

Ecological conservatism in the “living fossil” *Ginkgo*

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Abstract.—The living species *Ginkgo biloba* is phylogenetically isolated, has a relictual distribution, and is morphologically very similar to Mesozoic and Cenozoic congeners. To investigate what adaptations may have allowed this lineage to persist with little or no morphological change for over 100 Myr, we analyzed both sedimentological and floral data from 51 latest Cretaceous to middle Miocene *Ginkgo*-bearing fossil plant sites in North America and northern Europe. The resulting data indicate that throughout the late Cretaceous and Cenozoic *Ginkgo* was largely confined to disturbed streamside and levee environments, where it occurred with a consistent set of other plants. These inferred habitats are surprising because the life-history traits of *Ginkgo* (e.g., slow growth rate, late reproductive maturity, extended reproductive cycle, large and complex seeds, large and slowly developing embryos) are counter to those considered advantageous in modern disturbed habitats. Many flowering plant lineages first appeared or became common in disturbed riparian habitats, and are inferred to have had reproductive and growth traits (e.g., rapid reproduction, small easily dispersed seeds, rapid growth) suited to such habitats. Paleocological inferences based on both morphology and sedimentary environments thus support the idea that *Ginkgo* was displaced in riparian habitats by angiosperms with better adaptations to frequent disturbance.

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Introduction

Members of the Ginkgoalean clade remained a moderately important to minor associate of mid- to high-latitude paleofloras from the mid-Mesozoic to the mid-Cenozoic (Tralau 1967, 1968; Vakhrameev 1991). However, reconstructing the ecology of the group is problematic, given the extreme taxonomic isolation (Chamberlain 1935; Gifford and Foster 1989) and highly relictual distribution of what might well be only semi-wild stands of *Ginkgo biloba* L., the sole survivor of this once moderately diverse clade (Vasilevskaya 1963; Tralau 1968). The objective of this study was to determine whether some aspects of the paleoecology of *Ginkgo* could be recovered from (1) an interpretation of the sedimentary context in which its fossils occur; (2) the autecology of the modern descendants of its important fossil associates; and (3) a contextual study of the fragmentary ecology of its surviving species.

According to Tralau (1968), the order Ginkgoales consists of six families and 19 genera.

Ginkgoales first appeared in the Permian and achieved maximum diversity during the Jurassic and Early Cretaceous. Its most plausible ancestral group is the pteridosperms (“seed ferns”) (Thomas and Spicer 1987), and especially the Peltaspermales (Meyen 1987: p. 146). However, the clade is so isolated evolutionarily that efforts to establish its closest extant sister group have remained controversial. Nevertheless, there is a growing consensus, favored by molecular data, that cycads are the most plausible closest living relative (Meyen 1984; Thomas and Spicer 1987; Raubeson and Jansen 1992; Chaw et al. 1993, 1997; Rothwell and Serbet 1994; Boivin et al. 1996; Hickey 1996; Hasebe 1997) rather than conifers (Chamberlain 1935; Pant 1977; Stewart 1983; Crane 1985; Doyle and Donoghue 1986, 1987).

Undoubted remains of the genus *Ginkgo* (*G. digitata* [Brongniart] Heer) first appeared in the Early Jurassic (Tralau 1968; but see Vasilevskaya and Kara-Murza 1963 for a questionable attribution to the Late Triassic), making it the oldest extant genus among seed plants (Arnold 1947). At least a dozen species have

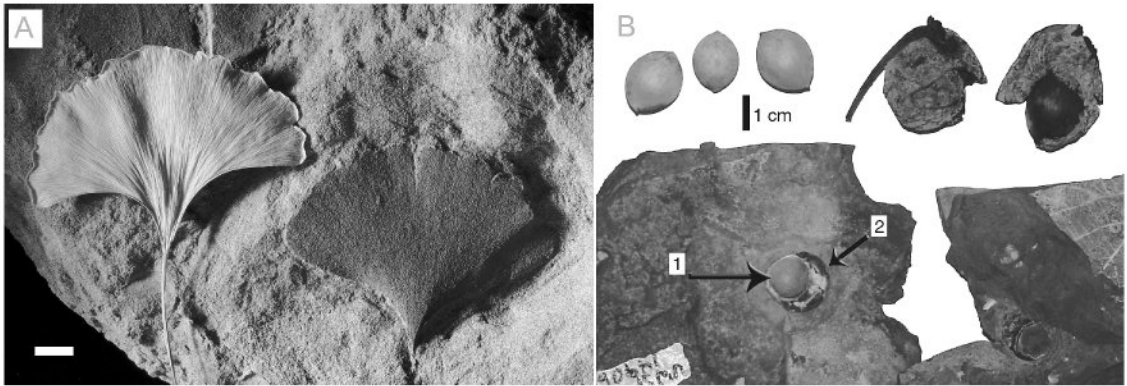


FIGURE 1. A, Leaf of *Ginkgo biloba* (left) and fossil *G. adiantoides* (right) (scale bar, 1 cm). Fossil leaf from Colgate Member of Fox Hills Formation (Maastrichtian; YPM 7004). Photo by W. K. Sacco. B, Seeds of extant *G. biloba* and Paleocene *Ginkgo* seeds from Almont, North Dakota. *G. biloba* seeds above on left have been removed from their sarcotestas; those on the right have not. Paleocene *Ginkgo* seed on left (UWSP 14906) shows both sclerotesta (arrow 1) and sarcotesta (arrow 2), as does fossil seed on right (UWSP 2493). Photo courtesy of Mike Nowak.

been assigned to *Ginkgo*, which achieved its greatest diversity during the Early Cretaceous (Tralau 1968). Of particular interest for this study is *G. adiantoides* (Unger) Heer, which is morphologically identical to *G. biloba* (Seward 1919: p. 29; Shaparenko 1935; Manum 1966; Tralau 1968; Möslle et al. 1998). These similarities have led some authors to consider *G. adiantoides* conspecific with *G. biloba* (Seward 1919; Tralau 1967, 1968: p. 87). *Ginkgo adiantoides* first appeared in the Early Cretaceous and was relatively common during the Late Cretaceous and Paleogene (Tralau 1968; Vakhrameev 1991).

Although several additional Northern Hemisphere species of Cenozoic *Ginkgo* have been formally established, all but one of these are morphologically identical, or nearly so, to *G. adiantoides* (and *G. biloba*). One example is *G. beckii* Scott, Barghoorn, & Prakash, a species of Miocene wood associated with *G. adiantoides* foliage, which shows a striking similarity to *G. biloba* wood, with the possible exception of fewer pits per unit length on the radial walls of its tracheids (Scott et al. 1962; Mastrogioseppe et al. 1970). The only Cenozoic form that possibly merits recognition as a separate species is *G. gardneri* Florin (Tralau 1968), which has more-prominent papillae and less-sinuuous adaxial epidermal cells than does *G. adiantoides* (Manum 1966). *G. gardneri* is found only in the late Paleocene deposits on the Isle of Mull, Scotland (e.g., Boulter and Kvaček 1989). Giv-

en this lack of morphological diversity, it is possible that Ginkgoales has been monospecific (or nearly so) in the Northern Hemisphere for the entire Cenozoic. In the Southern Hemisphere a different, more strongly digitate type of *Ginkgo* leaf persists into the Eocene, but we lack data on its occurrence and do not discuss it further here.

