the structure of the

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Figs. 22–29 *Trapago angulata* (Newberry) McIver and Basinger. Fig. 22, Stem of floating rosette showing relationship of node with submerged leaves (at arrows) to nodes with emergent leaves. Note remnants of emergent leaves toward apex. S38457B; × 2. Fig. 23, Node of horizontal rhizome showing branching, bud scale (*BS*), and highly dissected rhizome leaves (*RL*). Arrow indicates the probable base of a diverging rosette axis. S38518A; × 3. Fig. 24, Branching rhizome showing attachment of root (*RT*) at node on rhizome (*R*). S38516; × 2. Fig. 25, Enlargement of rhizome in fig. 24 showing prominent node (*N*), bud scale (*BS*), branch, and branching root. Note characteristic crenulate surface pattern of rhizome. S38516; × 3. Fig. 26, Nodal region of branching rhizome showing prominent pairs of bud scales (*BS*) and diverging roots (*RT*). Note sediment between lower bud scale and the basal part of the upper bud scale at left. S38516; × 3. Fig. 27, Branching rhizome (*R*) showing characteristic morphology of rhizome leaf (*RL*). S38521; × 1.5. Fig. 28, Rhizome showing three nodes (*N*) and attached organs, including bud scales (*BS*) at left and rhizome leaves (*RL*) attached to node at right. S38527; × 1. Fig. 29, Segment of emergent branch showing morphology of submerged leaves. Note distinctively different morphologies of these leaves and submerged rhizome leaves (*RL* in fig. 27). S38544; × 3.



flowers is not clear from the few specimens available at the present time, they appear to have been epigynous with a floral cup and perhaps several ovules.

The preconceived idea that *Trapago* was, in fact, *Trapa* has clouded our ideas of what would be expected morphologically for the flowers or fruits of these plants. As McIver and Basinger (1993) have stressed, many of the supposed fruits probably belong to other families and genera, and association evidence alone is not enough to assign the fruits to these plants. While these authors discuss the topic in some detail and refigure one of Brown and Houldsworth's (1939, fig. 1) specimens (McIver and Basinger 1993, pl. 34, fig. 7), they do not comment on the second specimen figured by Brown and Houldsworth (1939, fig. 2). It is clear from Brown's refiguring of these two specimens in 1962 (pl. 58, figs. 1, 2), and his discussion, that he thought that this second specimen was abnormal in some way and "misshapen" (Brown and Houldsworth 1939). As described above, our reexamination of the second specimen illustrated by Brown and Houldsworth (1939, fig. 2) reveals that it also is not attached. However, this specimen shows a great similarity in size, shape, and in mode of putative attachment to our specimen from the Cardston area. As a result, the Brown and Houldsworth specimen may not, in fact be "misshapen." Rather, it may have been broken from its attachment to the pedicel during or after burial and, therefore, reflect the true morphology and mode of attachment for a young *Trapago* fruit. It is significant to note that these specimens are not similar to fruits of the genus *Trapa*. We hope that with further collecting of *Trapago* specimens a clearer picture of the reproductive portions of this plant will become better understood. It is clear, however, that *T. angulata* was very successful at vegetative growth and was capable of covering the surfaces of shallow water ponds because of its prolifically branching rhizomes.

Although leaflets of *T. angulata* were first described as species of *Neuropteris* Brongniart (Newberry 1861), it became clear by the late 1800s that these plants were not ferns but, in fact, angiosperms because of their more complex venation patterns (Lesquereux 1878; Dawson 1887; Ward 1887; Knowlton 1899). Many authors since that time have included these specimens in the genus *Trapa* based on the rosettes of floating leaves (Knowlton 1900; Hollick 1930; Berry 1935; Brown and Houldsworth 1939; Dorf 1942; Brown

1962). Several species names were given to the isolated leaflets, but the slight variation in venation patterns and leaflet shape have been discussed by several authors (see summary in McIver and Basinger 1993). Other authors such as Bell (1949) treated these remains in the genus *Nymphaeites* because of their many aquatic features, such as the presence of aerenchyma, trichomes, and some similarities in leaf type to genera such as *Cabomba* Aubl. While this interpretation has not been accepted by most authors, there is still disagreement as to the affinities of these plants. Hickey (1977) in his treatment of the Golden Valley flora had very few specimens from this Paleocene site but agreed with Dorf (1942) that the assignment of these specimens to extant *Trapa* was doubtful. McIver and Basinger (1993) put these remains into a new genus *Trapago* but still retained it in the Trapaceae.

