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# WINGED FRUITS OF LINNAEEAE (CAPRIFOLIACEAE) IN THE TERTIARY OF WESTERN NORTH AMERICA: DIPLODIPELTA GEN. NOV.

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Recent phylogenetic analyses of the Caprifoliaceae and related families have paved the way for critical study and interpretation of the fossil record. A new extinct genus, *Diplodipelta,* is established on the basis of winged fruits from the Eocene, Oligocene, and Miocene of western North America, with two species: *Diplodipelta reniptera* (Becker) comb. nov. and *D. miocenica* (Berry) comb. nov. Although formerly attributed to *Ptelea* and *Dodonaea,* detailed comparative studies demonstrate that the fossils actually represent the Caprifoliaceae, tribe Linnaeeae, on the basis of elongate, indehiscent, longitudinally ribbed fruits with a sterile apical neck and persistent, epigynous calyces, and "supernumerary bracts." The samaroid dispersal units resemble those of extant *Dipelta* because the bracts are enlarged into wings that function in wind dispersal. However, *Diplodipelta* differs from *Dipelta* by the presence of a pair of fruits, rather than just one fruit, per dispersal unit, by the adnation of lateral wings to the peduncle, and by a peculiar transverse folding of the median wing. On the basis of available characters, *Diplodipelta* appears to be the sister group to *Dipelta.* The stratigraphic record of *Diplodipelta,* together with the occurrence of genuine *Dipelta* fruits in the late Eocene of England, indicates that the divergence of these genera occurred during or prior to the late Eocene. The fossil record of Caprifoliaceae is reviewed, and previous reports of fossil *Abelia* fruits are discounted.

## Introduction

The literature that has accumulated over the past century on fossil leaf assemblages of western North America contains many references to elliptical and ovoid winged fruits attributed to the rutaceous genus *Ptelea* (see, e.g., LaMotte 1952; Taylor 1990). Although careful study indicates that fruits of *Ptelea* are indeed present in the North American Tertiary (Call and Dilcher 1995), most of the fossil fruits previously attributed to the genus were misidentified. Some of them recently have been determined to represent samaroid capsule valves of *Craigia* (Tiliaceae; Kvaček et al. 1991). Most of the fossil fruits that have been treated as *Ptelea* from the Tertiary of western North America are here shown to represent samaroid partial infructescences allied to *Dipelta,* an extant Chinese genus of the Caprifoliaceae. These fossils from Washington, Oregon, Idaho, Montana, and Colorado provide the first unequivocal evidence for the recognition of the Linnaeeae tribe of the Caprifoliaceae in the Tertiary of North America and are complementary to the record of *Dipelta* fruits in the Tertiary of England (Reid and Chandler 1926).

Fruit characters are particularly important in the classification of extant genera of the Caprifoliaceae. Fruits range from fleshy and multiseeded (Lonicerae) to capsular (Diervilleae) to achene-like (Linnaeeae). Adaptations for wind dispersal are seen in *Abelia* and *Heptacodium,* with wings formed by the accrescent calyx, and in *Dipelta,* with a samara-like structure formed by the enlargement of inflorescence bracts. Wind-dispersed fruits have a good fossil record because they are readily blown into basins of sedimentary deposition and may be preserved in shales along with fossil leaves. The fossil record of fruits provides information on the antiquity of extant and extinct genera and of particular character states considered to be of phylogenetic importance in the history of this family. The fruits described in this article represent a new genus of Linnaeeae and are significant as the only known extinct genus of Caprifoliaceae.

In this article we recognize two species of the new genus *Diplodipelta,* review the classification of extant Caprifoliaceae, evaluate the probable systematic position of the fossil genus relative to extant genera of the family, discuss the evolution of winged dispersal units in Linnaeeae, and give a brief overview of other fossil Caprifoliaceae.

## Material and methods

Fossils were examined from many paleobotanical collections, including those of the University of California Museum of Paleontology, Berkeley (UCMP; courtesy H. Schorn), Museum of Natural History, Albertson College of Idaho, Caldwell (ACI; courtesy Eric Yensen), University of Michigan, Ann Arbor (UM; courtesy R. Burnham), United States National Museum, Washington, D.C. (USNM; courtesy S. L. Wing and J. Ferrigno), and Yale University, New Haven, Connecticut (YPM; courtesy L. J. Hickey and L. Klise). The greatest number of specimens, collected by the late Herman F. Becker, are in the

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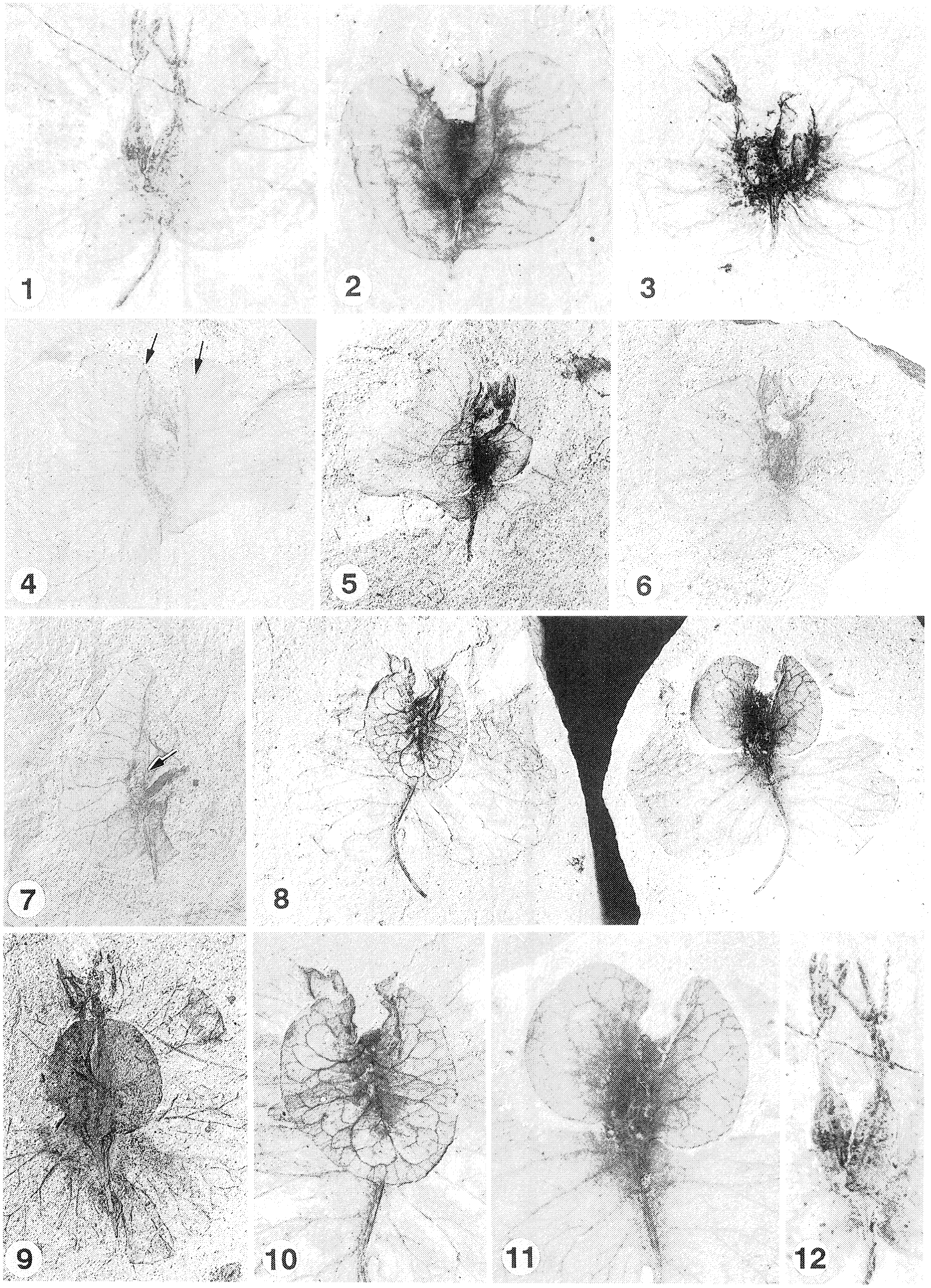

**Figs. 1–12** *Diplodipelta reniptera* (Becker) comb. nov. from the late Eocene/early Oligocene of southwestern Montana. Fig. 1, Specimen showing peduncle and two fruits with persistent, digitate calyces; also showing radiating venation of two lateral wings. Paratype, UM 33622, × 5. Fig. 2, Dispersal unit showing the two lateral wings, the distal lobe of the median wing, and the persistent calyces of two fruits. UM 36946, × 5. Fig. 3, Holotype showing the two lateral wings and a central darkened

New York Botanical Garden paleobotanical collection now housed at YPM. Additional specimens, provided by David Dilcher, Howard and Darlene Emry, Gary Eichhorn, and Allen Marquette, are deposited at the Florida Museum of Natural History, Gainesville, Florida (UF).