A number of Mesozoic species of *Ginkgo* closely match the extant species as well. For example, Möslle et al. (1998) found strong similarities between the cuticles of the Early Cretaceous *G. coriacea* Florin and *G. biloba*. Villar de Seoane (1997) reported similar results for the cuticle of Early Cretaceous *G. tigrensis* Archangelsky from Argentina. Zhou (1993) compared the megaspore membranes of middle Jurassic *G. yimaensis* Zhou & Zhang with *G. biloba*, and noted few morphological differences. Van Konijnenburg-van Cittert (1971) concluded that the pollen of middle Jurassic *G. huttoni* (Sternberg) Heer was morphologically identical to *G. biloba*. Thus, *Ginkgo* is a highly conservative morphologically, with the long-ranging fossil species *G. adiantoides* indistinguishable from modern *G. biloba*.

Ecology of Ginkgo biloba.—*Ginkgo biloba* (Fig. 1) has been cultivated for more than 2000 years in China and for some 1000 years in Japan as a source of food, shade, and beauty (Li 1956; He et al. 1997); small stands are sometimes present within the forests customarily preserved adjacent to Buddhist and Taoist

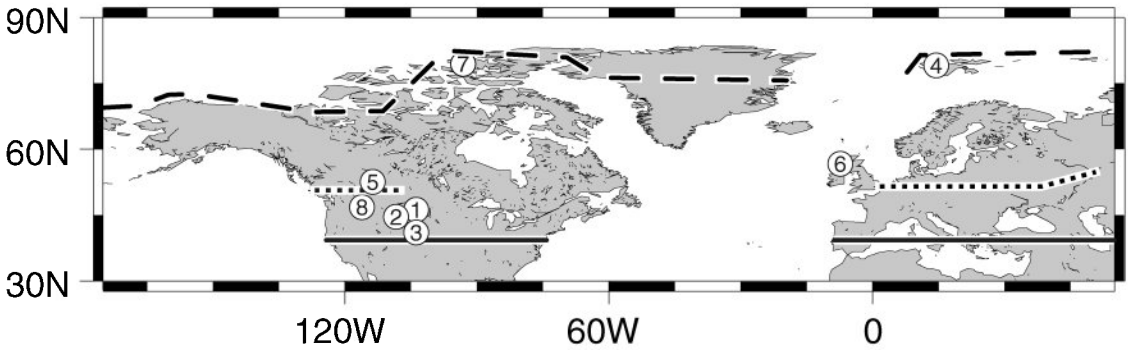


FIGURE 2. Geographic distribution of *Ginkgo*-bearing localities used in this study. Numbers refer to the following field areas: 1 = Williston Basin; 2 = Bighorn Basin; 3 = Denver Basin; 4 = Spitsbergen; 5 = south-central Alberta; 6 = Isle of Mull; 7 = Axel Heiberg Island; 8 = north-central Idaho. Solid line represents the southern extent in the Northern Hemisphere of the genus *Ginkgo* for the Jurassic–Miocene. Dashed and dotted lines represent the northern extent of the genus *Ginkgo* during the Cretaceous–Eocene and the Miocene, respectively. Data from Tralau (1967).

temples (Li 1956). However, the natural ecology of *G. biloba* is largely unknown because no unequivocally natural stands remain today (see discussions in Li 1956; Franklin 1959; Del Tredici et al. 1992; He et al. 1997). The last remaining natural populations are (or were) largely in the low coastal and interior mountains straddling the Yangtze River. This is the region where *G. biloba* was first cultivated and also harbors relictual stands of other taxa with long fossil records such as *Cryptomeria*, *Liriodendron*, *Metasequoia*, *Nothotaxus*, and *Pseudolarix*. The area lies at about 30°N latitude and has a warm temperate mesic climate (mean annual temperature = 9–18°C; mean annual precipitation = 600–1500 mm) (Li 1956; Del Tredici et al. 1992; He et al. 1997). In cultivation *Ginkgo* tolerates a wide variety of seasonal climates, ranging from Mediterranean to cold temperate, where winter temperature minimums can reach –20°C. Interestingly, nearly all fossil occurrences of *Ginkgo* lie poleward of 40° and, concomitant with cooling and increased seasonality during the Tertiary, its geographical range progressively constricted toward 40°N, and it disappeared all together from the Southern Hemisphere (Tralau 1967; Ziegler et al. 1996) (see Fig. 2). Thus, both its broad modern range of climatic tolerance and the paleobotanical data suggest that the climatic parameters of its current (semi-)natural range at 30°N are anomalous in terms of the long-term history of *Ginkgo* (Ziegler et al. 1996).

Ginkgo is a tree of medium height, reaching approximately 30 m (Del Tredici et al. 1992; He et al. 1997), and can live as long as 3500 years (see He et al. 1997). Although *Ginkgo* is frequently described as slow growing, under favorable conditions with warm summers it exhibits growth rates of up to 30 cm/yr for the first 30 years or so of its life (Del Tredici 1989). During this “bolting” phase of their growth, seedlings and saplings have a straight main axis, with sparse, excurrent branches. After that, growth slows markedly—100-year-old trees may have attained only two-thirds of their mature height (Santamour et al. 1983; He et al. 1997)—and the young tree begins to fill out its crown (Del Tredici 1989). Plants do not produce viable seeds for 20 to 30 years (Wyman 1965; Santamour et al. 1983; He et al. 1997), but individual trees can remain fertile for more than 1000 years (S.-A. He personal communication 2000). *Ginkgo*’s fusiform seeds are large, ranging from 1 to 2 cm in length.

In addition to sexual reproduction, *Ginkgo* can reproduce clonally from embedded buds, called lignotubers (or basal chichi), that occur near the base of the trunk. If the soil in the immediate environment is disturbed, as by excessive erosion, positive geotropic growth is stimulated within these lignotubers. Once the apex of a lignotuber penetrates below ground, it forms rhizomatous tissue that can generate both aerial shoots and adventitious roots (Del Tredici 1992). In a modern “semi-wild” stand in the coastal mountains near the Yangtze Riv-

er studied by Del Tredici et al. (1992), 40% of the larger trees had at least two primary stems but few saplings were present, a clear indication of the reproductive importance of lignotubers. In older individuals, these buds also form within secondary stems and are called aerial chichi. As with lignotubers, aerial chichi develop in response to a disturbance (e.g., severe crown damage) and can lead to successful clonal reproduction (Fujii 1895; Del Tredici et al. 1992).

Modern *Ginkgo* is typically shade intolerant, growing best on exposed sites (He et al. 1997). Del Tredici et al. (1992) observed that seeds of *G. biloba* in a "semi-wild" stand require an open canopy for growth and development; Jiang et al. (1990) reported a similar requirement in another "semi-wild" stand. Many of the individual trees studied by Del Tredici et al. (1992: p. 202) were growing in disturbed microsites such as "stream banks, steep rocky slopes, and the edges of exposed cliffs." However, Del Tredici (1989) also suggests that *Ginkgo* may play a role as a gap opportunist and persist in the shady understory of the forest until a gap occurs that allows it to shoot up into the canopy.

