

FOSSIL CERATOPHYLLUM (CERATOPHYLLACEAE) FROM THE TERTIARY OF NORTH AMERICA¹

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ABSTRACT

Fossil fruits and a vegetative axis assignable to the extant genus *Ceratophyllum* are described from four North American Tertiary localities. Fossil fruits assignable to the extant species *C. muricatum* and *C. echinatum* are reported from the Eocene Green River and Claiborne formations, and the Miocene Esmerelda Formation, respectively. An extinct species, *C. furcatispinum*, is described from the Paleocene Fort Union Formation and represents the oldest published report of *Ceratophyllum* in the fossil record. The existence of extant angiosperm species in the Eocene is very unusual and may be attributable in this case to slow evolutionary rates and unusual evolutionary properties associated with hydrophily in the genus *Ceratophyllum*.

CERATOPHYLLUM is a submersed monoecious freshwater aquatic angiosperm with underwater pollination (hydrophily) and distinctive, often spiny fruits. One might expect such taxa to have an abundant fossil record, and in this paper we describe and illustrate fossil vegetative and reproductive *Ceratophyllum* specimens from four localities ranging in age from Paleocene to Upper Miocene. These specimens expand the known geological history of the group (Les, 1988a) and provide an opportunity to evaluate the suggestion that slow rates of evolution and low diversity are consequences of hydrophilous pollination in perennial aquatic genera (Les, 1988c). Inefficient pollen transfer, reduced sexuality, widespread clonal growth and diminished seed production have been suggested as causal factors to explain the low species diversity in many hydrophilous genera (Les, 1988c). Hydrophily occurs in a phylogenetically heterogeneous group consisting of seven families and 18 genera, 16 of which consist of fewer than ten species (Les, 1988c). The Ceratophyllaceae have been suggested to be a living representative of some of the oldest flowering plants (Les, 1988a). Therefore, the

fossil history of *Ceratophyllum* is of interest particularly because it should allow for an evaluation of some of the hypotheses concerning diversity and rates of evolution in hydrophilous taxa (Les, 1988c).

The Ceratophyllaceae have been reported previously in the paleobotanical literature. The extinct genus *Ceratostratiotes* Gregor from the Miocene of Europe has been suggested to have taxonomic affinities to *Ceratophyllum*. It is treated as a separate extinct genus in the Ceratophyllaceae because of differences from *Ceratophyllum* in placentation, fruit wall ornamentation and symmetry (Bůžek, 1982; Les, 1988a). In addition to the reports of fossil *Ceratophyllum* species cited in Les (1988a), several other reports are in the literature. *Ceratophyllum miodemersum* Hu and Chaney was reported from the Miocene of Shantung Province, China (Hu and Chaney, 1940). The fossil vegetative axes have whorled leaves which appear to be at least twice dichotomously divided. Reports of fossil material of twelve *Ceratophyllum* species, several of which were originally described in a number of different papers, are summarized by Dorofeev (1974). However, the report of *C. praedemersum* Ashlee (Ashlee, 1932; Brown, 1937) is erroneous. The axis illustrated by these authors is perhaps an immature platanoid inflorescence, not a vegetative shoot of *Ceratophyllum*. The Ceratophyllaceae appear to have been relatively diverse in the past. Thus the paleobotanical record provides an understanding of the extent of past morphological diversity as compared to that observed in extant *Ceratophyllum* species.

Historically, taxonomic studies of *Cerato-*

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phyllum species have yielded widely varying treatments with 1–30 species being recognized. Recent systematic studies of *Ceratophyllum* species throughout the world (Les, 1985, 1986a, b, 1988a, b) have clarified the taxonomy of the group and facilitated a critical evaluation of the taxonomic affinities of the fossils presented in this paper.