Specimens studied are from several localities in western North America: the late Eocene Florissant flora of Colorado (MacGinitie 1953), the Oligocene Ruby and Mormon Creek floras, Montana (Becker 1960, 1961, 1972), the Oligocene Gray Ranch assemblage of the Bridge Creek flora, Oregon (Chaney 1927), the Miocene Grand Coulee flora of Washington (Berry 1931), the Miocene Succor Creek flora of Oregon and Idaho (Fields 1992), and the late Eocene Haynes Creek flora near Salmon, Idaho (currently under study by D. Axelrod).

About 75 fossil specimens of *Diplodipelta* were available for this investigation. It was necessary to examine a large number of specimens to locate examples showing all of the relevant parts. Each fracture plane was studied carefully under a dissecting microscope to discern the morphology and relative position of wings within the samaroid dispersal unit. Details of the wings, receptacle, fruit, and calyx were exposed as necessary by chipping away sediment with fine needles. In order to determine the relative position of the fruits and each of the wings, it was necessary to study and partially dissect both part and counterpart halves of well-preserved specimens.

Fruits of extant Caprifoliaceae were examined at the Missouri Botanical Garden Herbarium (MO) and at the Harvard Herbaria (A and GH). In addition, fresh specimens of *Dipelta floribunda* and other Caprifoliaceae were obtained from the Arnold Arboretum in Jamaica Plain, Massachusetts. The original specimens of *Dipelta europaea* from the Tertiary of England (Reid and Chandler 1926) were studied through the courtesy of a loan from the Natural History Museum, London, England.

## Systematics

### FAMILY—CAPRIFOLIACEAE

### TRIBE—LINNAEEAE

### GENUS—DIPLODIPELTA GEN. NOV.

ETYMOLOGY. *Diplo-* (Greek, *Diploos* = twofold, double) + *Dipelta,* referring to the occurrence of paired fruits in contrast to the solitary fruits of extant *Dipelta.*

DIAGNOSIS. Dispersal unit a bilaterally symmetrical samara-like structure consisting of two fruits, a pair of large lateral wings, and a small median wing. Fruits achene-like, elongate, and fusiform with longitudinal striations and a long sterile neck topped by a thickened region and five digitate calyx lobes. Wings entire-margined with radiating reticulate venation forming intramarginal loops; the two lateral wings each asymmetrical, approximately semicircular, spreading mainly in a common plane that also contains the two fruits, adnate to the peduncle below the point of fruit attachment such that the two wings meet to give a cordate outline to the base of the dispersal unit; the median wing more or less symmetrical, arising at or slightly below the level of attachment of the two fruits, with a prominent midvein giving rise to radiating reticulate venation, widely elliptical on the proximal end, narrowly elliptical on the distal end, folded transversely over the shoulder region between the sterile necks of the two fruits. Type species = *Diplodipelta reniptera* (Becker) comb. nov.

Two species of *Diplodipelta* gen. nov., distinguished primarily on the basis of size of wings and calyx lobes, are recognizable in the North American Tertiary. As in extant *Dipelta,* the fruit-dispersal units have three enlarged wings including a pair of large lateral wings and a smaller median wing. Both species of *Diplodipelta* are

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area where the two fruits were positioned. Three of the five calyx lobes can be seen arising from a thickened region at apex of fruit at left (the other two presumably are buried in the sediment). UM 33621, × 5. Fig. 4, Dispersal unit showing typical venation of the two lateral wings, with a strong ascending primary vein in each wing (arrows). YPM 9443a, × 3. Fig. 5, Opposite counterpart of specimen in fig. 4 showing two calyces (indicating two fruits), microexcavated beneath the level of the fruits to show the proximal end of the median wing. YPM 9443b, × 3. Fig. 6, Dispersal unit with both lateral wings nearly complete, and showing two fruits with persistent calyces. YPM 9445, × 3. Fig. 7, One of the lateral wings torn from the dispersal unit showing the ascending primary vein and the scar of fruit attachment (arrow). YPM 9441, × 3. Fig. 8, Two counterparts of the same fossil. Both halves show the prominent peduncle and same pair of large lateral wings, but each shows a different shape and venation pattern of the median wing. YPM 9435a, b, × 3. Fig. 9, Dispersal unit with faintly preserved lateral wings, and well-preserved median wing with apically protruding digitate calyx lobes. YPM-NYBG 412, × 3. Fig. 10, Distal lobe of the median wing from the specimen in fig. 8, showing subelliptical outline, with reticulate, looping venation radiating downward with respect to the infructescence axis. × 5. Fig. 11, Detail of the right counterpart of specimen in fig. 8, showing proximal end of the median wing with cordate base, thick midvein and U-shaped tear at its top. × 5. Fig. 12, Detail of the fruits from specimen in fig. 1, showing longitudinal striations, fusiform outline, sterile neck, and digitate calyx lobes. × 6.5. Localities: figs. 1–3, 8–12, Ruby Paper Shale; figs. 3–7, Mormon Creek.

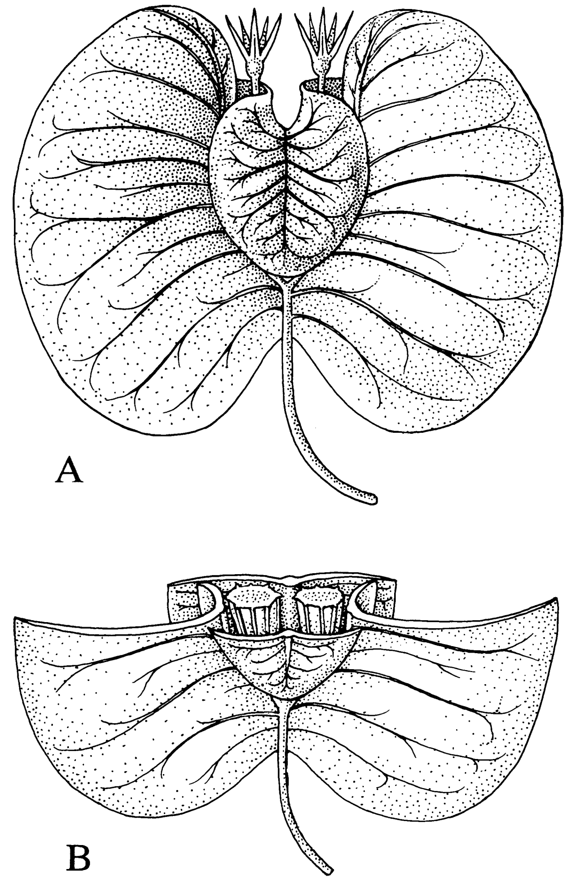


**Fig. 13** Diagrammatic reconstruction of *Diplodipelta reniptera*. *A*, Complete dispersal unit with symmetrical lateral wings, small median wing, and the apices of two fruits with prominent calyx lobes, showing distal lobe of the median wing with its venation fanning downward from the apical fold, modeled after figs. 2, 8, 10. *B*, Basal half of disseminule, transversely sectioned, showing the position of wing laminae relative to each other and the two fruits, as observed by dissection of fossil specimens.

readily distinguished from those of *Dipelta* as indicated in the following key:

Dispersal unit consisting of a single fruit and three enlarged wings; lateral wings free from the peduncle (adnate only to the fruit) and spreading in two different planes; median wing not folded . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Dipelta* spp.

Dispersal unit consisting of a pair of fruits and three enlarged wings; lateral wings adnate to the peduncle, mostly spreading in a single plane; median wing folded transversely, enveloping the two fruits between its proximal and distal portions . . . . . . . . . . . . . . . . . . . . . . . . . . *Diplodipelta* spp.

Dispersal unit small to medium, mostly 0.9–1.8 cm wide, calyx lobes long (1.5–2 mm) . . . . . . . . . . . . *Diplodipelta reniptera* (Becker) comb. nov.

Dispersal unit medium to large, mostly 2.0–2.9 cm wide, calyx lobes short (<1 mm) . . . . . . . . . . . . . . *Diplodipelta miocenica* (Berry) comb. nov.

