

IN SITU CERCIDIPHYLLUM-LIKE SEEDLINGS FROM THE PALEOCENE OF ALBERTA, CANADA¹

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ABSTRACT

Fossil seedlings and seeds of an extinct *Cercidiphyllum*-like plant occur in the Paskapoo Formation (Late Paleocene) at Joffre Bridge near Red Deer, Alberta. Cotyledon and early seedling leaf stages are preserved in growth position. Morphological details of seedlings and seeds support a close relationship between the Paleocene fossils and extant *Cercidiphyllum*, and suggest that during the Upper Cretaceous and Tertiary (Paleogene) *Cercidiphyllum*-like plants were important early colonizers of open flood-plain environments.

IN RECENT YEARS paleobotanical studies have devoted increasing attention to investigating the reproductive biology of fossil plants (e.g., Taylor, 1977; Stockey, 1978; Crepet, 1979; Dilcher, 1979; Taylor and Millay, 1979; Rothwell, 1981). Despite many examples of exceptional preservation, knowledge of early seedling stages in the life-cycle of fossil plants is extremely limited. The few examples of preservation of seedlings in the fossil record include araucarian conifers (Kendall, 1949; Stockey and Taylor, 1978; Nishida, 1981), a voltzialean conifer (Grauvogel-Stamm and Grauvogel, 1975) and two genera of viviparous angiosperms (Rhizophoraceae) (Chandler, 1964; Wilkinson, 1981). In this paper, fossil seeds and seedlings of a *Cercidiphyllum*-like flowering plant from the Paskapoo Formation of central Alberta are described. These remains provide a remarkable example of what must have been nearly instantaneous preservation. In addition the seedlings provide important information with respect to the systematic relationships, paleoecology, and life cycle of this widespread Upper Cretaceous and Tertiary (Paleogene) fossil plant.

MATERIALS AND METHODS—Over 8,000 fossil seedlings have been collected from the Joffre Bridge locality (Paskapoo Formation) 14 km east of Red Deer, Alberta (UN226940). Fossil mammals (Krause, 1978; Fox, 1983) date the sediments as Tiffanian (Late Paleocene) in age.

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Plant fossils occur in a pale green-gray to buff, fine-grained siltstone 7–10 mm below a hard calcareous layer containing abundant freshwater mollusks, and 15–30 cm above a sandstone layer. Overlying and underlying sediments contain abundant plant remains including leaves, fruits and seeds of a *Cercidiphyllum*-like plant, leaves and fruits of *Platanus*, shoots and cones of *Glyptostrobus* and *Metasequoia*, rhizomes and tubers of *Equisetum*, *Azolla*, and fragments of a variety of other angiosperm taxa. The associated fauna includes insects (Kevan and Wighton, 1981; Wighton, 1982), fish (Wilson, 1980), amphibians, reptiles, and mammals (Fox, 1983).

The seedlings are confined to a layer 1–3 cm thick that can be traced laterally for 50–60 m. Within this layer, seedlings are abundant, often occurring at densities of 20–40 per 10 cm². Most are preserved upright in growth position; less than 1% are compressed laterally. Over 99% of the seedlings that occur at the Joffre Bridge locality are those of a *Cercidiphyllum*-like plant. Most of the remainder are referable to *Platanus*. The current study deals only with the seeds and seedlings of the *Cercidiphyllum*-like plant. The authors plan a detailed investigation and whole plant study in a forthcoming publication.

All specimens are deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

RESULTS AND DISCUSSION—Seedlings are preserved at different stages of development. Many have only cotyledons present (Fig. 1, 3) whereas most have cotyledons and first or second leaves (Fig. 4, 5, 7). None of the seedlings show more than three pairs of leaves, suggesting that all probably germinated at approximately the same time. Germination was epi-