While both *Trapa* and *Trapago* have rosettes of floating, aerenchymatous leaves, with a generally similar venation pattern, *Trapa* has only simple leaves that are borne first oppositely (submerged) and then helically on floating rosettes with truncate or cuneate bases and inflated petioles. *Trapago* has both simple and compound leaves borne in opposite pairs with rounded to rarely cuneate to truncate bases of leaves or leaflets that lack inflated petioles. The venation patterns of the leaves show some overall similarities to *Trapa* in their pinnate, craspedodromous major venation with the mid-vein and secondaries thinning toward the leaf margins. Secondary veins dichotomize and converge with a marginal vein near the tooth. However, the marginal vein in *Trapago* is more pronounced than in *Trapa*, and the secondary vein often branches as it approaches the sinus and joins the fimbrial vein. In *Trapa* (figs. 38–40; Golovneva 1991) there is a vein that appears marginal but follows the margin closely only on the basal side of the tooth. On the apical side, veins do not always parallel the leaf edge as they appear to do in *Trapago*. As McIver and Basinger (1993) point out, the margins of *Trapa* leaves also show double mucronate tips, while *Trapago* always shows single tips. *Trapa* usually grows with elongate stems that are mostly simple, flexible, submerged, and bottom-rooted (Cook 1990). Submerged leaves are sessile, linear, and entire, and lateral roots originate in the submerged leaf axils. These roots are often mistaken for submerged leaves in the literature (Cook 1990).

McIver and Basinger (1993) came to the conclusion

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Figs. 30–40 *Trapago angulata* (Newberry) McIver and Basinger. Fig. 30, Node of rhizome showing branch emerging from between paired bud scales (BS). Note short internode of branch, rhizome leaves, and characteristic crenulate surface pattern of rhizome. S38539; × 3. Fig. 31, Cross section submerged node of emergent stem showing leaves and central area that may represent stele surrounded by four peripheral areas that may represent lacunae in cortex. S38548; × 3. Fig. 32, Cross section near apex of emergent stem showing divergence of compound leaves at two adjacent nodes. S38528; × 4. Figs. 33–34, Part and counterpart of possible *Trapa*-like fruit found associated with *Trapago*. S36001A and B; × 4. Fig. 35, Cross section of rhizome showing morphology of rhizome leaves. S38542A; × 3. Fig. 36, Enlargement of single flower or immature fruit in figure 7 showing remnants of possible perianth parts (arrows) at apex and possible ovary basally. S38523; × 8. Fig. 37, Isolated tubular flower showing structures that may represent the ovary (O), and lobes of calyx and sympetalous corolla. S38526; × 8. Figs. 38–40, *Trapa* L. Fig. 38, Leaf apex and margin showing characteristic double tooth and lack of distinct marginal vein; × 4. Fig. 39, Leaf surface showing abundant trichomes; × 10. Fig. 40, Apical portion of cleared leaf showing pinnate, craspedodromous venation, dichotomizing secondary veins, and symmetrical base; × 1.2.