MATERIALS AND METHODS—The fossil specimens examined in this study are from five different Tertiary localities. Two localities are in the Eocene Green River Formation in southwestern Wyoming. These are fossil fruits from the Wilkins Peak Member, Little Mountain flora (MacGinitie, 1969; housed in the paleobotanical collections at Indiana University) and a vegetative axis from the F-1 fossil fish beds, Lincoln Co., Wyoming (Grande, 1984; housed at the Field Museum of Natural History, Chicago, IL). The Eocene Claiborne Formation fruit is from Fayette Co., Tennessee (housed at the U.S. National Museum, USNM). Berry (1916, 1930), Potter and Dilcher (1980), and Parks (1971, 1975) provide details of the geology and paleobotany of the Claiborne Formation. Fruits of the Miocene Esmeralda Formation, Coal Valley flora (Berry, 1927; Axelrod, 1940) are from western Nevada (housed at USNM). The Paleocene Fort Union Formation fruits are from 7 Mile Creek, Stipek, Montana (housed at USNM). Brown (1962) and Hickey (1977) provide general treatments of the Paleocene floras of the Rocky Mountains and Great Plains.

Fossil specimens were examined, photographed, and fruit body length, width, spine number and lengths were recorded. When possible, matrix was degaged to reveal entire spines. Fruit body and spine measurements are important features taxonomically for evaluating the affinities of the fossil fruits.

SYSTEMATICS—*Ceratophyllum muricatum* Cham. subspecies *incertum* (Berry) Herendeen, Les and Dilcher, comb. et stat. nov.

Ceratophyllum incertum Berry 1930, USGS Prof. Pap. 156, p.71, pl. 33, fig. 7, 8 (USNM 316783).

Green River Formation (L. and M. Eocene) Southwestern Wyoming and Claiborne Formation (M. Eocene) Tennessee.
Figures 1–6, 9, 18–20.

Diagnosis—This subspecies is distinguished from the other subspecies in *C. muricatum* by having smaller fruits with longer lateral spines. The fossil fruits are 2.8–4.0 mm long ($\bar{x} = 3.4$) and 2.0 to 2.3 mm wide ($\bar{x} = 2.2$) and bear 8–

11 lateral spines. The maximum lateral spine lengths are 1.7 to 3.3 mm ($\bar{x} = 2.5$).

Description—The fossils consist of approximately 20 isolated fruits, 2.8–4.0 mm ($\bar{x} = 3.4$) in length, 2.0–2.3 mm ($\bar{x} = 2.2$) in width, having 8–11 lateral spines, paired basal spines, and a stylar spine. The maximum lateral spine lengths are 1.7–3.3 mm long ($\bar{x} = 2.5$ mm), basal spines 2.6–4.4 mm long ($\bar{x} = 3.3$ mm) and the partial lengths of incomplete stylar spines are 1.6–1.9 mm long ($\bar{x} = 1.8$ mm). There is no indication of lateral expansions of the spine bases or a marginal fruit wing. The spines are simple. The two basal spines project downward and the lateral spines radiate out more or less evenly from the fruit margins. The average length to width ratio of the fruit body is 1.65 (range 1.4–1.9). The peduncle is 1.5 mm long. Stylar spines are incomplete and no stylar groove or pore was observed. The external surface of the fruit wall appears smooth and no evidence of tubercles or facial spines or appendages was observed. Some compressed material at the base of the fruit suggests the presence of an involucre (Fig. 6). One vegetative shoot is also known from the Green River Formation. The axis is 26.4 cm long and 2 mm wide with 17 nodes having about 6–8 finely dichotomously-dissected leaves at each node. Each leaf is divided by at least two orders of dichotomy. The maximum leaf whorl diameter is 40 mm. The leaves are fine with slender segments, and we observed no indication of inflated segments or marginal and apical denticles. The basal nodes are leafless and the nodes appear swollen along the length of the shoot. The apex of the shoot is not preserved. This vegetative shoot is associated with a fruit (Fig. 18, 20) with remnants of the stylar spine but the lateral and basal spines are poorly preserved. The single fruit from the Eocene Claiborne Formation (Fig. 9) (Berry, 1930) is similar to the Green River fossils in nearly all respects, differing only in having slightly longer lateral spines.

Holotype—USNM 316783.

Paratypes—IU 15882-7455a–e pt. and cpt., 15882-8200, 15882-8201 pt. and cpt.

Other material—*Vegetative axis*: Field Museum of Natural History PF 12455 pt. and cpt.

Number of specimens examined—20.