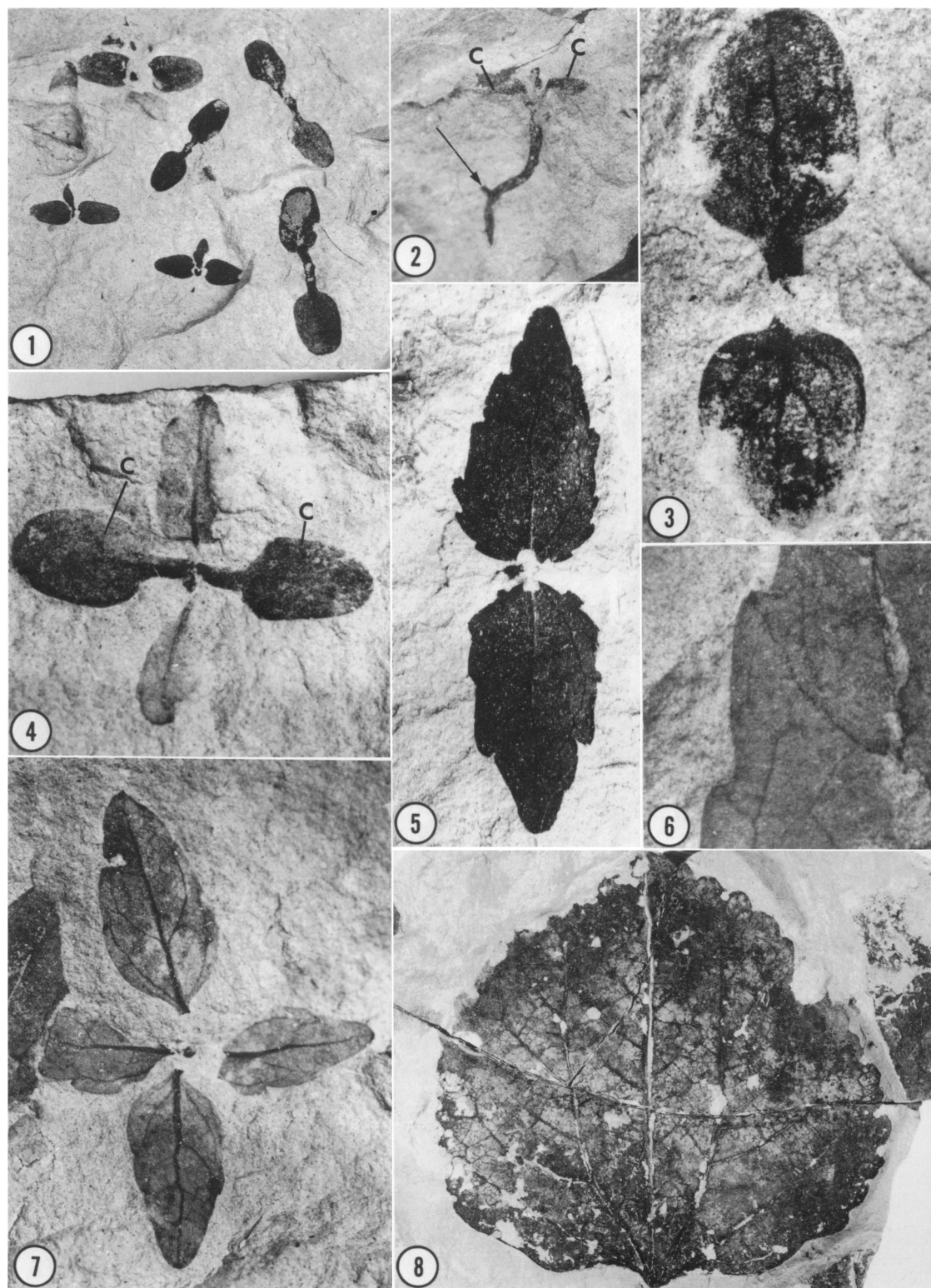


Fig. 1–8. Fossil *Cercidiphyllum*-like seedlings and associated leaf. 1. Seedlings with cotyledons. S10715. $\times 2.7$. 2. Laterally compressed seedling with two cotyledons (c) and lateral root (arrow). S11786. $\times 3.3$. 3. Cotyledon venation. S12103. $\times 11.8$. 4. Seedling with cotyledons (c) and first leaves. S10717. $\times 5.7$. 5. Seedling leaves showing crenate margin. S12102. $\times 4.8$. 6. Details of tooth venation on seedling leaf. S8947. $\times 10$. 7. Seedling with first and second leaves. S11226. $\times 4.8$. 8. Mature *Cercidiphyllum*-like leaf from overlying sediments. S9559. $\times 0.8$.