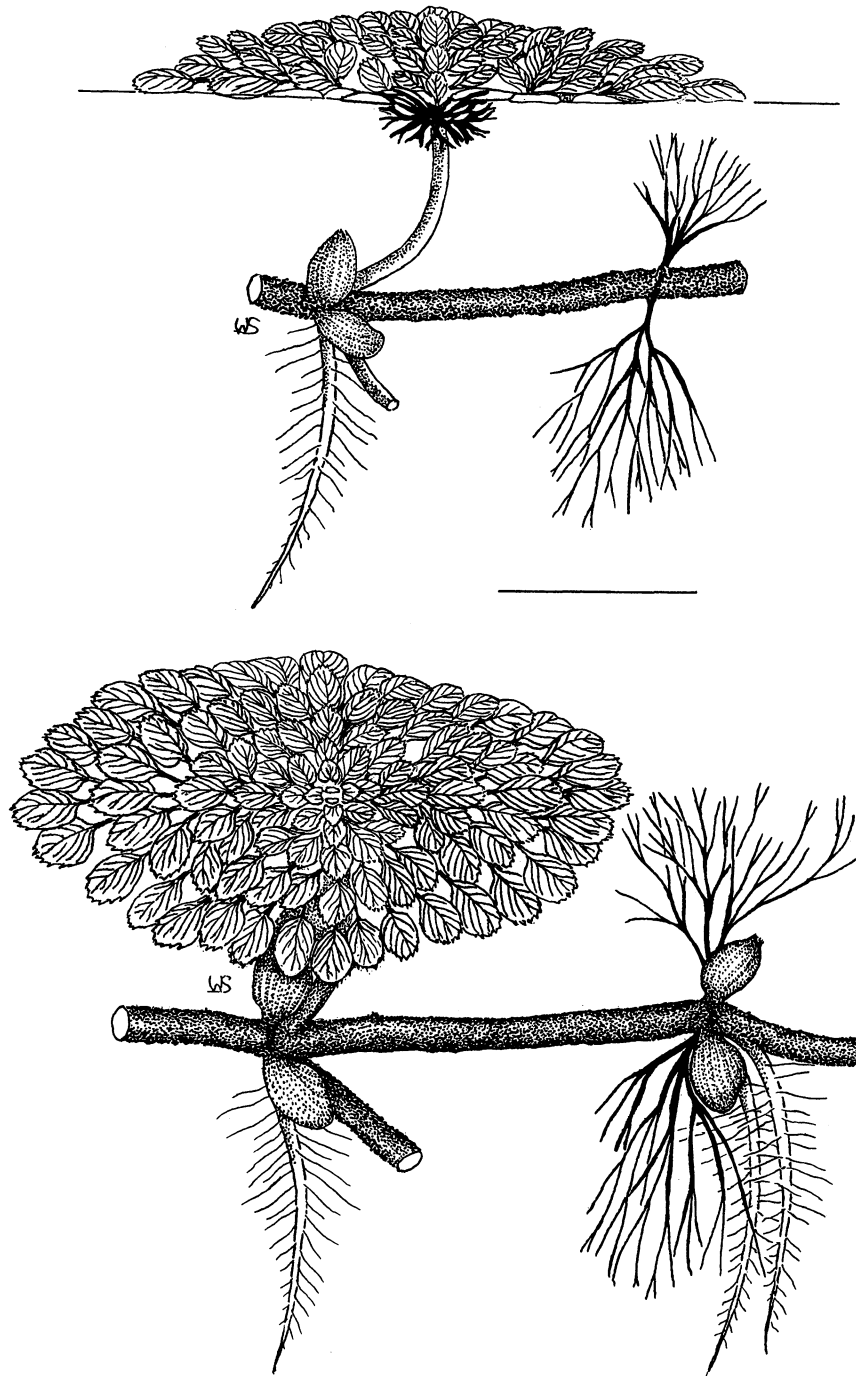


Fig. 41 *Trapago angulata* (Newberry) McIver and Basinger. Reconstructions showing overall growth form and distribution of the various leaf morphologies. Upper drawing illustrates floating rosette from side, while lower drawing shows it from the top. Scale = 5 cm.

that despite the differences between *Trapa* and *Trapago*, they should be included within the same family of dicots. There are many character changes between these two genera, and until the reproductive structures are understood with certainty this conclusion remains tentative. Our reconstruction of *T. angulata* (fig. 41) reveals that most of the similarities to the living genus *Trapa* are common to a large number of only distantly related aquatic angiosperms (Cook 1978). These in-

clude rosettes of leaves on erect, unbranched stems, heterophylly, and linear or dissected submerged leaves. Cook (1978) has termed this the “*Hippuris* syndrome.” While most species with this syndrome, including *Trapa* (Cook 1990), have simple leaves, a few, such as *Myriophyllum* and *Cabomba* (Cook 1978) and the fossils described in this article, have dissected leaves.

Evidence that there is more than one type of plant

of Cretaceous and Tertiary age that had a leaf morphology and growth habit similar to *Trapago* comes from several recent studies by Russian workers (Samylina 1988; Golovneva 1991, 1994). Kryshstovovich, as early as 1938, argued that the specimens formerly described as *Macclintockia sachalinensis* Kryshst., *Metadictyozamites mirabilis* Kryshst., and *Trapa? microphylla* by Lesquereux (1878), Hollick (1930), and Berry (1935) should be treated as the same taxon (Kryshstovovich 1938a). In 1953, Kryshstovovich included several other taxa in synonymy, including specimens from Japan, Alaska, Portugal, and east Asia, and *Trapa angulata* from western North America. In 1938, Kryshstovovich (1938b) described some elliptical fruits under the genus *Quereuxia*. He compared these to the "attached" fruits in Brown and Houldsworth's (1939, fig. 1) article and accepted their attachment to the *Trapa*-like plants. Thus, he included all of the apparently similar material from the Cretaceous and Tertiary worldwide in the genus *Quereuxia*. As has been stated above, however, the attachment of these fruits with this type of foliage has not been proven (McIver and Basinger 1993). McIver and Basinger did not accept this taxonomic placement and erected the genus *Trapago* for the North American material. The Russian literature, however, has generally accepted Kryshstovovich's (1953) use of the generic name *Quereuxia* for plants of this type, and several species have now been described (e.g., Krassilov 1979; Samylina 1988; Golovneva 1991, 1994).