### SPECIES — DIPLODIPELTA RENIPTERA (BECKER) COMB. NOV. (figs. 1–15, 27*A, D*)

BASIONYM. *Dodonaea reniptera* (Becker 1961, p. 82, pl. 26, figs. 3–8).

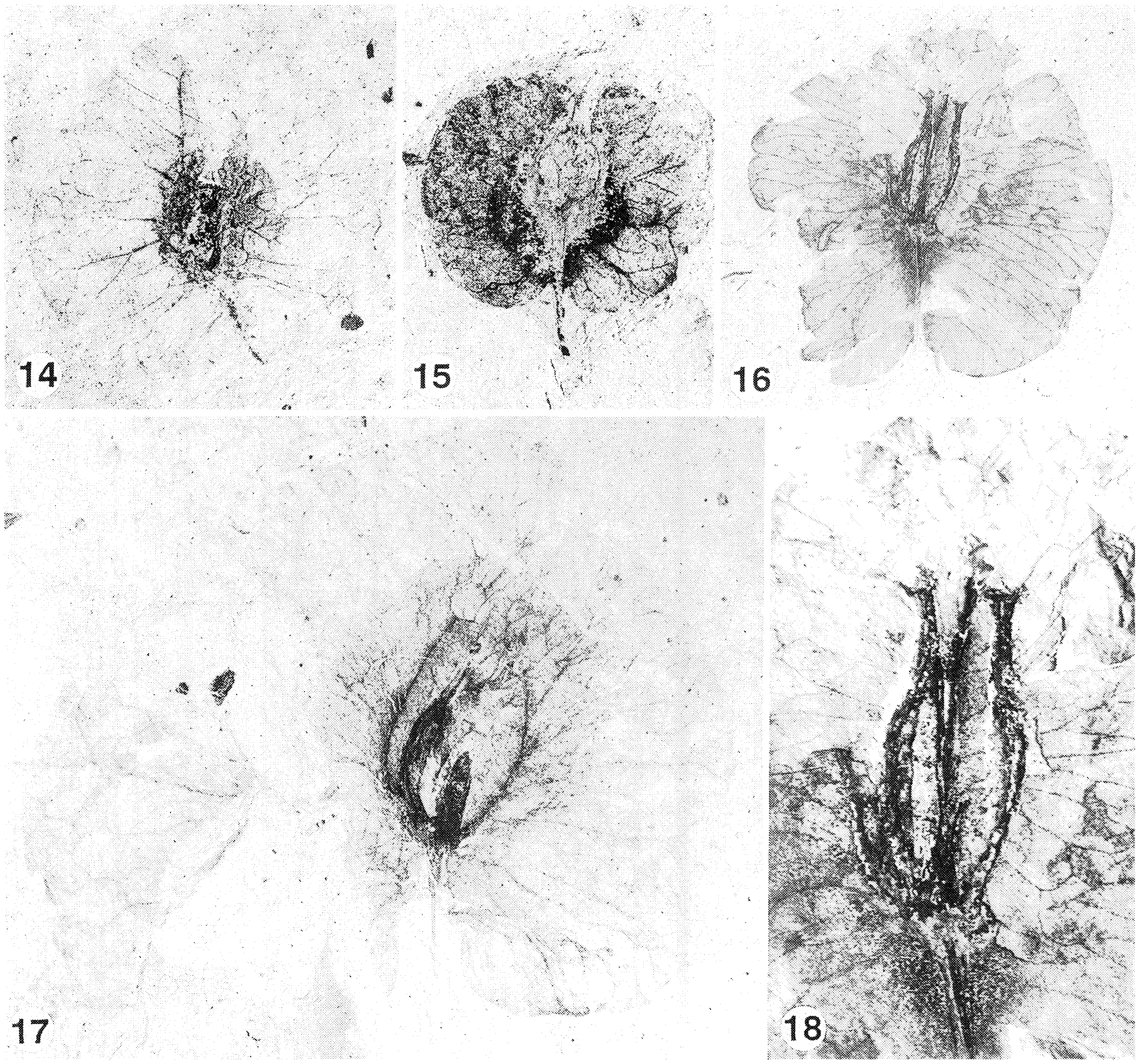
EMENDED DIAGNOSIS. Samara-like dispersal units of *Diplodipelta* with the following dimensions: peduncle 0.1 mm thick, 6 mm long. Dispersal unit width 9–21 mm, height 7–17 mm; fruits 3.5–5 mm long exclusive of calyx lobes, 0.9–1.1 mm wide, with a constricted sterile neck 1 mm long, calyx lobes 1.6–1.9 mm long, 0.2–0.6 mm wide, with a midvein and pinnate secondary veins. Lateral wings 7–17 mm high, 3–6.5 mm wide. Median wing 4.5–6 mm wide, 4–4.5 mm high on the proximal side, folded transversely over the shoulder region between the two fruits, with the distal lobe 2.6–3.5 mm wide, 3–3.5 mm high.

SPECIMENS. Holotype UM 33621, paratype UM 33622 from Ruby flora, Montana. Other specimens according to locality. Florissant: USNM 312724, 312725, 387544, 387545, 405863, YPM 25266, 25267. Ruby paper shale: YPM 9435, 9436, YPM-NYBG 408, 410, 412, 413, 884, 885. Mormon Creek: YPM 9437–9446.

NOMENCLATURE. These fossils were treated previously as *Ptelea cassioides* (Lesq.) MacGinitie (MacGinitie 1953, pl. 48, fig. 3; Becker 1961, pl. 23, figs. 16–18). However, the type of that species (*Rhus cassioides;* Lesquereux 1883) is a fossil leaf that is distinct from these fruiting remains; the epithet *cassioides* thus does not apply to the fruits under consideration. The epithet with priority is *reniptera,* based on *Dodonaea reniptera* Becker (1961).

COMMENTS. This species has been recovered exclusively from Eocene and Oligocene lake deposits in areas of volcanic ash deposition. It is known from Florissant, Colorado (10 specimens), and from the Ruby (15 specimens) and Mormon Creek (12 specimens) floras of southwestern Montana. Specimens from Florissant were figured and described previously as *Dodonaea* (Lesquereux 1883, p. 182, pl. 36, fig. 5), *Ulmus* (Lesquereux 1883, p. 161, pl. 27, fig. 8 only), and *Ptelea* (MacGinitie 1953, p. 128, pl. 48, fig. 3). Those from the Ruby Basin were illustrated and described as *Dodonaea* (Becker 1961, p. 82, pl. 26, figs. 3–8) and as *Ptelea* (Becker 1960, p. 110, pl. 21, fig. 8, pl. 30, figs. 11–13; Becker 1969, p. 107 [only two of the fruits figured by Becker (1969) belong to *Diplodipelta:* pl. 33, figs. 9, 11; the other figured fruits are *Craigia* sp.]; Becker 1972, p. 42, pl. 10, figs. 12–14).

Although first documented from the Florissant



**Figs. 14–18** *Diplodipelta* spp. from the late Eocene of Colorado and Idaho. Figs. 14, 15, *D. reniptera* from the Florissant flora, Colorado. Fig. 14, Specimen showing peduncle and both lateral and median wings. The prominent ascending primary vein is clearly preserved on the left lateral wing. USNM 455138, × 2.5. Fig. 15, Smaller specimen. USNM 405863, × 3.3. Figs. 16–18, *D.* cf. *miocenica* from the Haynes Creek flora, Idaho. Fig. 16, Complete dispersal unit showing pair of fruits surrounded by wings. UF 14767, × 2.5. Fig. 17, Especially large specimen with two unequally developed fruits. UF 14765, × 2.5. Fig. 18, Detail of fruits from fig. 16. Each fruit tapers to an apical neck topped by the perianth. × 7.

flora (as *Dodonaea* and *Ulmus;* Lesquereux 1883), the best-preserved and most informative specimens of this species are from the Ruby and Mormon Creek floras. Even outlines of individual cells are preserved in the fine-grained sediment of the Ruby paper shales. The Ruby material, like that from Florissant, is heavily compressed. The least compressed specimens, which are the best for determining the original orientation and positioning of wings, are from Mormon Creek.

The two large lateral wings are readily observed in all specimens because they form the dominant plane of weakness in the sediment along which the fossils are exposed when the rock is split open. Depending on the nature of preservation and the precise position of the plane of fracture exposing the fossil, one may also observe either the pair of fruits (figs. 1, 6) or the median wing (figs. 2, 5, 8, 9). The fruits are longitudinally striated with about six to eight ribs and are fusiform with a sterile neck. At the top of the sterile neck is a thickened region around which arise five digitate calyx lobes (figs. 1–3, 12). In many specimens the body of each fruit is hidden or not preserved, but even in these the sterile neck and calyx are usually preserved and the presence of two distinct calyces arising side by side (figs. 2, 5, 9) indicates that the fruits were borne in pairs.