Discussion—Because of the similarities between the Green River and Claiborne fossils,

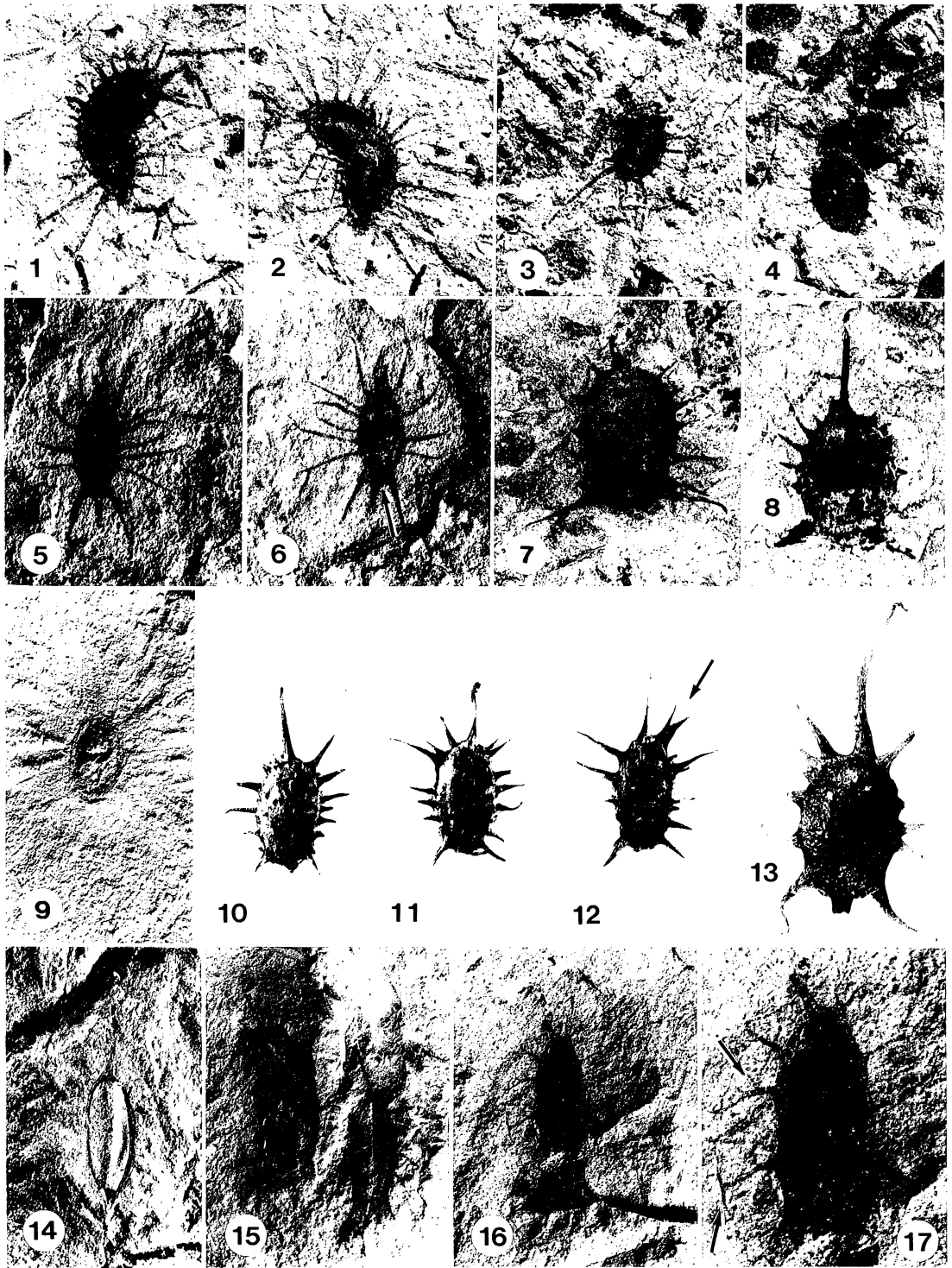


Fig. 1–17. Fossil and recent *Ceratophyllum* fruits. 1–6. *C. muricatum* fossil fruits, Little Mountain flora, Green River Formation, Eocene. 1, 2. IU 15882-7455. $\times 4$ and 5, 6. IU 15882-8201. $\times 4$ are counterparts. Arrow on Fig. 6 indicates possible remains of involucre at base of fruit. 3. IU 15882-7455c. $\times 4$. 4. IU 15882-7455d. $\times 4$. 7, 8. *C. echinatum* fossil fruits from the Esmerelda Formation, Miocene. 7. USNM 175765. $\times 4$. 8. USNM 175764. $\times 4$. 9. *C. muricatum* fossil fruit from the Claiborne Formation, Eocene USNM 316783. $\times 4$. 10–12. Modern fruits of *C. muricatum* subsp. *australe* [Lewis 2216 (OS)] $\times 4$. Arrow on Fig. 12 indicates coalcesced spines. 13. Fruit of recent *C. echinatum* [Les 436 (OS)] $\times 4$. 14–17. *C. furcatispinum* sp. nov. fossil fruits from the Fort Union Formation, Paleocene. 14, USNM 422513. $\times 4$. 15. USNM 422514. $\times 4$. 16, 17. USNM 422512. 16. $\times 4$. 17. Arrows indicate T-shaped spine apex and an unequally branched spine. $\times 8$.



Fig. 18–20. Fossil *Ceratophyllum muricatum* from the F-1 fossil fish beds, Green River Formation, Eocene PF 12455. 18. Fossil *Ceratophyllum* fruit with poorly preserved lateral margins, $\times 4$. Enlarged from region of upper arrow on Fig. 20. 19. Axis with swollen nodes and whorled, finely divided leaves, $\times 4$. Enlarged from region of lower arrow on Fig. 20. 20. Vegetative axis showing whorls of finely dissected leaves and swollen nodes. Fossil fish is *Knightsia eocaena* $\times 0.5$. Arrows indicate illustrations of details in Fig. 18, 19.

we conclude that they both belonged to a single geographically wide ranging taxon. The measurements of fruit length and width, lateral and basal spine lengths and number of lateral spines on the fossil fruits all fall within the range reported for modern *C. muricatum* (Les, 1988b).

There are three extant subspecies recognized in *C. muricatum*, however, and comparisons between the three subspecies and the fossils are complex. Three fruits from *C. muricatum* subsp. *australe* are illustrated in Fig. 10–12 for comparison with the fossil material.