Most of the fruits associated with North American specimens of *Trapago* leaves are not similar to those of *Trapa*. Since none of these previously described North American fruits is attached (McIver and Basinger [1993] suggest that they might belong to *Viburnum* or some other genus), the use of the species name *Quereuxia angulata* (Newberry) Kryshstovovich based on Newberry's (1861) type seems unfounded.

Recently, Golovneva (1991) described a new genus, *Palaeotrappa*, with three species, *P. aculeata*, *P. bicornata*, and *P. triangulata*. This genus is based on fruits from the Maastrichtian of the Koryak Upland that are similar in morphology to living *Trapa* and to the fruits described as *Quereuxia* by Kryshstovovich (1938b, 1953). The relationship of these spiny fruits with *Trapago*-like leaves has been noted and links between the species have been suggested, but so far attachments have not been found (Golovneva 1991, 1994).

Leaf form and venation of North American specimens cannot be distinguished from the Russian and east Asian forms that Kryshstovovich (1953) and Samylina (1988) both described as having simple and compound leaves on the rosettes. However, it appears to us that at least some of the Russian and east Asian vegetative material described as *Q. angulata* by Krassilov (1979), Samylina (1988), and Golovneva (1991, 1994) and reconstructed by Samylina (1988) in fact represents a different genus (or genera) altogether. Krassilov's (1979) material clearly shows elongate dichotomizing axes that bear "tufts" or rosettes of what

were probably floating leaves. We see no evidence of dichotomous branching of our rosette axes (or in any other North American specimens described so far) which appear to have been short with smooth surfaces.

Samylina's (1988, fig. 18) reconstruction of the east Asian taxon is based on more than 150 specimens. Structures similar to bud scales that occur on the rhizome system of our specimens are seen attached just below the floating rosettes in the Russian reconstruction (Samylina 1988). Axes that bear the rosettes in the Samylina reconstruction are elongate and bear what appear to be whorls of dissected leaves similar to what we see on our horizontal rhizomes. The rosette-bearing axes of the Russian material dichotomize and are shown attached to rhizome systems, but not at a node. Simple adventitious roots are illustrated attached to the rhizome system, also not at nodes. While the justification for the growth habit of these east Asian plants is not completely clear to us from the illustrated specimens, what is clear is that the branching patterns of these plants are distinctly different from those of our specimens of *Trapago angulata* (fig. 41).

Recently, Golovneva (1991) described two new species of *Quereuxia*, *Q. flabellata* and *Q. rotundifolia*, based on vegetative remains. It is not clear to us how these specimens differ from aquatic plants described in the genus *Fortuna* (McIver and Basinger 1993). *Fortuna marsilioides* (Bell) McIver and Basinger leaves have rounded apices, cuneate bases, and toothed margins and appear to have formed rosettes of opposite, simple leaves. These leaves are also found at Cardston attached to rhizome systems and will be the subject of another study, but they have been confused with leaves of *Trapago* by several authors including perhaps Bell (1949), Kryshstovovich (1953), and Golovneva (1991, 1994). Another specimen described as *Trapa palula* by Brown (1962, pl. 58, fig. 13) may show some similarity to the aquatic plants from Cardston and to the Russian material. However, its growth habit appears to be distinct from either reconstructed plant. What is clear from these studies is that there are several aquatic angiosperm taxa in Cretaceous and Paleocene sediments that need to be reinvestigated as whole plants. Only then will we be able to distinguish them from one another, to determine the geographic and stratigraphic ranges of each, and to put them into the proper phylogenetic context.

As Crane and Stockey (1986) illustrated with the fossil and living representatives of the family Cercidiphyllaceae, similar and indistinguishable leaf types may have been present on plants that had entirely different growth habits and arrangements of reproductive structures. Only by carefully reconstructing these individual taxa can we hope to understand their evolutionary significance. We suggest that the same may be true of the Cretaceous and Tertiary aquatic plants from North America and Asia.

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