At least in cultivation, *Ginkgo* grows best in "sandy loam soils. . . along dams. . . or at the foot of hill slopes" (He et al. 1997: p. 377), environments that are well watered and well drained. *G. biloba* is very successful as an urban street tree (e.g., Handa et al. 1997), owing in part to its tolerance to air pollution (Kim and Lee 1990, Kim et al. 1997) and its high resistance to insects (Major 1967; Kwon et al. 1996; Ahn et al. 1997; Honda 1997), fungi (Major et al. 1960; Major 1967; Christensen and Sproston 1972), bacteria (Mazzanti et al. 2000), and viruses (Major 1967), as well as its ability to competitively grow on exposed sites. *Ginkgo's* resistance to disease is due, in part, to its high production of secondary defense compounds (e.g., Yoshitama 1997).

Implications for Fossil Ginkgo.—Although the close morphological similarity of *Ginkgo adiantoides* to *G. biloba* makes it tempting to infer the paleoecology of the fossil species from what is known of the living, the extreme relictual nature of the modern form suggests that such surmises should be made cautiously and only

with corroboration from the fossil record (see Hickey 1977). Uemura (1997) thought that *Ginkgo* was ecologically conservative through time, and required moist environments. Kovar-Eder et al. (1994) studied Neogene occurrences in central Europe and considered *G. adiantoides* an accessory element in riparian communities. Spicer and Herman (2001) reported similar depositional associations for mid-Cretaceous *G. adiantoides* in northern Alaska. In this paper, we will provide a quantitative description of the floral associates (defined here as the plants that co-occur with *Ginkgo*) and sedimentological contexts of fossil *Ginkgo*, concentrating primarily on the putative conspecific of *Ginkgo biloba*, *G. adiantoides*, which ranged in age from latest Cretaceous to middle Miocene. Through the interpretation of *Ginkgo's* sedimentological contexts and the modern ecology of the nearest living relatives of its floral associates, two independent lines of evidence will be used to interpret the paleoecology of the genus.

Methods

Sources of Data.—Sedimentological and floral data were obtained through field observations and the literature. Most data are from the Fort Union and Willwood Formations (Big Horn Basin) and the Hell Creek Formation (Williston Basin). The geographic extent of our sampling is shown in Figure 2. Data sources are given in Appendix 1.

Recognition of Sedimentological Contexts.—We assigned sites to environments of deposition according to the lithology, grain size, primary stratification, and overall cross-sectional and plan-view shape of their deposits, along with their organic content and nature of their contacts with surrounding sediments, using criteria developed by J. R. L. Allen (1964, 1965), Hickey (1980), Wing (1984), and Miall (1992). We will use the following terms for the environments of deposition that we recognize here: relief channel, abandoned channel, crevasse splay, active trunk channel, backswamp, and distal floodplain.

Relief channels are represented by thin, shallow-lenticular, laterally restricted bodies of silt to sand-sized sediment that fill minor stream axes used in time of flood. Abandoned

channels represent a segment of a stream or river that was intermittently or permanently cut off from its main channel, whose original depth can be reconstructed from the thickness of the total sedimentary package. They often have claystone or mudstone in their axes. The basal contacts of both types of channels are frequently down-cut, concave upward, and veneered with a coarse (often pebble-sized) basal lag deposit. Plant remains within these deposits are typically parautochthonous (Wing 1984; Gastaldo et al. 1989). These channel deposits are characterized by relatively thin (<5 cm for relief channels and <1 m for abandoned channels) couplets of coarser sandstone and siltstone with finer siltstone and mudstone that represent the alternating periods of flooding or channel reactivation and slack-water or subareal phases (Wing 1984). Intervals within abandoned channels often show evidence of standing water, such as aquatic plants and invertebrates, and successions of small-scale, fining-upwards sequences (Wing 1984).

Crevasse splay deposits are floodplain deposits formed by the breaching of a levee, typically during flood events. They are characterized by sand- or silt-sized sediments with generally tabular beds that are sometimes cross-bedded or cross-laminated. These often overlie finer-grained, massive floodplain sediments. Proximal to the break-through point, downcut contacts with concave-upward bedding and scour and fill structures are more common, but distal to the break-through point basal contacts tend to be more parallel with one another. Beds of sandstone in splays represent multiple reactivation events and range in thickness from centimeters to more than a meter. Often these grade upward into progressively finer sediments that represent low-energy floodplain conditions. The modal grain size of the sediments in these reactivation events usually coarsens upwards because of the progressive lateral shift of the stream axis toward a given point in the crevasse splay (Miall 1992). Crevasse splay deposits are generally more laterally extensive than relief channels but are not traceable for long (>10² m) distances.

Other sedimentological contexts distin-

guished here include backswamps, which are dominated by carbonaceous shale; active trunk channels, which are characterized by massive cross-bedded sandstone; and ponds/lakes, which are distinguished by laminated mudstone and the presence of aquatic plants and animals. Because of the convergence of their properties, we assigned large abandoned channels to the pond/lake category.

Floral Associates.—We generated floral lists for most sites. When possible, we limited these lists to the individual beds within a deposit where *Ginkgo* was found. In general, we follow the taxonomic terminology of Wing et al. (1995). In two cases, we combined closely related species of the family Platanaceae into single counting units. The first of these units consists of the broadly trilobed *Platanus raynoldsii* Newberry and *P. guillelmae* Goepfert, and the second of the narrowly five-lobed *Macginitiea gracilis* (Lesquereux) Wolfe & Wehr and *M. brownii* (Berry) Wolfe & Wehr.

All but two of our sites contain *Ginkgo adiantoides*. *G. spitsbergensis*, found at one site, is considered conspecific with *G. adiantoides* by Tralau (1968), whereas *G. gardneri*, found at one site on the Isle of Mull, may be a distinct species, as discussed above.

Results

Sedimentological Contexts.—Our sampling of 48 sites spanning the latest Cretaceous to middle Miocene indicates that *Ginkgo* is most often found in relief/abandoned channels (44% of all sites) and crevasse splays (38%) (Table 1; raw data presented in Appendix 2). In most relief/abandoned channel deposits, *Ginkgo* occurs within the coarser-grained intervals. *Ginkgo* is rarely preserved in backswamps (4%). Certain depositional environments are preserved more commonly than others or are more likely to preserve fossil plants. The high proportion of relief/abandoned channels and crevasse splays might therefore simply reflect the numerical abundance of these deposits containing plant fossils. To normalize for this potential bias, we determined the distribution of sedimentological contexts for all fossil plant sites (including *Ginkgo*-bearing sites) documented by Johnson (2002) ($n = 157$ sites) and Wing et al. (1995) ($n = 131$). Together, these

TABLE 1. Summary of the distribution of sedimentological contexts and floral associates. Description of columns are as follows: (1) % occurrence at all *Ginkgo*-bearing sites; (2) % occurrence at *Ginkgo*-bearing sites that overlap with the data sets of Johnson (in press) and Wing et al. (1995); (3) % occurrence at all sites (including *Ginkgo*-bearing sites) from the data sets of Johnson (in press) and Wing et al. (1995); (4) % difference between the two restricted sets (i.e., column [2]–[3]); (5) level of significance between the two restricted sets (*G*-test of independence; Sokol and Rohlf 1995: p. 729). Because the sedimentological contexts are not independent of one another (i.e., columns add up to 100%), these *p*-values were adjusted using the Dunn-Šidák method in the following manner: $\alpha' = 1 - (1 - \alpha)^{1/k}$, where $k = 6 =$ the number of significance tests (Sokol and Rohlf 1995: p. 239).