The two lateral wings are joined together medially in their lower halves by fusion to the peduncle to form a more or less symmetrical paired structure with a cordate base and apex (figs. 2, 3, 6). Above the level of fruit attachment these wings are free from each other. Each of them has a primary vein (figs. 4, 7) that runs along the line of fusion until the point of fruit attachment, where it is deflected slightly to a position just inside the "inner" wing margin and continues its course to the apex; this vein produces nine to 14 secondary veins that run straight or with dichotomous branching to form loops at the "outer" margin. Only a few veins run toward the inner margin from the primary vein. It appears that the wing tissue was folded along the primary vein, because the inner, narrow part lies at a slight angle to the rest of the wing (fig. 13*B*).

The three-dimensional morphology of *D. reniptera* is reconstructed in figures 13 (*A, B*) and 27 (*A, B*). The configuration of the median wing is difficult to observe directly because the specimens typically split open directly across the two larger wings, leaving one or both surfaces of the median wing hidden in sediment. A particularly informative specimen from the Ruby paper shale shows both counterpart impressions of a single dispersal unit with opposite impressions of the same pair of large lateral wings (fig. 8). A central wedge of sediment, which would have encased the pair of fruits, was lost in collecting the specimen, but the two halves show nicely the relative positions of all of the wings. One of the counterparts, enlarged in figure 10, shows an oval median wing that is constricted, folded, and torn near the upper end. The other counterpart, enlarged in figure 11, shows a corresponding mirror-image constriction and tear at its upper end, but the median wing is wider and has a cordate base and a thick midvein. The matching constriction and tear indicates that this is a single laminar structure that has folded over the shoulder region between the two fruits (fig. 27*A, B*). We describe the attachment end (figs. 11, 27*A*) as the proximal side and the other side of the fold, with its "upside-down" venation, as the distal lobe (figs. 10, 13*A*), as diagrammed in figures 13 and 27 (*A, B*). If the median wing were "unfolded" it would expose the two fruits, as diagrammed in figure 27*B*.

Thus, in addition to the two prominent lateral wings, each disseminule bears a small median wing that is transversely folded over the pair of fruits, leaving only the sterile necks and calyces protruding (figs. 2, 5, 9, 13). The distal lobe is oval and slightly higher than wide, with venation radiating downward with respect to infructescence axis (figs. 2, 10); the wing on its proximal side is circular to wide ovate and basally cordate, with a very thick vertical midrib (figs. 4, 9, 11).

### SPECIES — DIPLODIPELTA MIOCENICA (BERRY) COMB. NOV. (figs. 16–24)

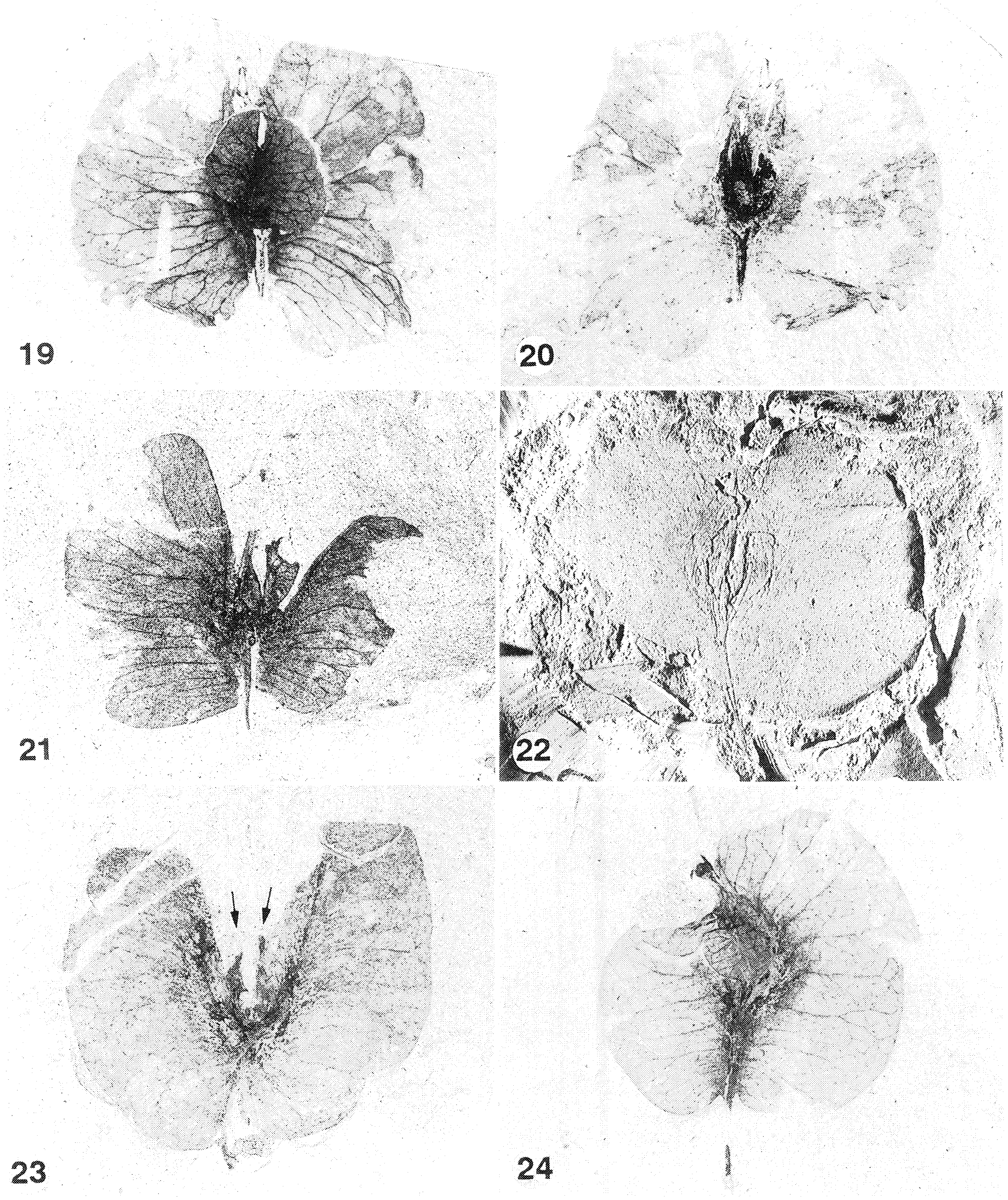
BASIONYM. *Ptelea miocenica* (Berry 1931, p. 39, pl. 12, fig. 7), from Grand Coulee, Washington.

EMENDED DIAGNOSIS. Samara-like dispersal unit resembling that of *D. reniptera,* but with larger wings and shorter calyx lobes. Peduncle 0.2–0.5 mm thick, 9 mm long. Dispersal unit width 22–29 (–38) mm, height 17–25 mm, the fruits 5–8 mm long exclusive of calyx lobes, 1.5–2 mm wide, calyx lobes 0.5–0.8 mm long. Lateral wings 8–15 mm wide, 17–25 mm high. Median wing 6–10 mm wide, 6–10 mm high on the proximal side, folded transversely over the shoulder region between the two fruits, with the distal lobe 4.5–6 mm wide, 5–10 mm high.

SPECIMENS. Holotype USNM 38649, Miocene Grand Coulee, Washington. Other specimens UF 14505–14510, 15041, 15042, ACI 2381–2387, Miocene Succor Creek flora, Idaho-Oregon border.

COMMENTS. *Diplodipelta miocenica* is based on Miocene material from volcanic ash and siltstone lake deposits in Oregon, Idaho, and Washington. Most specimens are from the Succor Creek flora of eastern Oregon and western Idaho (ca. 25 specimens examined). The type specimen from the Grand Coulee flora of Washington was illustrated both by Berry (1931) and by Brown (1937), but in each instance the photos were retouched, so that the authors' interpretation of detail cannot be distinguished from the original image. Brown (1937) pointed out that Berry's rendering of the venation was incorrect and provided a more accurately retouched photograph of the specimen. The same specimen is illustrated once again here, unretouched, in figure 22. The specimen is an impression with no pigmentation and only very faintly preserved venation; it would be difficult to describe the species in detail only on the basis of this holotype. Fortunately, the specimen shows some important features that allow it to be linked to better-preserved specimens from other localities of similar age. These features include a pair of large semicircular wings adjoined along a medial longitudinal vein that bifurcates in the lower one-third of the wing (corresponding to the peduncle and pair of pedicels).