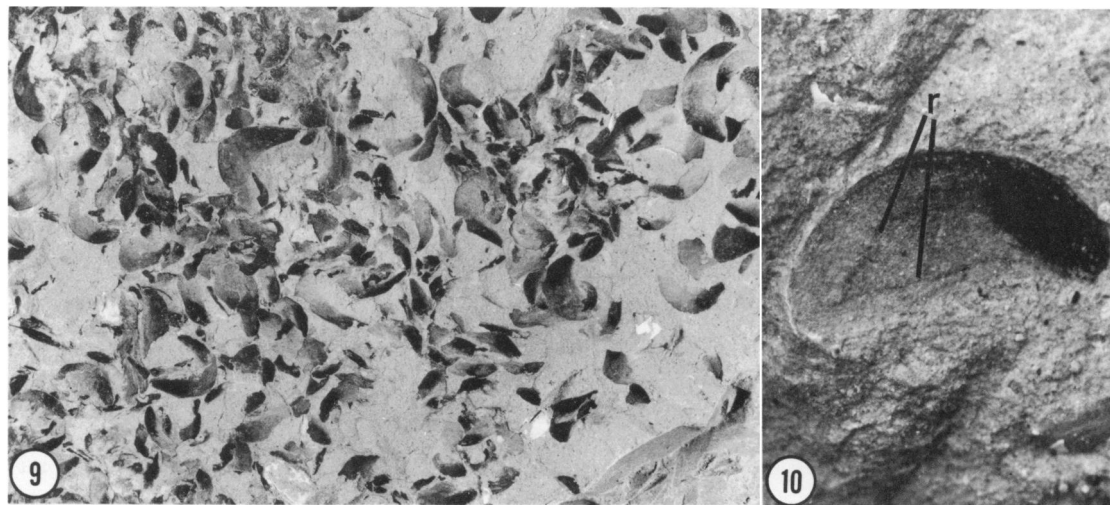


Fig. 9–10. Fossil *Cercidiphyllum*-like seeds. 9. Numerous winged seeds. S11886. $\times 1.8$. 10. Seed showing raphe (r) in wing. S10817. $\times 8.4$.

geal, producing a thin hypocotyl and two cotyledons (Fig. 2). Two laterally compressed specimens show the first lateral root approximately 5.5 mm below the cotyledonary node (Fig. 2).

The major veins in seedling leaves are generally well preserved, but details of venation in teeth and cotyledons are only visible in a few specimens (Fig. 3, 6). Neither cotyledons nor seedling leaves have cuticle preserved, but some show cellular details preserved as poor impressions in the matrix.

Cotyledons are broadly ovate to oblong, 2.0–4.0 mm long and 1.5–3.0 mm wide, with an entire margin and rounded apex (Fig. 1, 3, 4). The base tapers abruptly into a short petiole (Fig. 4). Venation is pinnate and camptodromous, with a prominent midrib running to the apex and two to three pairs of opposite to subopposite lateral secondary veins (Fig. 3). The lowermost secondaries arise above the base of the cotyledon at a low angle and extend for half the length of the cotyledon. The more distal secondary veins arise at higher angles and are generally less prominent than the pair below (Fig. 3).

Seedling leaves are borne in opposite pairs, with first and second leaves showing similar architecture. These leaves are ovate with an acute to rounded apex, and an obtuse base decurrent into the petiole (Fig. 7). Margins are sparsely crenate with glandular teeth (Fig. 5, 7). Venation is similar to that of the cotyledons but more pronounced, with up to six pairs of secondary veins. In the lower part of the leaf the secondary veins form weak brochidodromous loops (Fig. 7). Teeth are glandular with

an opaque papillate tip inset into the lamina (Fig. 6). On either side of the leaf are 3–6 teeth (Fig. 5, 7) each supplied by a single tertiary vein that branches from the adjacent brochidodromous secondary loop (Fig. 6). Two lateral tertiary veins converge towards the apex of each tooth, which is therefore of the chloranthoid type (Hickey and Wolfe, 1975). The first pair of leaves are usually 2.0–8.0 mm long and 2.0–4.5 mm wide, whereas the second pair are 6.0–14.0 mm long and 3.0–7.0 mm wide.