Variation in fruit characters in the three extant *C. muricatum* subspecies and the Green River and Claiborne fossils is summarized in Table 1. The fossil fruits are close in size but slightly smaller than the fruits in all three extant subspecies. The length to width ratio is close to the value observed in *C. muricatum* subsp. *australe*. The single peduncle length measurement for the fossils is at the high end of the range observed in *C. muricatum* subsp. *australe*. Both mean basal spine length and mean number of lateral spines on the fossils are approximately intermediate between the values observed for *C. muricatum* subsp. *muricatum* and *australe*. However, sample sizes for these measurements are small. It is interesting to note that although the mean basal spine length for the fossils (3.3 mm) is slightly closer to that observed for *C. muricatum* subsp. *muricatum* and subsp. *kossinskyi* (3.8 mm), there were no basal spines on the fossils with maximum measurements approaching the relatively long basal spines that occur in these subspecies (6–8 mm). In fact, the maximum basal spine length observed on the fossils (4.4 mm) falls within the range observed for *C. muricatum* subsp. *australe* (max. 4.5 mm). The mean maximum lateral spine length is 1.1 mm longer than in *C. muricatum* subsp. *australe*, the subspecies with the longest lateral spines. However, the measurements fall within the range observed in *C. muricatum* subsp. *australe* and subsp. *muricatum*.

The sample size available for the fossils is small, however, and for most characters, the range of values observed for these specimens can be accommodated within the range of variation known to occur in populations of both *C. muricatum* subsp. *muricatum* and subsp. *australe* (Table 1). It would be particularly helpful to have more measurements of peduncle length and basal spine length and additional numbers of lateral spines.

From these data it is evident that the fossils are distinct from extant subspecies in some respects. The fossil fruits tend to be smaller and bear longer lateral spines as compared to the extant subspecies. In terms of basal spine length and number of lateral spines, the fossils appear to be intermediate between subsp. *muricatum* and subsp. *australe*. The fossils are more similar to the tropical American subspecies *australe* in length to width ratio and in peduncle length. It is for these reasons that we recognize these fossils as a distinct subspecies within the extant species *Ceratophyllum muricatum*.