Specimens from the Succor Creek flora show more details of wing morphology and venation (figs. 19, 21, 23, 24) and the shape and position of fruits (figs. 20, 23). One of the most informative specimens is illustrated with both counterparts, showing on one side (fig. 19) the centrally positioned median wing, and on the other side (fig. 20) the compressed remains of the two fruits situated in the plane underneath the median wing. Further dissection of the same specimen revealed



**Figs. 19–24** *Diplodipelta miocenica* (Berry) comb. nov. from the Miocene of Oregon, Idaho, and Washington, all × 2.5. Fig. 19, Typical dispersal unit showing pair of lateral wings and proximal end of the smaller median wing. UF 14505. Fig. 20, Counterpart of specimen in fig. 19 with median wing partially excavated away to show the two dark carbonaceous fruits. Fig. 21, Another specimen partially degraded, showing the two lateral wings and torn remnants of the median. UF 15073. Fig. 22, Holotype showing the two lateral wings and the peduncle that bifurcates indicating the position of two fruits. USNM 38649. Fig. 23, Specimen showing the attachment of two fruits (arrows) near the junction of two lateral wings. Also shows the primary vein in each of the wings. UF 15074. Fig. 24, Specimen showing long peduncle, two lateral wings, median wing, and the protruding sterile neck of a fruit topped by the calyx lobes. UF 14506. Localities: figs. 19–21, 23, Succor Creek flora, Idaho; fig. 24, Succor Creek flora, Oregon; fig. 22, Grand Coulee, Washington.

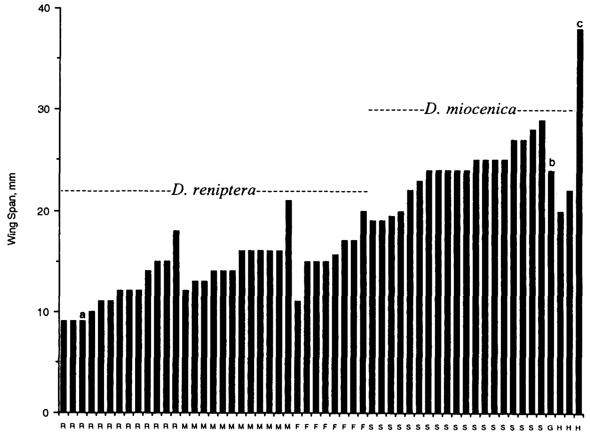


**Fig. 25** Bar graph showing the size distribution of *Diplodipelta* fruits from different localities. *a* = holotype of *D. reniptera* (fig. 3); *b* = holotype of *D. miocenica* (fig. 22); *c* = unusually large specimen from Haynes Creek flora (fig. 17). Localities: *R* = Ruby, Montana, late Eocene; *M* = Mormon Creek, Montana, late Eocene; *F* = Florissant, Colorado, late Eocene; *S* = Succor Creek, Idaho-Oregon border, middle Miocene; *G* = Grand Coulee, Washington, middle Miocene; *H* = Haynes Creek, Idaho, late Eocene(?).

the distal lobe of the median wing in a plane of sediment just beneath the two fruits of figure 20.

It is clear from the arrangement of wings and the paired fruits that *D. miocenica* belongs to the same genus as the *D. reniptera. Diplodipelta miocenica* differs from *D. reniptera* by the larger fruits and wings and shorter calyx lobes. The fruits of *D. miocenica* are about 1.5–2 times longer than those of *D. reniptera.* However, there appears to be the opposite size relationship in calyx lobes, with those of *D. reniptera* being larger. Calyx lobes are not preserved in most specimens of *D. miocenica* but where preserved they are shorter than those of *D. reniptera.* Measurements on UF 14506, which shows complete calyx lobes (fig. 24), give a calyx lobe length of 0.5–0.8 mm, which is less than half the length of those in *D. reniptera* (1.6–1.9 mm), despite the larger overall size of the *D. miocenica* disseminules.

Although differences in fruit size and in sepal length appear to be the most reliable way to distinguish the two species, preservation of many specimens does not allow recognition of these characters. The wing span of the disseminule, measured across the pair of lateral wings, provides another means of identifying most specimens, as shown in figure 25. The wing span ranges from 22 to 29 mm in *D. miocenica,* vs. 9–21 mm in *D. reniptera.* The largest specimens of *D. reniptera* overlap with the smallest of *D. miocenica* (19 mm). However, the populations as a whole are readily separated on the basis of size: 92% (35/38) of the specimens of *D. reniptera* are less than 18 mm wide and 91% (21/23) of the specimens of *D. miocenica* are more than 19 mm wide.

Although *D. miocenica* is best known from Miocene occurrences, new collections from the upper Eocene Haynes Creek flora of Idaho (age courtesy D. Axelrod, unpublished data) contain specimens that appear to represent *D. miocenica* (figs. 16–18). Only three specimens of *Diplodipelta* are known from Haynes Creek, but all three are large, two falling into the normal range of *D. miocenica,* and one (fig. 17) with the largest wing span of any *Diplodipelta* specimen so far observed (38 mm). Calyx lobes are short or not preserved (fig. 18). These specimens are placed provisionally in *D. miocenica,* although more specimens are needed for a thorough comparative study of this Eocene material. If this determination is correct, and if the late Eocene age assignment (ca. 35 million years old) is correct, then the fossil record of this species extends back as far as that of *D. reniptera.* Although *D. reniptera* apparently became extinct after the early Oligocene (perhaps ca. 30 million years ago), *D. miocenica* persisted until the middle Miocene (ca. 14 million years ago).

## Discussion

### SYSTEMATIC POSITION OF DIPLODIPELTA

The resemblance of these fruits to those of *Ptelea* (Rutaceae), suggested by previous taxonomic assignments, is only superficial. *Ptelea* fruits have a basal disk where the pedicel attaches, indicating hypogynous perianth, and the fruit wing is derived from the ovary rather than from bracts. Additional characters important in recognizing authentic *Ptelea* fruits in the fossil record are presented by Call and Dilcher (1995). The resemblance to samaras of *Dodonaea* (Sapindaceae) is also superficial. *Dodonaea* fruits are also derived from flowers with hypogynous perianth and have wings that form from the ovary. In addition, *Dodonaea* fruits are schizocarpic, splitting down the midline into two distinct halves. *Diplodipelta* differs from both of these genera and their families by the presence of an epigynous perianth.

*Diplodipelta* conforms to Caprifoliaceae in the possession of pentamerous flowers and fully inferior ovary. Paired flowers occur sporadically in the family, having been derived by various trends of inflorescence reduction (Weberling 1989). Although the vegetative axes of *Diplodipelta* remain unknown, the paired lateral wings of the infructescence might be taken as an indication of opposite phyllotaxy, another feature of the Caprifoliaceae. Other characters of Caprifoliaceae, such as the zygomorphic corolla, nectaries, and tricolporate, echinate pollen, are not preserved in the fossil material, but there are derived characters that unite *Diplodipleta* to subgroups within Caprifoliaceae, as discussed below, which further support placement in this family.

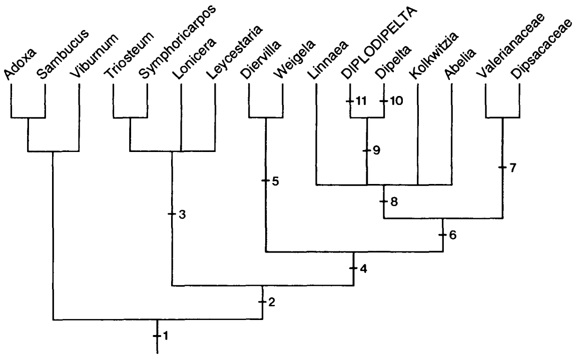


**Fig. 26** Cladogram showing relationships among Caprifoliaceae and related families (following Judd et al. 1994), with the placement of *Diplodipelta* based on the following characters: *1,* opposite leaves/inflorescence bracts; *2,* fully inferior ovary; *3,* polytelic inflorescence; *4,* elongate ovary with sterile apical neck; *5,* fruit capsular, many seeds; *6,* indehiscent, achene-like fruit; *7,* calyx reduced or bristle-like; *8,* supernumerary bracts (placement of this character could be on the branch labeled *6* if the "epicalyx" of Dipsacaceae is homologous with supernumerary bracts; see text for discussion); *9,* enlarged bracts, winged dispersal unit; *10,* one flower (probable abortion of laterals); *11,* two flowers (probable abortion of terminal flower), folded medial wing.