	<i>Ginkgo</i> sites (%)		All sites from restricted set (weighted %)	Difference in restricted set (%)	<i>p</i>
	All	Restricted set			
Sedimentological contexts	(<i>n</i> = 48)	(<i>n</i> = 41)	(<i>n</i> = 288)		
Relief channel/abandoned channel	43.8	41.5	14.3	27.2	0.004
Crevasse splay	37.5	41.5	17.8	23.7	0.012
Channel	8.3	9.8	5.5	4.3	0.98
Backswamp	4.2	4.9	53.2	-48.4	<0.001
Distal floodplain	4.2	4.9	0.8	4.0	0.60
Other (mostly stable ponds/lakes)	4.2	0.0	8.4	-8.4	0.08
Floral associates	(<i>n</i> = 47)	(<i>n</i> = 41)	(<i>n</i> = 289)		
(<i>Ginkgo adiantoides</i>)			8.4		
<i>Cercidiphyllum genatrix</i>	59.6	63.4	32.9	30.5	<0.001
<i>Metasequoia occidentalis</i>	44.7	46.3	27.7	18.7	0.022
<i>Platanus raynoldsii/guillelmae</i>	42.6	48.8	23.3	25.5	0.002
<i>Glyptostrobus europaeus</i>	29.8	31.7	44.3	-12.6	0.19

data sets span the interval from the latest Cretaceous to the early Eocene and include the late Cretaceous Hell Creek Formation and earliest Paleocene part of the Fort Union Formation in the Williston Basin and the Paleocene through early Eocene Fort Union and Willwood Formations in the Bighorn Basin. We considered only our *Ginkgo*-bearing sites included in these data sets (*n* = 41 sites) and weighted the full data sets of Johnson (2002) and Wing et al. (1995) to reflect the distribution of these *Ginkgo*-bearing sites (22% from the Williston Basin, 78% from the Bighorn Basin).

For these two geographic regions, *Ginkgo* is preferentially found in both relief/abandoned channel (42% for *Ginkgo* localities vs. 14% for all plant localities) and crevasse splay (42% vs. 18%) deposits (Table 1, Fig. 3). Equally striking is that the likelihood of finding *Ginkgo* in a backswamp is far less than the background percentage of backswamp deposits (5% vs. 53%). The differences for all three of these sedimentological contexts are significant at the $\alpha = 0.02$ level (*G*-test of independence).

Floral Associates of Ginkgo.—A sampling of 47 *Ginkgo*-bearing sites spanning the latest Cretaceous to middle Miocene reveals that *Ginkgo* most commonly is fossilized with *Cer-*

cidiphyllum genatrix (Newberry) Hickey (co-occur at 60% of all *Ginkgo* sites), *Metasequoia occidentalis* (Newberry) Chaney (45%), *Platanus raynoldsii/guillelmae* (43%), and *Glyptostrobus europaeus* (Brongniart) Heer (30%) (Table 1; raw data presented in Appendix 3). All four of these associates have temporal ranges that span the latest Cretaceous to middle Miocene. Analogous to the potential sedimentological taphonomic bias, it is possible that these floral associates simply dominate the megafloreal record during this interval, which, if true, would diminish the paleoecological significance of our results. As with the data on sedimentary environments, then, we compared a weighted average of the overall floral distribution patterns for the Hell Creek and Fort Union Formations in the Williston Basin (*n* = 158 sites) (Johnson 2002) and the Fort Union and Willwood Formations in the Bighorn Basin (*n* = 131) (Wing et al. 1995) with the *Ginkgo*-bearing sites that overlap with these studies (*n* = 41). *C. genatrix* and *P. raynoldsii/guillelmae* occur more often with *Ginkgo* relative to their overall occurrence rate (63% vs. 33% and 49% vs. 23%, respectively) (Table 1, Fig. 3). These differences are significant at the $\alpha = 0.003$ level (*G*-test of independence). *Ginkgo* also preferentially associates with *M. occidentalis* (46%

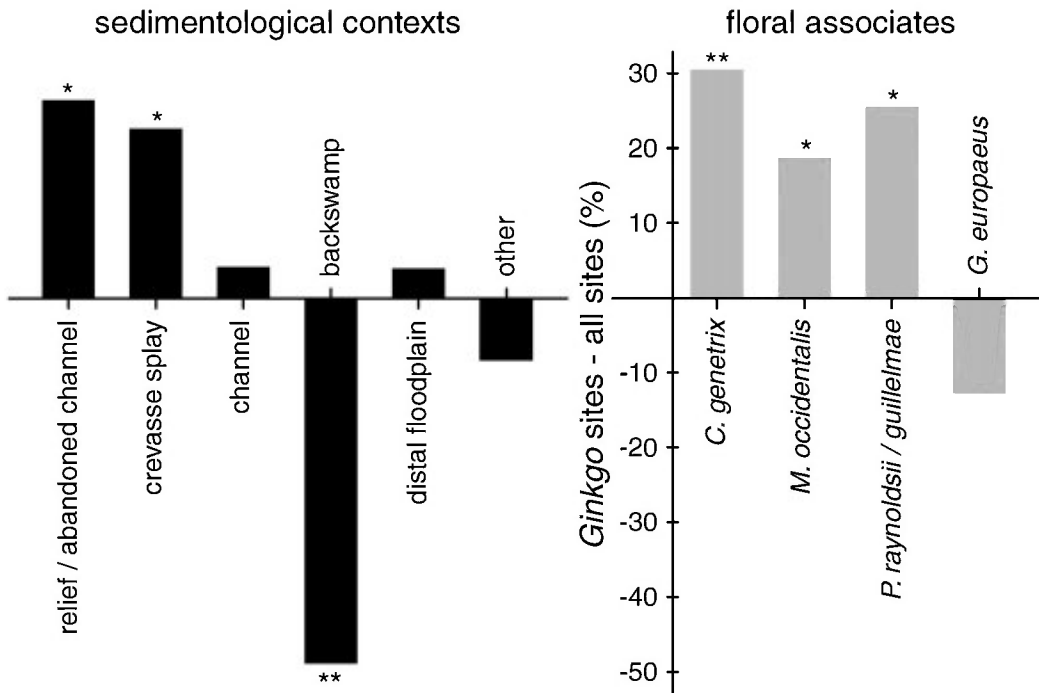


FIGURE 3. Deviations of the proportion of sedimentological contexts and floral associates at *Ginkgo*-bearing sites from the background occurrence rate of these sedimentological contexts and floral associates. Data taken from second-to-last column in Table 1. Methodology of calculation discussed in text. Asterisks represent whether the differences in proportionality are significant at the $\alpha = 0.05$ level (*) or $\alpha = 0.001$ level (**) (*G*-test of independence).

vs. 28%; $p = 0.02$; *G*-test of independence). The background occurrence rate of *G. europaeus*, however, is higher than its co-occurrence rate with *Ginkgo* (44% vs. 32%) (Table 1, Fig. 3), suggesting that it is not useful in determining the paleoecology of *Ginkgo*.