The hypothesis that the divergence of *C. muricatum* subsp. *australe* and subsp. *muricatum*

TABLE 1. Variation in fruit characters in extant *Ceratophyllum muricatum* subspecies and the Green River and Claiborne fossils

	Body length ^{a,b}	Body width	L/W ratio	Peduncle length	Basal spine length	Lateral spine length	Lateral spine number
<i>C. muricatum</i> subsp. <i>muricatum</i>	3.7 (3.0–4.5)	2.5 (2.0–3.0)	1.48	0.75 (0.4–1.0)	3.8 (0.0–8.0)	0.6 (0.0–3.5)	7.7 (0–19)
<i>C. muricatum</i> subsp. <i>kossinskyi</i>	3.8 (3.5–4.0)	2.4 (2.0–2.5)	1.58	0.95 (0.5–1.5)	3.8 (1.5–6.0)	0.4 (0.0–2.5)	2.6 (0–8)
<i>C. muricatum</i> subsp. <i>australe</i>	4.0 (3.0–4.5)	2.5 (2.0–3.0)	1.6	1.25 (0.8–1.5)	1.5 (0.0–4.5)	1.4 (0.0–4.0)	11.6 (0–20)
<i>C. muricatum</i> subsp. <i>incertum</i>	3.4 (2.8–4.0)	2.2 (2.0–2.3)	1.65	1.5 (—)	3.3 (2.6–4.4)	2.5 (1.7–3.3)	9.5 (8–11)
Green River fossils	N = 8	N = 8	N = 8	N = 1	N = 3	N = 6	N = 4
Claiborne fossil	3.5	2.1	1.7	—	—	3.4	8

^a Including mean (and range).

^b Data for extant taxa from Les (1986a, 1988b). Ranges are not given for the Claiborne fossil since only one specimen is available.

catum is attributable in part to isolating effects resulting from the opening of the Atlantic Ocean (Les, 1989), is useful for interpreting the morphological similarities of the Eocene age fossils from North America to these extant subspecies. This hypothesis would predict that the North American fossils (*C. muricatum* subsp. *incertum*) would be more or less intermediate morphologically between the two extant subspecies. Because this morphological pattern is generally what we see in comparing the Eocene fruits with extant fruits of these subspecies, the hypothesis appears to be supported by the available paleobotanical evidence. The greater similarity of the fossils to *C. muricatum* subsp. *australe* suggests an affinity of these Eocene plants in central and southeastern North America with the extant flora of Mexico and Central America (Miranda and Sharp, 1950; Taylor, 1988; Dilcher, in preparation).

Ceratophyllum echinatum A. Gray

Ceratophyllum fossilium Berry 1927, Proc. U.S. Natl. Mus. 72(23), p. 10, pl. 1, fig. 2–4 (USNM 175763, 175764, 175765).

Esmeralda Formation, Upper Miocene Nevada. Figures 7, 8.

Description—The fossils consist of two isolated fruits 5.4–5.9 mm (\bar{x} = 5.0) long by 3.5–3.7 mm (\bar{x} = 3.6) wide having 10–11 lateral spines, distinct paired basal spines, and a pronounced stylar spine. The maximum lateral spine lengths are 1.9–2.2 mm (\bar{x} = 2.1 mm), the maximum basal spine length is 3.1 mm (only 1 measurement possible), and the maximum stylar length is 4.1 mm (only 1 measurement possible). Lateral spines have conspicuous webbed bases which coalesce to form a narrow lateral wing around the fruit. The fruit body length/width ratio is 1.6. No stylar groove or pore could be observed. No associated vegetative material is known.

Number of specimens examined—3.

Discussion—These fossil fruits of *Ceratophyllum* are similar in nearly all features to fruits of the extant North American species *C. echinatum* (Fig. 13) and this demonstrates the presence of this section of the genus by the Upper Miocene (Les, 1989). They are considerably larger than the Eocene specimens of *C. muricatum* from the Green River Formation and the Claiborne Formation, a feature that readily separates them morphologically from that species. Today *C. echinatum* occurs only in North America and has a disjunct distri-

bution between the east central and the upper northwest regions (Fig. 21; Les, 1986c). In the northwest extant material has never been found living further south than Siltcoos Lake, Oregon (Les, 1986c). The fossil material demonstrates that *C. echinatum* had a broader distribution during the Miocene and the species may have once ranged broadly across northern North America (Les, 1986c).