Several phylogenetic analyses of Caprifoliaceae and related taxa have been conducted on the basis of extant species. Donoghue (1983) argued that *Viburnum* is closely related to *Sambucus* and *Adoxa,* and that these genera may not be closely related to Caprifoliaceae in the strict sense (Caprifolioideae *sensu* Hara [1983]). He also reviewed earlier suggestions that Caprifoliaceae *sensu stricto* may be more closely related to Valerianaceae and Dipsacaceae. These preliminary hypotheses have been corroborated by an analysis of nucleotide sequences of the chloroplast gene *rbcL* (Donoghue et al. 1992; also see Chase et al. 1993; Olmstead et al. 1993), by restriction site characters from the cpDNA inverted repeat (Downie and Palmer 1992), and by a more detailed analysis of morphological data (Judd et al. 1994). On the basis of these findings, the *Viburnum-Sambucus-Adoxa* clade is now recognized as Adoxaceae, and the Caprifoliaceae have been recircumscribed to refer to Caprifoliaceae s.s., Valerianaceae, and Dipsacaceae (Judd et al. 1994). This treatment is supported by additional phylogenetic analyses including *rbcL* sequences from all genera of Caprifoliaceae s.s., as well as by a combination of morphological and molecular characters (M. J. Donoghue, R. G. Olmstead, J. Smith, and P. Reeves, unpublished data).

The Caprifoliaceae, as circumscribed by Judd et al. (1994), are united by generally zygomorphic corolla tubes, large pollen grains with supratectal spines, nectary tissue of unicellular hairs, capitate stigmas, and a reduction to marginal carpel vasculature. Within Caprifoliaceae, a clade consisting of *Leycestaria, Lonicera, Symphoricarpos,* and *Triosteum* is the sister group to the rest of the family (fig. 26). The rest of the family is united by a reduction in the number of nectaries, elongation of the ovary, and the presence of a sterile "neck" toward the apex of the ovary. Within this group, a clade consisting of *Weigela* and *Diervilla* (Diervilleae; Hara 1983) appears to be the sister group of the remaining taxa (fig. 26), which are characterized by a reduction to one nectary, four stamens, a base number of eight chromosomes, abortion of two of the three (or four) carpels, and the production of a dry indehiscent fruit. This clade includes the Linnaeeae of Caprifoliaceae s.s., as well as the Valerianaceae and Dipsacaceae.

Relationships within the Linnaeeae-Valerinaceae-Dipsacaceae are not confidently resolved by morphological characters. The link between Valerianaceae and Dipsacaceae is supported by several characters, including simple vessel perforations, modification of the calyx lobes, and reduction in the amount of endosperm. Whereas the presence of "supernumerary bracts" (Troll and Weberling 1966; Weberling 1989) emerged as evidence for the monophyly of Linnaeeae in the analysis by Judd et al. (1994), a recent analysis of Dipsacaceae and Valerianaceae (Caputo and Cozzolino 1994) supports an alternative hypothesis that the extra bracts evolved in the common ancestor of Linnaeeae, Valerianaceae, and Dipsacaceae, with subsequent loss in some Valerianaceae and extreme modification to form the characteristic epicalyx in Dipsacaceae (Hofmann and Gottman 1990). Under this interpretation, it is possible that Linnaeeae is paraphyletic with respect to Valerianaceae plus Dipsacaceae, although this depends on the treatment of several other morphological and chemical characters (A. Backlund and M. J. Donoghue, unpublished data).

Our concept of the systematic position of *Diplodipelta* within the Caprifoliaceae (*sensu* Judd et al. 1994) is shown on the cladogram (fig. 26). The fossil genus is united with the clade comprising Diervilleae, Linnaeeae, Valerianaceae, and Dipsacaceae (fig. 26) based on the elongate ovary with sterile neck, which matures into a dry fruit, and more specifically with Linnaeeae, Valerianaceae, and Dipsacaceae by the presumably indehiscent single- or few-seeded achene-like fruits (as opposed to the elongate, many-seeded capsules of Diervilleae). The wings of *Diplodipelta* are interpreted as supernumerary bracts, a character diagnostic of Linnaeeae (or possibly of Linnaeeae + Valerianaceae + Dipsacaceae, as discussed above). The persistence of calyx lobes in fruit is a characteristic feature of Linnaeeae. The calyx lobes of *Diplodipelta* are not enlarged to the extent seen in *Abelia,* in which they provide a mechanism for wind dispersal, but they are in the size range commonly encountered in the other extant genera (*Linnaea, Kolkwitzia,* and *Dipelta*). Variation in calyx lobe width, length and venation provides a basis for species distinction in *Dipelta* (Ying et al. 1993) and other modern genera as well as in *Diplodipelta.*

Four extant genera are assigned to the Linnaeeae: *Abelia* (25 species, including *Zabelia;* deciduous to evergreen shrubs, up to 3300 m elevation, Himalayas to eastern Asia, Mexico), *Dipelta* (three species; deciduous shrubs, 600–3600 m elevation, central to south central China), *Kolkwitzia* (one species; deciduous shrubs, 350–1900 m elevation, central China), and *Linnaea* (one species; evergreen procumbent dwarf shrubs, cool circumboreal). A fifth genus, *Heptacodium* (two species; deciduous small trees, 600–1000 m elevation, central and eastern China), has been allied with this group by some authors (Hara 1983), but alternatively may be related to *Leycestaria* and *Lonicera* of the Caprifolieae (Weberling 1966; Fukuoka 1972). *Heptacodium* was not included in the analysis by Judd et al. (1994) owing to limited information on several critical morphological characters; *rbcL* sequences, although inconclusive, imply that it is not directly related to Linnaeeae (M. J. Donoghue, R. G. Olmstead, J. Smith, and P. Reeves, unpublished data).

It is not possible, based on the presently available fossil material, to determine the number of carpels, or the nature of any carpel or ovule abortion that may have occurred in *Diplodipelta.* The abortion of two carpels is a feature of all extant Linnaeeae (Wilkinson 1949; Fukuoka 1972). In *Abelia, Kolkwitzia,* and usually in *Linnaea* there are three carpels in the ovary, but only one of them enlarges and bears a seed. In *Dipelta* (and sometimes in *Linnaea*) the ovary has four carpels, of which two enlarge and bear seeds. It would be desirable to know the number of locules in fruits of *Diplodipelta* for comparison with extant Linnaeeae but this must await the discovery of better-preserved fossil material.

*Kolkwitzia* often produces paired, syngynous fruits that could be compared with the paired fruits of *Diplodipelta,* but in *Kolkwitzia* the paired fruits are unequally developed, being derived from a terminal and a lateral flower (Wilkinson 1948; Weberling 1989), whereas the paired fruits of *Diplodipelta* are usually equal in size and symmetrically positioned, suggesting that they represent two lateral flowers with an aborted terminal (see discussion below). *Kolkwitzia* is also distinguished by the presence of elongate (ca. 2 mm) bristles covering the fruit and peduncle, by bracts that do not enlarge during fruit formation, and by a fruit with a rounder body at the base and longer sterile neck.

Of extant genera in the Linnaeeae, *Dipelta* appears to be the most closely related to *Diplodipelta* (fig. 27*C–F*). We interpret these genera as sister groups (fig. 26), because they share the enlargement of supernumerary bracts to form dispersal wings. The chief differences between *Diplodipelta* and *Dipelta* are the occurrence of two vs. one fruit per dispersal unit and the arrangement and morphology of wings. *Dipelta* has as an autapomorphy the development of peltate, nearly circular lateral wings attached directly to the fruit wall rather than to the peduncle. *Diplodipelta* is distinguished by lateral wings that have become highly asymmetrical and decurrent along the peduncle, and a median wing that wraps over the tops of the two fruits (figs. 27*A, B*).

### DERIVATION OF DISPERSAL UNITS IN DIPELTA AND DIPLODIPELTA

*Dipelta* and *Diplodipelta* both have fruits that are shed as samara-like units with papery wings (fig. 27). In *Dipelta* each dispersal unit has only a single fruit and three wings that are significantly expanded (fig. 27*C–F*). The flower is subtended by two closely spaced pairs of "supernumerary bracts" (Troll and Weberling 1966; Fukuoka 1969; Weberling 1989), the configuration also seen in *Abelia, Kolkwitzia,* and *Linnaea.* Below these bracts are the two caducous prophylls, positioned at the "middle of the peduncle" (Ying et al. 1993). Of the four bracts, the inner (upper) pair enlarges most, forming two more or less equal and orbicular lateral wings that are peltately attached directly to the fruit wall. Of the lower pair of bracts, one expands into an ovate median wing smaller than the two laterals, and the other persists but remains relatively small and narrow (fig. 27*C*). Each of the wings is supplied with palmate, reticulate venation that forms loops near the margin. In the mature fruit, the margin of the small wing rests against the sides of the larger wings, forming a trigonal structure (fig. 27*F*) that effectively hides the fruit.