Discussion

Paleoecology of Ginkgo.—The sedimentological features at the majority of *Ginkgo* localities indicate that it grew primarily in disturbed environments along stream margins and the distal sides of levees. These environments are typically well watered (owing to a shallow water table) yet well-drained (owing to their primarily coarse-grained substrate and higher elevation relative to other flood plain settings). Because of their high disturbance rate, open-canopy forests are common in these settings (e.g., Hack and Goodlett 1960; Everitt 1968; Carr 1998).

As reported above, *Cercidiphyllum genatrix* and a form of *Platanus* delimited by the pair *P. raynoldsii* and *P. guillelmae* are two of the more

common floral associates of *Ginkgo*. *C. japonicum* Siebold & Zuccarini, the nearest living relative (NLR) of *C. genatrix*, grows in the wild today in Japan and China. It usually occurs in small gaps or along stream margins (Seiwa and Kikuzawa 1996). It is a fast growing pioneer species, often reproduces by sprouting, and prefers mesic, disturbed sites (Ishizuka and Sugawara 1989). Interestingly, at mid-elevations (1450–3500 m) in the mountains of south-central China, *C. japonicum* occurs on scree slopes (Tang and Ohsawa 1997) and in other highly disturbed habitats (Wang 1961). Although plant remains are rarely preserved in alluvial fan facies, at Ardtun Head (Isle of Mull, Scotland) *Ginkgo* is found in fine-grained sediments within an alluvial fan deposit (see Appendix 2). As noted above, modern *Ginkgo* has been observed growing on steep rocky slopes and along edges of exposed cliffs (Del Tredici et al. 1992). It is possible, then, that disturbance is the overriding ecological filter for *Ginkgo*, and that the fluvial deposits where *Ginkgo* is most commonly pre-

served represent only a small fraction of its potential habitat range.

The NLRs of *P. raynoldsii* and *P. guillelmae* are *P. occidentalis* L., *P. orientalis* L., and their hybrid *P. × acerifolia* Willdenow. These living species are most commonly found in riparian habitats (Tang and Kozłowski 1982; Ware et al. 1992; Thomas and Anderson 1993; Atzmon and Henkin 1998; Everson and Boucher 1998); for example, *P. occidentalis* often grows on the lowest stream terrace (McClain et al. 1993), where flood frequency is highest (Bell 1980). *P. occidentalis* can develop adventitious roots and lenticels in response to flooding (Tsukahara and Kozłowski 1985); however it appears to require aerated soils during the growing season (Everson and Boucher 1998).

Metasequoia occidentalis, another common *Ginkgo* associate (Table 1), has remained largely unchanged morphologically throughout the Cenozoic (Chaney 1951; Christophel 1976; Liu et al. 1999) and is represented today by *M. glyptostrobooides* H. H. Hu & Cheng. Like *Ginkgo*, the geographic range of *Metasequoia* has been severely restricted; however, areas of near-natural stands still grow in one mountain valley in south-central China. It occurs there along stream banks and at seepages at the bases of slopes (Chu and Cooper 1950). These modern observations contrast in part with the paleobotanical observations that show *Metasequoia* most often occurring in swamp, swamp margin, and distal splay environments (e.g., Hickey 1980; Momohara 1994; Wing et al. 1995; Falder et al. 1999). This discrepancy may result either from the fact that most of the valley floor where *Metasequoia* presently makes its last stand has been converted to agriculture and habitat space has been lost, or from a shift in the ecological niche of *Metasequoia* during the Cenozoic.

In summary, the sedimentological record strongly indicates that *Ginkgo* most commonly grew along streamsides and on the proximal slope of levees. The ecology of the NLRs of two genera of *Ginkgo's* common floral associates (*Cercidiphyllum* and *Platanus*) supports these sedimentological interpretations. *Ginkgo's* association with *Metasequoia* proves problematic, however, as the latter most commonly grew in swamps and distal levees during the

Tertiary. It is possible, then, either that *Ginkgo* also grew in more stable distal floodplain settings or that *Metasequoia* was a minor associate in disturbed levee and riparian-type environments. This latter option is supported, albeit weakly, by modern ecological observations of *Metasequoia*.

In general, NLR-derived paleoecological interpretations are less reliable than sediment-derived interpretations because a given lineage of plants can shift its ecological tolerances over geologic time (e.g., Hickey 1977; Wolfe 1977), and because few late Cretaceous and early Tertiary plants have close modern relatives. In contrast, the sedimentology of an autochthonous fossil plant site retains a primary paleoecological signal. Only recently have paleobotanists begun to analyze the sedimentological contexts of their assemblages in an effort to extract paleoecological information (e.g., Hickey 1980; Spicer 1980; Burnham 1988, 1994; Wing et al. 1995; Spicer and Herman 2001; Spicer et al. 2002). The results of this study highlight the potential of applying sedimentological data from a large number of fossil plant sites, and we hope that the application of such data becomes more common in the future.

Implications for the Relationship between G. biloba and G. adiantoides.—Analysis of our data indicates that there were no striking changes in the sedimentological context of *Ginkgo* during the latest Cretaceous to early Eocene (Fig. 4A). *Ginkgo* consistently associated with unstable crevasse splay and relief/abandoned channel environments. Although there is a shift to more relief/abandoned channel localities in the early Eocene, this is driven by a drying trend in the Bighorn Basin that restricted the preservation of fossil plants to these environments and to tabular carbonaceous layers representing swampy floodbasins (Wing 1984).