The architecture of seedling leaves is similar to that of *Cercidiphyllum*-like foliage found at Joffre Bridge (Fig. 8). Other organs of this fossil plant are also present and are currently under investigation. *Cercidiphyllum*-like seeds are particularly abundant (Fig. 9) and occur scattered throughout the seedling layer. These seeds are 3.5–7.0 mm long and 1.5–3.5 mm wide, winged and typically crescentic with one edge convex and the other straight to slightly concave (Fig. 10). The seed body is elliptical and positioned close to the convex edge at one end of the wing (Fig. 10). The seed surface is finely striated. Some seeds show the position of the raphe as a dark line in the wing (Fig. 10). The raphe follows the straight margin of the seed for over three-quarters of the length of the wing, then turns abruptly to follow a curve parallel to the convex margin before entering the base of the seed body.

Interpretations of the systematic relationships of Upper Cretaceous and Paleogene *Cercidiphyllum*-like plants have varied with different authors. Some have assigned the leaves, fruits and seed remains to extant *Cercidiphyllum* (Brown, 1935, 1939; Chandrasekharam,

1974; Christophel, 1976), while others have assigned the remains to a variety of extinct and extant genera (Bell, 1949; Wolfe, 1966; Hickey, 1977; Crane, 1981). Re-evaluation of *Cercidiphyllum*-like fossils from the Late Paleocene and Lower Eocene of southern England (Crane, 1978, 1981) has shown that whereas the leaves closely resemble those of extant *Cercidiphyllum* significant differences occur, both in structure and arrangement of foliicles, and in cellular details of the seed. The Joffre Bridge seeds and seedlings, however, show some further similarities rather than differences between the fossil specimens and the extant genus. The seedling leaves are very similar to those of extant *Cercidiphyllum* (Swamy and Bailey, 1949, fig. 1b, c). They are borne in opposite pairs as in living *Cercidiphyllum*, and the distinctive course of the raphe is like that in seeds of *Cercidiphyllum*, *Trochodendron* and *Tetracentron* (Swamy and Bailey, 1949).

In addition to systematic information, the Joffre Bridge locality also provides some evidence of probable paleoecology of the *Cercidiphyllum*-like plant. The abundance of these plant remains in Upper Cretaceous and Paleogene floras (Brown, 1935; Schloemer-Jäger, 1958; Ilinskaya, 1974) has suggested a riparian habit (Brett, 1956). In the Reading Beds of southern England (Late Paleocene) *Cercidiphyllum*-like remains occur in clay and silt lenses associated with cross-bedded sands that are interpreted as fills of overbank ponds and abandoned channels in a fluvial system. This prompted Crane (1981) to suggest that the plant may have been a colonizer of open habitats. The seeds and seedlings at Joffre Bridge are abundant at a level in the outcrop which is otherwise poor in plant remains. The seedlings demonstrate unequivocally that at some stage the sediment surface was either exposed or only shallowly submerged by water and that seeds were able to germinate and colonize the open surface. The approximately similar ages of the seedlings suggest more or less synchronous, rapid germination, before they were quickly buried by a gentle influx of further fine-grained sediment. Unlike plant-bearing sediments in the Reading Beds, those at Joffre Bridge are not associated with evidence of high energy fluvial conditions, suggesting that the *Cercidiphyllum*-like plant may also have been effective at colonizing open habitats in quieter parts of the flood-plain.

Further information about the reproductive biology of these *Cercidiphyllum*-like plants from the London Clay is suggestive of an opportunistic, early colonizing habit. Pyritized locule casts (*Jenkinsella apocynoides* Reid and

Chandler, 1933, Chandler, 1961, 1964; Crane, 1978) show approximately 100 placental scars. Crane (1981) suggested that up to 50 of these ovules may have matured into seeds. Counts of extant *Cercidiphyllum* show that it typically produces 10–20 seeds per follicle. The numerous dispersed seeds at Joffre Bridge (Fig. 9) also provide circumstantial evidence of high production of small winged seeds indicative of colonizing species (Harper et al., 1970), that were well suited for dispersal by wind or water. Large numbers of small winged seeds, combined with the rapid, and apparently efficient, epigeal germination demonstrated at Joffre Bridge support the view that this fossil plant may have been an important early colonizer of open habitats in Upper Cretaceous and Paleogene flood-plain environments.

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