In *Diplodipelta,* the dispersal units have two fruits and three expanded wings (fig. 27*A, B*). No young flowering specimens are known from which to directly observe bract arrangement, but we can determine the arrangement and number of wings at fruiting stage through detailed observation of numerous specimens, and from this information attempt to deduce the original arrangement of bracts. The two lateral wings enlarge the most. One of them is attached to the base of each fruit. These wings are asymmetrically developed with more expansion on one side of the primary vein than the other, the larger portion with a convex margin (distal to the axis of infructescence symmetry) and the narrow part with a straight margin (proximal to the axis of symmetry). The fruit is epiphyllous on the primary vein, as is best documented by the attachment scar on a wing torn from the rest of the dispersal unit (fig. 7). Below

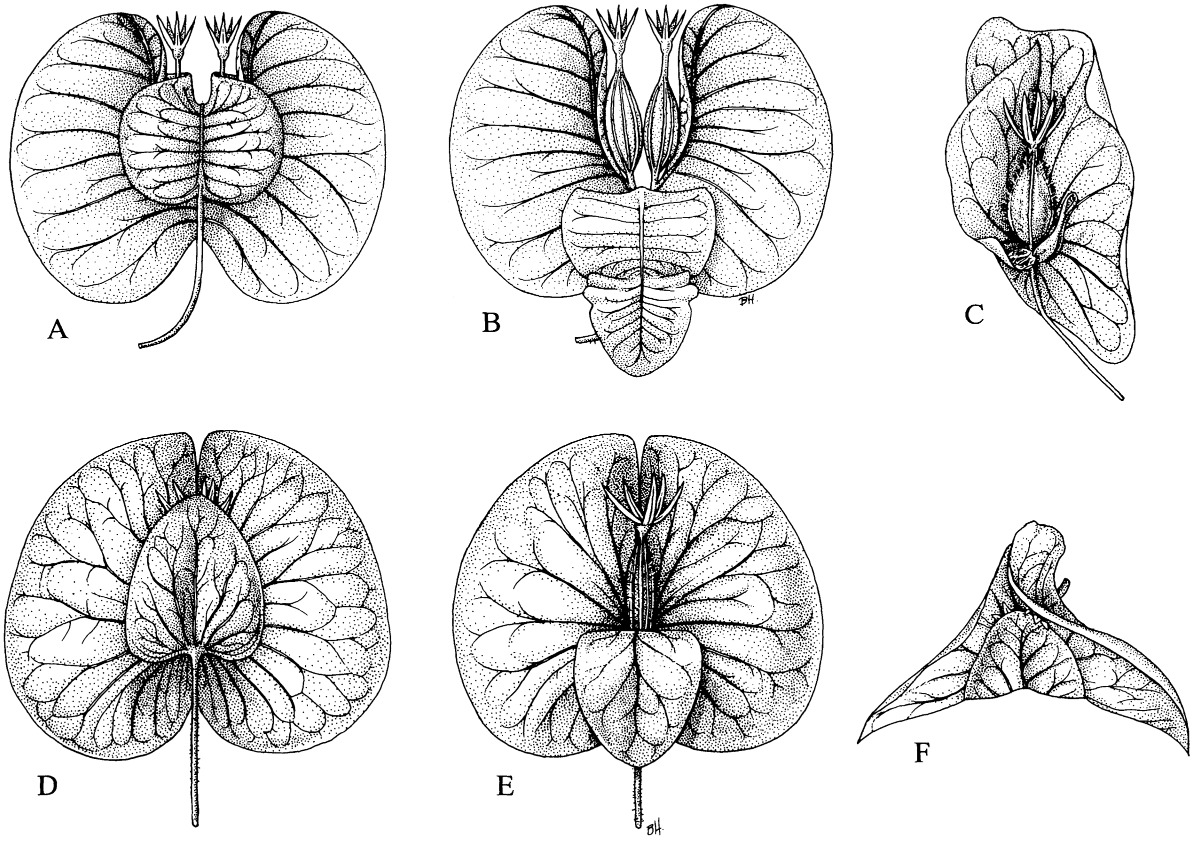


**Fig. 27** Morphological diagrams of fossil *Diplodipelta* and extant *Dipelta* disseminules. *A, B, Diplodipelta reniptera* (Becker) comb. nov. *A,* Reverse side of the dispersal unit diagrammed in fig. 13*A,* showing the large lateral wings, proximal portion of the median wing, and apices of the two fruits with prominent calyx lobes, modeled after figs. 5, 6, 8, 9, 11, 14. *B,* Same view, but with the median wing hypothetically unfolded to show the two fruits and their attachment to the lateral wings. *C–F,* Extant *Dipelta floribunda* Maxim. *C,* Lateral view with one of the large wings removed, showing median wing (left) and a less conspicuous median bract at base of the nut (right). *D,* Dispersal unit showing large lateral wings and smaller median wing. *E,* Same view with median wing folded down, as in *B,* to reveal the single fruit, with prominent calyx lobes. *F,* Apical view showing the triangular configuration and concave shape of the lateral wings.

the fruit attachment area the lateral wings are fused along the peduncle (e.g., figs. 2, 8, 16, 22, 24), except in a few specimens (figs. 1, 3). The main surfaces of the lateral wings of *Diplodipelta* lie approximately in a common plane (fig. 13*B*), whereas those of *Dipelta* are shallowly concave, spreading in separate planes (fig. 27*F*). The median wing attaches to the peduncle between the two fruits at or immediately below the position where the fruits are attached. The complete structure of the median wing is directly observable only in fossils with both counterparts available for dissection (e.g., figs. 4, 5, 8, 10, 11) because it is folded over the shoulder region between the two fruits such that the distal and proximal ends come to lie on the opposite sides of the fruits (fig. 27*A, B*). Depending on the precise plane within the sediment along which the fossil is split open, one may observe either the proximal or distal portion of the median wing, but not both. Additional microexcavation of the intervening sediment, where the two fruits are enclosed, is required to expose the other side. The proximal side has a thick midvein and a slightly cordate base (figs. 5, 9, 12, 14, 19, 27*A*). The distal side forms an ovate lobe with venation spreading "downward" toward the base of the dispersal unit (figs. 2, 10, 13*A*, 24). The wing is broader on the proximal side and is narrowed where it folds over the shoulder region between the sterile necks of the two fruits. From first appearances, we thought that the distal and proximal ends of this structure were two separate wings with emarginate apices derived from two separate bracts, but careful study by light microscopy shows that the wing tissue has torn or folded near the top of the infructescence and appears to be a single continuous lamina. Thus the median wing is interpreted as being derived from a single bract that folds over the tops of the two fruits during development (fig. 27*A, B*). This would effect coverage of the fruits at maturity.

We have not observed any unexpanded bracts in *Diplodipelta.* But it is possible that an unexpanded bract, like the one that occurs opposite the median wing in *Dipelta* (fig. 27*C*), would be