Ginkgo's floral associates also remain stable through the early Paleogene (Fig. 4B). This stability is striking considering the large number of factors that influence plant migrations and evolution. The one minor change in this time series is the lack of *Metasequoia* during the early Eocene, although this may be due to the paucity of early Eocene backswamp de-

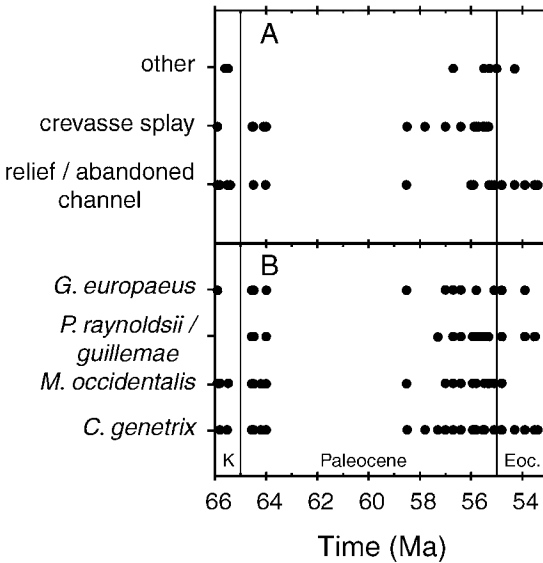


FIGURE 4. Temporal distribution of sedimentological contexts (A) and principal floral associates (B) for latest Cretaceous–early Eocene *Ginkgo*-bearing sites. Data from Appendices 2 and 3.

posits relative to the late Paleocene in the Big-horn Basin (Wing et al. 1995). If correct, this observation provides additional support for inferring *Ginkgo*'s preferential association for streamside and levee habitats.

Data are generally lacking for the Neogene. However, at the middle Miocene Juliaetta site in Idaho, *Ginkgo* occurs in sandy delta foreset beds (Appendix 2). Although the overall depositional setting is lacustrine, *Ginkgo* is found only in this high-energy delta environment, and so perhaps it grew in a nearby riparian setting and was carried by the river to the lakeshore. *Amentotaxus gladifolia* (Ludwig), Ferguson, Jähnichen, & Alvin is the single floral associate of *Ginkgo* at the Juliaetta site. *A. gladifolia* is also present in the late Paleocene Ardtun Head site, some 40 million years earlier. Its nearest living relative, *A. formosana* Li, grows along streams on mountain flanks (Page 1990).

On the basis of our sedimentological and floral data, *Ginkgo* appears to have been ecologically conservative throughout the Tertiary. Furthermore, the environments of growth of the modern *G. biloba* match the paleoecological interpretations generated here. This marked stability in ecology supports previous work,

based upon morphology alone, that *G. adiantoides* and *G. biloba* are conspecific.

The Ecological Paradox of Ginkgo and a Possible Mechanism for Its Decline.—Woody plants successful in highly disturbed habitats today usually share a suite of traits described as the competitive-ruderal strategy, sensu Grime (2001). These may include an early-successional habit, shade intolerance, high growth rates, ability for clonal reproduction (Everitt 1968; Eriksson 1993), early reproductive maturity, small seed size (Harper et al. 1970; Westoby et al. 1992), the production of few secondary defense compounds (Coley et al. 1985), short life span, and a rapid rate of evolution (Eriksson and Bremer 1992). *Ginkgo* shares some of these characteristics, namely shade intolerance, rapid early growth, and a clonal habit, but many of its life-history traits counter those considered beneficial in disturbed environments. *Ginkgo* requires more than 20 years to reach reproductive maturity, produces large seeds needing a protracted period for fertilization and embryo development, manufactures an impressive array of secondary defense compounds, can live more than 3000 years, and has an extremely slow rate of evolution.

Ginkgo therefore represents an ecological paradox: it appears to favor disturbed habitats, and has likely done so for more than 65 million years, yet the living species has few of the life-history traits typical of plants that prosper in modern disturbed settings. One solution to this paradox is to accept a non-uniformitarian view that plants in the geologic past operated in a different ecological regime, and that it is therefore not appropriate to pigeonhole *Ginkgo* into Grime's system of strategies. Angiosperms dominate the canopy today in most riparian and crevasse-splay-type environments, and are the principal taxon from which modern ecological concepts for disturbed habitats are derived. The Ginkgoalean clade first appeared in the Permian and the Genus *Ginkgo* in the early Jurassic, making it possible that, prior to the radiation of angiosperms early in the Early Cretaceous (Doyle and Hickey 1976), certain competitive-ruderal ecological strategies were less highly

developed than in the present (see Knoll 1984; Bond 1989; Midgley and Bond 1989).

It is difficult to test this hypothesis directly because detailed sedimentological data for pre-angiospermous Mesozoic plant fossil-bearing sites are rare, and many lineages that may have dominated these disturbed habitats are extinct. However, from at least the Jurassic, members of Ginkgoales at high latitudes are often associated with sandy channel deposits (Hughes 1976; Spicer and Parrish 1986; Falcon-Lang et al. 2001; Spicer and Herman 2001; Spicer et al. 2002; L.J.H. unpublished field data from the Jurassic in Yorkshire, England). In the subtropical Lower Cretaceous Wealden beds of northwest Germany, *Baiera* is restricted to barrier sands, whereas *Ginkgoites* is found in environments ranging from muddy floodplains to backswamps (Pelzer et al. 1992).

Before the flowering plants, ferns dominated the early seral stages in unstable, fluvial settings (Hughes 1976; Hickey and Doyle 1977; cf. Wing et al. 1993; Taylor and Hickey 1996) and probably provided the chief competition for *Ginkgo* from germination to the young sapling stage. In competition with the ferns, *Ginkgo's* large seed reserves and "bolting" habit are inferred to have been sufficient to carry it beyond the herbaceous pteridophyte canopy. Among arborescent plants, *Ginkgo's* chief competitors for crown space before the rise of the angiosperms were probably Bennettitales and various pteridosperms and tree ferns, plants whose sedimentary context, growth-habit, wood, and leaf structure suggest that they produced a relatively low, open canopy on disturbed sites (Hughes 1976; Crane 1985). The growth strategy of living *Ginkgo*, which undergoes rapid vertical elongation to a height of 10 m before elaborating lateral branches, would have been adaptive in such a situation.

Many of the early flowering plant lineages appear to have evolved in disturbed riparian habitats (Hickey and Doyle 1997; Taylor and Hickey 1996), and so could have been directly competing with *Ginkgo* for resources. For example, studies of the mid-Cretaceous (Albian-Cenomanian) of both northern Alaska (Spicer and Herman 2001) and the Antarctic Penin-

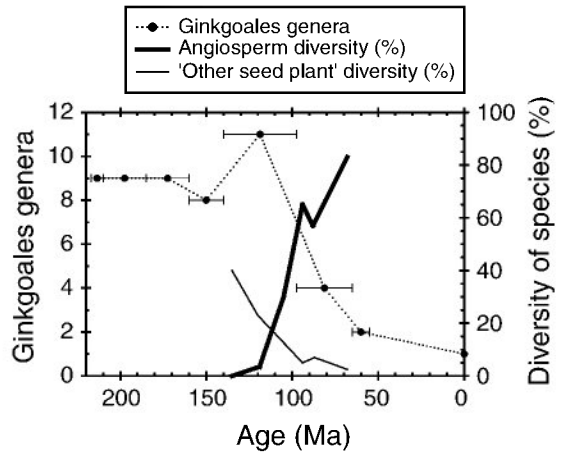


FIGURE 5. Temporal trends of the number of Ginkgoales genera and the percent of total plant species that are angiosperms and "other seed plants" (Ginkgoales, Bennettitales, Caytoniales, cycads, Czekanowskiales, and Gnetales). Ginkgoales data from Tralau (1968); other data from Ligard and Crane (1990).

sula (Falcon-Lang et al. 2001) indicate ginkgo-angiosperm-fern communities in riparian depositional environments. If the combination of rapid life cycles, high dispersal potential, and abundant foliage production in angiosperms was sufficient to out-compete *Ginkgo* in these settings, then it is possible that they played a role in the decline of *Ginkgo*.