Ceratophyllum furcatispinum Herendeen, Les and Dilcher sp. nov.

Fort Union Formation (Paleocene), Montana. Figures 14–17.

Diagnosis—This species is distinguished from all other *Ceratophyllum* species in having fruits bearing lateral spines that frequently terminate in a T-shaped branching pattern.

Description—The fossil fruits are 4.8 mm in length (only 3 measurements possible), 1.8 to 1.9 mm in width having 9–10 lateral spines and a stylar spine. Paired basal spines are very short. The lateral spines are 1.0–1.5 mm long (\bar{x} = 1.25 mm) and frequently terminate in a T-shaped pattern. Spines also branch unequally (Fig. 17). Lateral spines have thin webbing at the base that is coalesced to form a narrow lateral wing around the fruit. The stylar spine is 1.8–2.8 mm long with no evidence of a stylar groove. The stylar spine is eccentric on two specimens and central on one specimen. The average length to width ratio of the fruit body is 2.6 (range 2.6–2.7, N = 3). There is no evidence of an involucre preserved on this material. An embryo outline is preserved on several of the fruits. The position of the large cotyledons suggests that the fruit has apical placentation.

Holotype—USNM 422512 (Fig. 16, 17).

Paratypes—USNM 422513, 422514, 422515, 422516, 422517, 422518.

Number of specimens examined—12.

Discussion—The spiny nature of the fruit body indicates a probable affinity with the spiny margined species of *Ceratophyllum* (Les, 1988b). The length/width ratio of the fruit body and the number of lateral spines in the fossils is consistent with those features observed in the extant spiny-margined species *C. tanaiticum*. However the fossil differs from *C. tanaiticum* by the elongate stylar spine and the branched or coalesced lateral spines. Avakov (1962) reported *C. zaisanicum* Avakov from