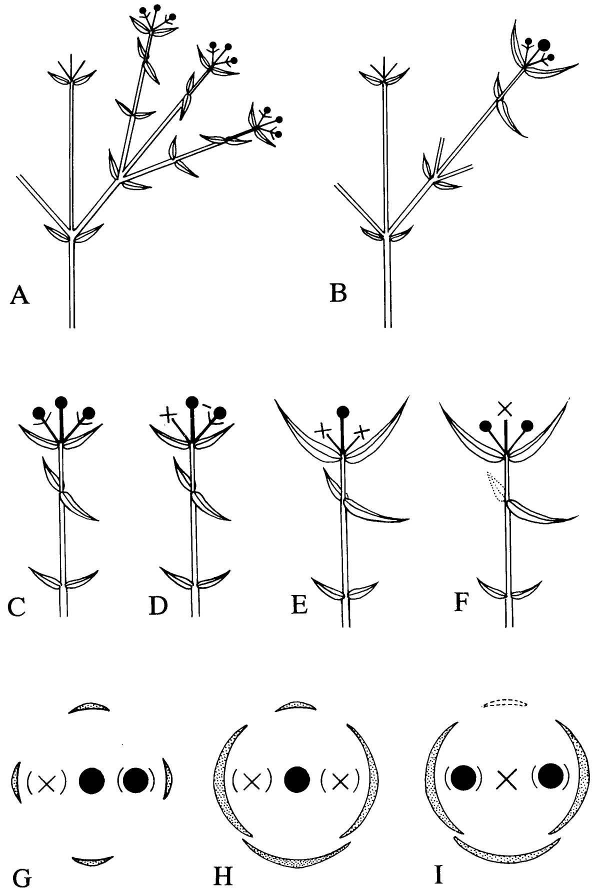


**Fig. 28** Schematic diagrams showing the apparent derivation of disseminules in *Kolkwitzia, Dipelta,* and *Diplodipelta. A,* Basic three-flowered Linnaeeae inflorescence unit as encountered in *Abelia rupestris* (modified from Weberling 1989, fig. 167). *B,* Hypothetical inflorescence structure with central flower dominating, a condition that may have led to the situation seen in extant *Dipelta. C–F,* Infructescence dispersal units. *C,* Hypothetical disseminule with both lateral flowers and terminal flower forming fruits (solid circles). *D, Kolkwitzia,* with one of the lateral flowers abortive (*x*) and the terminal and remaining lateral flower forming a syngynous fruit. *E, Dipelta* showing both lateral flowers abortive (*x*), and the terminal forming a fruit; with the upper pair of supernumerary bracts, and one of the lower pair, enlarging. *F, Diplodipelta,* lateral flowers forming fruits but the terminal abortive; with the upper pair of supernumerary bracts, and one of the lower pair, enlarging. *G, H,* Transverse diagrams of the dispersal unit, showing the arrangement and relative enlargement of bracts and the abortion of central or lateral flowers. *G, Kolkwitzia,* bracts not enlarging into wings. *H, Dipelta* with one of the bracts remaining relatively small. *I, Diplodipelta* showing three bracts that develop into fruit wings. The additional inferred inflorescence bract (dotted line), was not observed in the fossils, and was either absent or not sufficiently enlarged during fruit formation to be recognizable in the fossil material.

too small to be noticeable in fossil impressions. We suggest that the lateral wings are developed by enlargement of the upper pair of supernumerary bracts (fig. 28*F*). The median wing, which arises at a level at or slightly below the points of fruit attachment, may be formed by the expansion of one of the lower pair of supernumerary bracts. The possibility of one bract remaining small in *Diplodipelta* (fig. 28*I*) is supported by what happens to the lower pair of bracts in *Dipelta*: one forms a wing, yet the other remains relatively small and inconspicuous (fig. 28*H*).

The derivation of fruits from three-flowered units, of which one or two flowers abort (fig. 28*A, B*), is a common theme in Linnaeeae (Weberling 1989). In *Kolkwitzia,* both single and paired fruits occur on the same specimen. Whether paired or single, the fruits of this genus show four bracts that persist but do not expand (fig. 28*G*). The paired fruits of *Kolkwitzia* are asymmetrical, with the larger fruit developing from the terminal flower, and the smaller fruit from a lateral flower (fig. 28*D;* Wilkinson 1948). It is possible that the paired fruits of *Diplodipelta* are similarly derived from a terminal and a lateral flower. However, in *Diplodipelta,* the two fruits are usually equal in size (fig. 17 is a notable exception) and are attached equidistant from the infructescence axis, indicating that they probably represent a pair of lateral flowers, with the terminal flower abortive (fig. 28*F*).

In summary, the disseminules of *Diplodipelta,* with two fruits (fig. 27*B*), and those of *Dipelta,* with only one fruit (fig. 27*E*), can easily be derived from the same inflorescence plan, hypothesizing the three-flowered units to be the ancestral condition. Presumably in *Dipelta* the two lateral flowers abort and the fruit forms from the terminal one (fig. 28*E, H*) whereas in *Diplodipelta* the terminal flower aborts and the two laterals form fruits (fig. 28*F, I*).

## Fossil record of Caprifoliaceae

The Caprifoliaceae are relatively well represented in the fossil record. Fossil pollen of the family is known from the Tertiary of central Europe and has been placed in the genus *Lonicerapollis* (Krutzsch 1962). This genus accommodates tricolporate-echinate pollen of the type found in *Lonicera, Diervilla, Dipelta, Leycesteria, Linnaea, Symphoricarpos,* and *Triosteum* (Bohnke-Gutlein and Weberling 1981; Donoghue 1985). Fossil leaves have been attributed to various extant genera of the family (see Taylor [1990] for a listing from the North American literature), but reproductive characters of fruits and/or seeds provide the most reliable means of generic determinations for fossils within this family.

*Dipelta* is known from the late Eocene/early Oligocene Bembridge flora of southern England on the basis of well-preserved, thoroughly described samaroid fruits (Reid and Chandler 1926). We reexamined the type specimens of *Dipelta europaea* Reid et Chandler in comparison with *Diplodipelta.* The fossils possess two large lateral wings and a smaller oval median wing and have a longitudinally ribbed fruit with epigynous digitate calyx lobes. The specimens show only one fruit per dispersal unit and the median wing is not transversely folded (Reid and Chandler 1926, pl. 9, figs. 7, 8); we agree with Reid and Chandler's assessment that they belong to the extant genus. The occurrence of *Dipelta* in the Eocene of England is biogeographically significant because it occurs today only in eastern Asia (Ying et al. 1993). The time of appearance of *Dipelta* in England coincides approximately with that of *Diplodipelta* in western North America (table 1).

Given the Early Tertiary occurrences of *Dipelta* and *Diplodipelta,* it might be expected that other genera of the Linnaeeae might be recovered from the Tertiary as well. Although the extant genus *Abelia* has been reported several times based on fossil winged fruits (reviewed by Crane 1987), it has not been possible to confirm any of these reports as unequivocal records of the genus or family. Fruits named *Abelia quadrialata* from the late Eocene of England (Reid and Chandler 1926) and Hungary (Rásky 1960) recently have been found to have hypogynous, rather than epigynous, calyces (S. R. Manchester and L. Hably, unpublished data) and therefore cannot belong to *Abelia,* nor to the Caprifoliaceae. Similarly, fruits corresponding to *Abelia trialata* Reid and Chandler from the middle Eocene of Eckfeld, Germany, recently have been determined to have hypogynous perianth (V. Wilde, personal communication). A four-winged fruit from the middle Eocene of England, once assigned to *Abelia* sp. (Chandler 1964) was recently shown to represent the extinct juglandaceous genus *Cruciptera* (Manchester et al. 1994). Another four-winged fruit that was described and figured as "*Abelia* sp. 4" by Reid and Chandler (1926, p. 138, pl. 9, fig. 6) has wings with pinnate venation. This involucre, together with the isolated nutlet described by the same authors as "*Carpinus* sp." (1926, p. 96, pl. 6, fig. 10), is now considered to represent *Asterocarpinus,* an extinct betulaceous genus known from more complete specimens from latest Eocene and early Oligocene of western North America (Manchester and Crane 1987; S. R. Manchester, unpublished data). In our opinion, none of the previous reports of fossil *Abelia* can be accepted with certainty.

*Heptacodium* has been identified on the basis of fruits from the late Miocene of Japan (Ozaki 1980). *Weigela* has been recognized on the basis of its distinctive seeds from the Miocene and Pliocene of Poland (Łańcucka-Środoniowa 1967), the Miocene of Denmark (Friis 1985), the Oligocene and Miocene of western Siberia (Dorofeev 1963), and Mammoth Mountain, East Asia (Nikitin 1976). In the Adoxaceae, *Sambucus* has a good fossil record based on seeds extending from the late Eocene to Pliocene of Europe (Kirchheimer 1957), and leaves from the late Eocene of Florissant, Colorado, in North America (MacGinitie 1953). In the Valerianaceae, *Patrinia* is known from winged fruits from the Tertiary of western Siberia, the Pliocene of Baškiria, the Miocene of Poland (Łańcucka-Środoniowa 1979, and references therein) and the late Miocene of Japan (Ozaki 1980). The fossil record, when critically evaluated, has the potential to provide a good historical biogeographic case history of the Caprifoliaceae and related families, involving both extant and extinct genera, and may contribute to a better understanding of the evolution and phylogeny of the family.

Table 1

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF DIPLODIPELTA (A) AND DIPELTA (B)

| | Western North America | Western Europe | Eastern Asia |
|---|---|---|---|
| Recent | ... | ... | B |
| Pliocene | ... | ... | ... |
| Miocene | A | ... | ... |
| Oligocene | A | ... | ... |
| Late Eocene | A | B | ... |

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