Moreover, a striking temporal correlation exists between the rise of relative diversity in angiosperms (Ligard and Crane 1990; Lupia et al. 1999) and the decline in Ginkgoalean diversity (Tralau 1968) (Fig. 5). This comparison is not ideal as one must assume that all Ginkgoales possessed adaptive strategies similar to those of *G. adiantoides*. Nonetheless, even within the genus *Ginkgo* there is a large drop in diversity between the Early and Late Cretaceous (Tralau 1968). The relative diversity of "other seed plants" (see Fig. 5), consisting of Ginkgoales, Bennettitales, Caytoniales, Cycadales, Czekanowskiales, and Gnetales, but not conifers, also declines concomitantly with the rise of angiosperm diversity (Fig. 5) (Ligard and Crane 1990). The relative diversity of ferns, some of which preferred disturbed streamside environments (Taylor and Hickey 1996), drops sharply as well in the mid-Cretaceous, while the diversity of conifers, which preferred backswamp environments, remains

largely unchanged (Ligard and Crane 1990; Lupia et al. 1999). These observations further suggest that angiosperms restructured the ecology of disturbed floodplain environments during the Cretaceous.

Perhaps the most surprising fact is that *Ginkgo* survives to the present at all. The persistence of the *Ginkgo* lineage may relate to its occurrence in mid- and high-latitude areas (see Fig. 2). Wing and Boucher (1998) argued that lower temperatures and less light at higher latitudes make it more difficult for fast-growing competitive-ruderal trees to prosper, and that this explained the delayed increase in angiosperm diversity and dominance at higher latitudes during the Cretaceous (e.g., Lupia et al. 1999). If so, *Ginkgo* may have persisted because it was a mid- to high-latitude lineage for most of its existence (cf. Bond 1989); with growth limited by light and temperature, a relatively slow-growing competitive-ruderal such as *Ginkgo* could persist in the face of angiosperm competitors with the potential for faster rates of growth.

Conclusions

Ginkgo is an extreme example of a geologically long-lived genus, with its one living species arguably having a temporal range of >100 Myr. A quantitative survey of sedimentological and floral data from 51 *Ginkgo*-bearing fossil sites, spanning the latest Cretaceous to middle Miocene, indicates that *Ginkgo* was largely confined to disturbed stream margin and levee environments. Furthermore, the stability of *Ginkgo*'s sedimentological and floral associations through the time series parallels the morphological identity of the fossil species *G. adiantoides* and the living *G. biloba*. As many of *Ginkgo*'s life-history traits (e.g., long life span, large seeds, and late sexual maturity) are not considered advantageous today in highly disturbed habitats, it is possible that *Ginkgo* represents the survival of a pre-angiospermous strategy for growth in well-drained, disturbed habitats.

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Appendix 1
Sources of Data

Site	Source
Williston Basin	
Sedimentology and floral data	Johnson 2002; Crane et al. 1990 (Almont site)
Dating	Hicks et al. 2002
Bighorn Basin	
Sedimentology and floral data	Hickey 1980; Wing et al. 1995; field observations
Dating	Gingerich 2000; Wing et al. 2000 (Age Model 2)
Denver Basin (Site DMNH 2360)	
Sedimentology	R. S. Barclay unpublished data
Dating	Raynolds et al. 2001 (p. 25)
Basilika site (Spitsbergen)	
Sedimentology and floral data	Manum 1963
Dating	Kvaček et al. 1994
South-central Alberta	
Sedimentology and floral data	Speirs 1982; Hoffman and Stockey 1999
Dating	Fox 1990
Ardtun Head site (Scotland)	
Sedimentology and floral data	Boulter and Kvaček 1989
Dating	Royer et al. 2001
Stenkul Fiord site (Ellesmere I.)	
Sedimentology and floral data	Field observations
Dating	Kalkreuth et al. 1996
Beaver Creek site (Montana)	
Sedimentology and floral data	K. R. Johnson unpublished data
Dating	C. N. Miller unpublished data
Juliaetta site (Idaho)	
Sedimentology and floral data	Field observations
Dating	Reidel and Fecht 1986

Appendix 2

Summary of sedimentology at *Ginkgo*-bearing sites. W = Williston Basin (western North and South Dakota, U.S.A.); BHB = Bighorn Basin (Wyoming and Montana, U.S.A.); DB = Denver Basin (Colorado, U.S.A.); S = southwestern Spitsbergen (Norway); A = south-central Alberta (Canada); IM = Isle of Mull (Scotland); E = south-western Ellesmere Island (Canada); MT = western Montana (U.S.A.); ID = north-central Idaho (U.S.A.). Sedimentological contexts with question marks not included in analysis.

Site no.	Site name	Location	Age (Ma)	Sedimentary features	Interpretation
1	DMNH 571	W	65.9	Sandstone-mudstone couplets	Relief channel
2	DMNH 1492	W	65.9	Tabular sand with root traces on top	Crevasse splay
3	DMNH 572	W	65.8	Sandstone-mudstone couplets	Relief channel
4	DMNH 425	W	65.6	Cross-bedded sandstone	Channel
5	DMNH 2087	W	65.5	Sandstone-mudstone couplets	Relief channel
6	DMNH 568	W	65.5	Cross-bedded sandstone	Channel
7	DMNH 566	W	65.5	Gleyed mudstone with abundant root traces	Distal floodplain
8	DMNH 1489	W	65.4	Sandstone-mudstone couplets	Relief channel
9	KJ 83101/8415	BHB	64.5	Tabular sand	Crevasse splay
10	LJH 7423	BHB	64.5	Sandstone-shale-lignite upward sequence; <i>Ginkgo</i> in sand	Crevasse splay
11	LJH 7424c	BHB	64.5	Ledgey cross-bedded sandstone	Crevasse splay
12	LJH 7425/7653	BHB	64.5	Ledgey cross-bedded sandstone	Crevasse splay?
13	LJH 7659	BHB	64.5	Siltstone (relief channel) at base of clay plug (abandoned cutoff)	Relief channel
14	DMNH 2360	DB	64.1	Gray claystone w/ occasional fine/med sand partings	Crevasse splay
15	Basilika	S	64	~8 m siltstones/sandstones resting on ~30 cm pebble/cobble conglom.	Relief channel
16	LJH 7861	BHB	64	Siltstone/sandstone overlying lignite; <i>Ginkgo</i> in sand	Crevasse splay
17	Joffre Bridge	A	58.5	Carbonaceous mudstone; <i>Ginkgo</i> in hard mollusc layer	Abandoned channel
18	Burbank	A	58.5	Coarse sandstone bounded by shales	Crevasse splay
19	SLW 0029	BHB	57.8	Gray siltstone above carbonaceous shale	Crevasse splay
20	SLW 0025	BHB	57.3	Siltstone-mudstone couplets; <i>Ginkgo</i> mainly in siltstone	Relief channel
21	LJH 72127	BHB	57	Lignite-siltstone-sand sequence	Crevasse splay
22	SLW 0019	BHB	56.7	Cross-bedded medium to fine sandstone; large-scale cross-cuts	Channel
23	Chance	BHB	56.4	Coarsening-upwards sequence; <i>Ginkgo</i> in sand	Crevasse splay
24	Almont	W	56	Siliceous, iron-stained shale containing fish scales overlying fine sand	Abandoned channel
25	SLW 993	BHB	55.9	Base of channel fill directly above basal lag deposits (pebbles)	Abandoned channel
26	SLW 992	BHB	55.9	Interlaminated fine/coarse siltstones	Abandoned channel
27	SLW 991	BHB	55.9	Laminated gray siltstone	Crevasse splay
28	SLW 0051	BHB	55.9	Laminated siltstone and fine sandstone	?
29	LJH 72141-1	BHB	55.8	3 m above brown fissile lignite	Crevasse splay
30	SLW 9155	BHB	55.7	Interlaminated siltstone-sandstone	Crevasse splay
31	SLW 9427/9437	BHB	55.5	Thinly bedded sandstone	Crevasse splay
32	SLW 9411	BHB	55.5	Interbedded siltstone and sandstone above a carbonaceous shale	Crevasse splay
33	SLW 9412	BHB	55.5	Laminated fine sand	Crevasse splay
34	SLW 9438	BHB	55.5	Thinly bedded sandstone	Distal floodplain
35	SLW 9434	BHB	55.4	Interlaminated cross-bedded siltstone-sandstone; <i>Ginkgo</i> in siltstone	Crevasse splay
36	SLW 9050	BHB	55.3	Interlaminated siltstone-sandstone	Crevasse splay
37	SLW 9715/981	BHB	55.3	Laminated fining-upwards sequences; basal lag contains mollusks	Relief channel
38	SLW 9936	BHB	55.3	Siltstone overlying sandstone	?