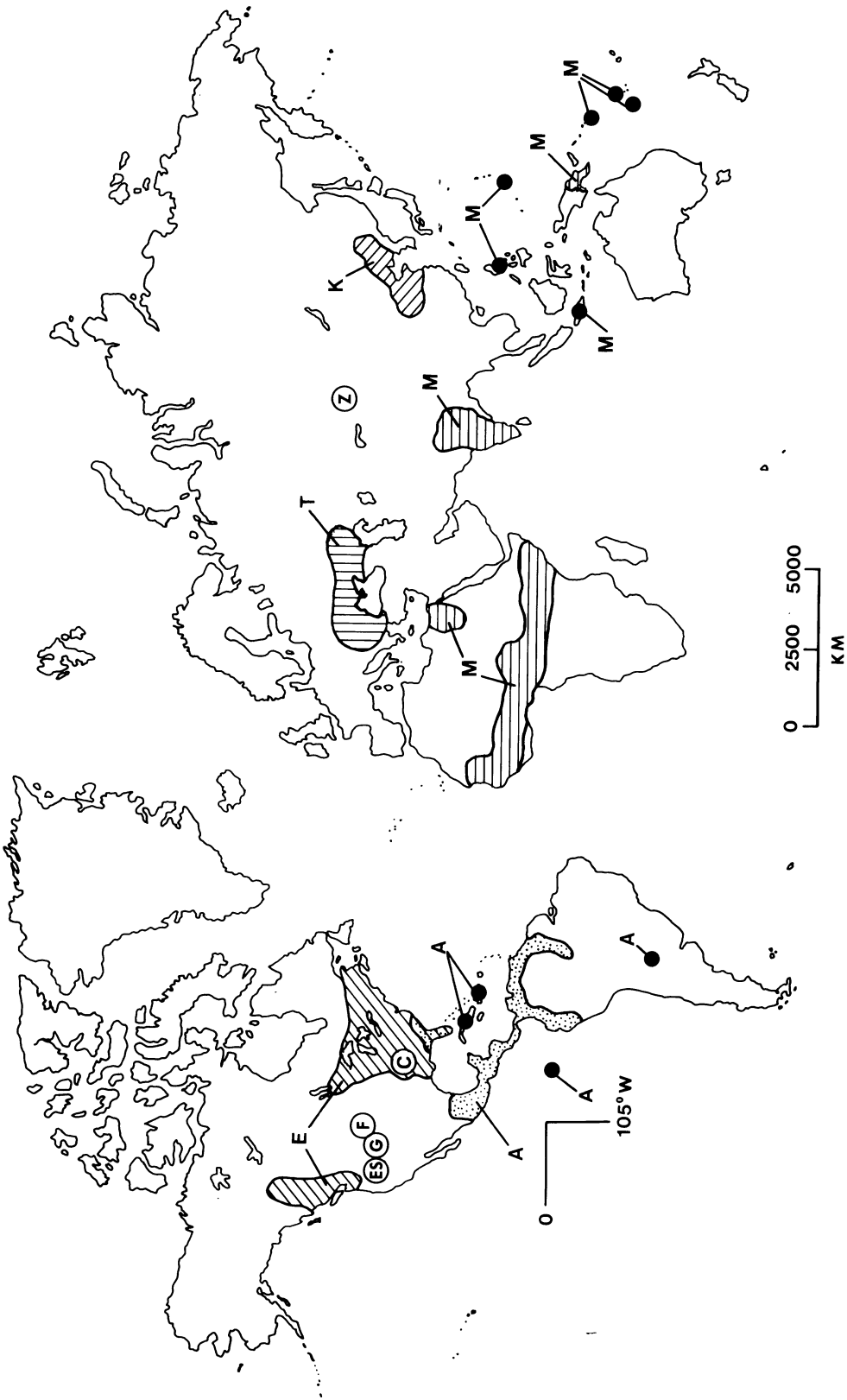


Fig. 21. Map showing distribution of extant spiny-margined *Ceratophyllum* (*C. muricatum*, *C. tanaiticum*, *C. echinatum*) (from Les, 1989) and the Green River, Claiborne, Esmerelda, and Fort Union fossil localities, and the Zaysan fossil *C. zaisanicum* (from Avakov, 1962) locality. E = *C. echinatum*, T = *C. tanaiticum*, K = *C. muricatum* subsp. *kossinskii*, M = *C. muricatum* subsp. *muricatum*, A = *C. muricatum* subsp. *australe*, Z = fossil site of *C. zaisanicum*, C = Claiborne Formation, F = Fort Union Formation, G = Green River Formation, ES = Esmerelda Formation.

the Oligocene of the Zaysan Basin (Kazakh SSR, Fig. 21) which resembles this fossil in all regards except for the branched spines. *Ceratophyllum zaisanicum* has a denticulate fringe with teeth 0.05–0.9 mm long formed by the extension of the lateral spines beyond the fringe. Perhaps the T-shaped branching of some of the lateral spines may have formed support for such a fringe in this fossil. No clear evidence of a fringe is preserved in *C. furcatispinum* but the T-shaped tips of the lateral spines curve parallel to the curvature of the fruit body and we suggest that they may have been marginal supports for a lateral fringe that is not preserved. This is offered here as a hypothesis as *C. furcatispinum* is the only species of the genus known to have branched lateral spines in such an orientation. Branched spines could either be derived from a coalescence of lateral spines or could represent simple branching of individual spines. A basal coalescence of spines sometimes occurs in the extant fruits of *C. muricatum* subsp. *australe* (Fig. 12).

Ceratophyllum tanaiticum occurs in areas around the west, northwest and northern border of the Black Sea extending east to the Caspian Sea (Fig. 21). The fossil *C. zaisanicum* was found in the Zaysan Basin, eastern Kazakh, SSR, as shown in Fig. 21. Although the occurrence of *C. furcatispinum* in North America greatly extends the range of these features geographically, we are uncertain whether *C. furcatispinum*, *C. tanaiticum*, and *C. zaisanicum* are closely related species, or that the former evolved independently in North America.

DISCUSSION—Climate—Distributions of several modern *Ceratophyllum* species, as well as locations of the fossils described in this paper are shown in Fig. 21. The occurrence of *C. muricatum* in predominantly subtropical and tropical regions supports previous suggestions that the climate during the Eocene in southwestern Wyoming and western Tennessee was subtropical or tropical (Dilcher, 1973; Wolfe, 1978, 1985). Similarly, the occurrence of *C. echinatum* in temperate North America is also consistent with a more temperate climate during the Upper Miocene in western Nevada (Wolfe, 1985). While interpreting climate based upon the ecology of the nearest related taxon has some limitations, our interpretations are based upon living representatives of what appear to be the same species. Evidence from foliar physiognomy from other plant taxa reported in these fossil floras (Dilcher, 1973; Wolfe, 1978, 1985), as well as from vertebrate remains from the Green River Formation such as crocodiles and alligators, supports our in-

terpretation of the climate of this region (Grande, 1984).