Appendix 2. Continued.

Site no.	Site name	Location	Age (Ma)	Sedimentary features	Interpretation
39	SLW 8612	BHIB	55.3	Carbonaceous shale	Backswamp
40	Ardtun Head	IM	55.2	White/gray clay in a clay/sandstone sequence interbedded with basalt	Relief channel
41	SLW 9812	BHIB	55.1	Gray shale-mudstone couplets	Relief channel
42	Stenkul Fiord	E	55	Medium to fine cross-bedded sandstone with climbing ripples	Channel
43	SLW 9911	BHIB	54.8	Mudstone/siltstone couplets; green sand at base	Relief channel
44	SLW 9915	BHIB	54.8	Sandstone-carbonaceous shale-siltstone unit; <i>Ginkgo</i> in top siltstone	Relief channel
45	SLW 841	BHIB	54.3	Carbonaceous shale	Backswamp
46	SLW LJ	BHIB	53.9	Coarse carbonaceous siltstone	Relief channel
47	SLW H	BHIB	53.5	Sandy siltstone	Relief channel
48	SLW near YPM 67	BHIB	53.5		Relief channel
49	LJH 9915	BHIB	53.4	Thin carbonaceous lenticular paper shale sandwiched between soils	Relief channel
50	Beaver Creek	MT	36		Lake
51	Juliaetta	ID	16.5	Coarse sand; delta foresets	Lake

Appendix 3. Extended.

Site name																				
LJH 72141	SLW 9155	SLW 9427	SLW 9411	SLW 9412	SLW 9438	SLW 9434	SLW 9050	SLW 9715	SLW 9936	SLW 8612	Ardtun Head	SLW 9812	SLW 9911	SLW 9915	SLW 841	SLW LB	SLW H	YPM 67	LJH 9915	Juliaetta
29	30	31	32	33	34	35	36	37	38	39	40	41	43	44	45	46	47	48	49	50
55.8	55.7	55.5	55.5	55.5	55.5	55.4	55.3	55.3	55.3	55.3	55.2	55.1	54.8	54.8	54.3	53.9	53.5	53.5	53.4	16.5
12	4	8	4	4	11	3	5	5	1	4	8	7	6	10	5	22	22	3	3	2
X		X			X							X	X	X	X	X	X		X	
X	X	X		X	X		X	X		X		X		X		X	X	X		
X												X	X	X		X	X	X		
		X		X		X		X					X	X		X	X			
	X	X			X		X									X	X			
		X	X	X	X	X														
			X	X	X	X														
								X												
X												X			X	X	X		X	
X										X		X			X	X				

Appendix 4

Complete list of species names with authors used in the text and appendices

- Acer silberlingii* Brown
Aesculus hickeyi Manchester
Amentotaxus formosana Li
Amentotaxus gladifolia (Ludwig) Ferguson, Jähnichen, & Alvin
Archaeampelos acerifolia (Newberry) McIver & Basinger
Athyrium Felix-femina L.
Averrhoites affinis (Newberry) Hickey
Baiera sp. F. Braun
Beringiaphyllum cupanoides (Newberry) Manchester, Crane & Golovneva
 Betulaceae sp. 1 (sensu Wing et al. 1995)
Cercidiphyllum genatrix (Newberry) Hickey
Cercidiphyllum japonicum Siebold & Zuccarini
Corylus insignis Heer
Dryophyllum subfalcata Lesquereux
Erlingdorflia montana Johnson
 "Ficus" *artocarpoides* Lesquereux
 "Ficus" *planicostata* Lesquereux
Ginkgo adiantoides (Unger) Heer
Ginkgo beckii Scott, Barghoorn & Prakash
Ginkgo biloba L.
Ginkgo coriacea Florin
Ginkgo digitata (Brongniart) Heer
Ginkgo gardneri Florin
Ginkgo huttoni (Sternberg) Heer
Ginkgo spitsbergensis Manum
Ginkgo tigrensis Archangelsky
Ginkgo yimaensis Zhou & Zhang
Ginkgoites Seward
Glyptostrobus europaeus (Brongniart) Heer
Leepierceia preartocarpoides Johnson
Macginitiea brownii (Berry) Wolfe & Wehr
Macginitiea gracilis (Lesquereux) Wolfe & Wehr
Menispermites parvareolatus Hickey
Metasequoia glyptostroboides H. H. Hu & Cheng
Metasequoia occidentalis (Newberry) Chaney
Nyssidium arcticum (Heer) Iljinskaya
Paranymphea crassifolia (Newberry) Berry
 Platanaceae
Platanus × *acerifolia* Willdenow
Platanus guillelmae Geoppert
Platanus occidentalis L.
Platanus orientalis L.
Platanus raynoldsii Newberry
 "Rhamnus" *cleburni* Lesquereux
Taxodium olrikii (Heer) Brown
Trochodendroides nebrascensis (Newberry) Dorf
Vitis stantoni (Knowlton) Brown
Wardiaphyllum daturaeifolia (Ward) Hickey
Zingiberopsis isonervosa Hickey
Zizyphoides flabella (Newberry) Crane, Manchester & Dilcher