Evolution—Interpreting the systematic affinities of fossil angiosperms must be approached with great care. This is because some fossil organs, such as leaves, sometimes lack sufficient diagnostic characters to permit systematic determination at the generic level (Dilcher, 1974; Jones and Dilcher, 1980). In addition, assigning systematic determinations to isolated fossilized organs without detailed examination of the extant genera or families to which the fossils are assigned can result in erroneous conclusions, as shown by Roth and Dilcher (1979). Thus, care was taken in this study to examine the overall diversity known in the living and fossil fruits and associated vegetative material to determine which taxa of living angiosperms are similar, and the extent of that similarity. Only one family was found to be similar: the Ceratophyllaceae which consists of one extant genus, *Ceratophyllum*, of six species and three subspecies. Therefore the fossils were compared carefully to extant material of these taxa. The nature of the fruits (size; presence, size and distribution of spines) is important in the differentiation of the extant species and subspecies. Although we were initially reluctant to extend species back to the Middle Eocene (ca. 45 million years BP), it became apparent using those same characters that are used to differentiate the extant species that some of the fossils and living material can be differentiated only at the subspecies level. Other fossils, such as *C. furcatispinum* from the Paleocene, can be differentiated only at the species level, and other fossil material, such as *Ceratostratioites*, can be differentiated at the generic level.

The fossil fruits and vegetative axis described here are significant in a consideration of the evolution of angiosperms for several reasons. First, they document the occurrence of the extant genus *Ceratophyllum* as early as the Paleocene. In addition, fossil fruits from the Green River and Esmerelda formations document that several extant *Ceratophyllum* species have undergone little morphologically detectable evolution since the Middle Eocene and Upper Miocene, respectively. The occurrence of extant angiosperm species in the Eocene and Miocene is particularly intriguing. The presence of an extant species in the Eocene is in marked contrast to the extinct genera more often encountered in Eocene floras (Manchester, Dilcher, and Tidwell, 1986). However, it is interesting to note that at least two extant species of sea grasses (*Cymodocea*) have been

recognized based on Eocene fossil material (reviewed in Hartog, 1970). However these reports have been questioned by Daghljan (1981). The fossil history of these plants is significant because the sea grasses and *Ceratophyllum* are biologically analogous in that they are submersed hydrophilous plants. Thus, one might expect some similarities in the rates of morphological evolution in these groups.

As Dilcher and Daghljan (1977) pointed out with the occurrence of the extant genera *Philodendron* and *Sabal* in the Middle Eocene, carefully made determinations of extant genera from 45 million year old sediments may reflect as much the nature of the systematic delimitation of extant taxa as it may reflect the rates of evolution of particular groups. The *Ceratophyllum* fossils described here could be interpreted to suggest that there has been relatively little evolutionary change in some *Ceratophyllum* species since the Eocene. Slow rates of evolution and diversification have been hypothesized for various hydrophilous genera (Hartog, 1970; Les, 1988c) and have been suggested to be a consequence of the relative uniformity of aquatic environments (Hartog, 1970; Tiffney, 1981) and the ubiquity of vegetative reproduction in hydrophytes (Les, 1988c). It is interesting to note that *C. muricatum* and *C. echinatum*, reported here from the Eocene and Miocene respectively, are among the *Ceratophyllum* species that reproduce sexually more often today (Les, 1988b).

Based upon our ability to recognize extant species by the Eocene, one could infer from these fossils that the initial diversification of *Ceratophyllum* must have occurred significantly earlier than the Eocene and we anticipate that the genus should have an earlier occurrence in the fossil record. Although there is insufficient paleobotanical data available at present, studies of additional fossil collections, as well as reexamination of previously published material, are likely to yield additional fossil material referable to the Ceratophyllaceae, as well as a clearer understanding of the timing of evolution and diversification in this family.

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