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Attached leaves and fruits of myrtaceous affinity from the Middle Eocene of Colorado

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Abstract

A new myrtaceous genus, *Syzygioides* Manchester, Dilcher et Wing, gen. nov., is established based upon compressed twigs showing the attachment of leaves, with axillary panicles of flowers and fruits from the Eocene of the Rocky Mountain region. The new combination *Syzygioides americana* (Lesquereux) Manchester, Dilcher et Wing, comb. nov. applies to leaves that formerly were attributed to *Eucalyptus* and *Eugenia*. The opposite, decussately arranged leaves are similar in architecture to those of extant *Syzygium fluviatilis* (Hemsley) Merrill et Perry and *S. jambos* (L.) Alston, but the attached leathery fruits, with incurved persistent calyx and short capitate stigmas, are unlike those of extant *Eucalyptus*, *Syzygium*, *Eugenia* and other extant genera. *Syzygioides americana* first appears in the Lower Eocene of the Rocky Mountain region and is common in the Middle Eocene. The improved understanding of this fossil shows the presence of an extinct myrtaceous genus in the Eocene and demonstrates the need for caution in attempting to identify isolated fossil leaves to extant genera of the Myrtaceae.

Keywords: palaeobotany; Eocene; Myrtaceae; Colorado; Green River Formation; leaves; fruits

1. Introduction

Fossil leaves with venation characteristic of extant Myrtaceae have long been recognized in the fossil record of North America. Usually they have been placed in extant genera that have species with leaves possessing prominent intramarginal veins, e.g. *Eugenia*, *Eucalyptus*, *Calyptranthes*, and *Myricia*. Fossil flowers of Myrtaceae have not been recorded from the North American fossil record before, but fruits with anatomically preserved seeds corresponding closely to extant *Psidium* have been identified from the Upper Paleocene of North Dakota (Crane et al., 1990) and from the Middle Eocene of southern British Columbia (Pigg et al., 1992). Previously, the fossil record of the Myrtaceae and related families has been known only from isolated organs, particularly leaves and fruits. Here we consider a fossil species known from twigs bearing attached leaves and infructescences.

Myrtalean fossil leaves in the Eocene Green River Formation were first reported by Lesquereux (1872, 1878), who named them *Eucalyptus*? *americana*. The foliage occurs at many localities of the Green River Formation in Colorado, Utah and Wyoming and was assigned most recently to *Eugenia americana* (Lesquereux) MacGinitie, 1969. It is now pos-

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sible to describe this species in greater detail based upon twigs with attached leaves, flowers and fruits. Although leaf architecture and phyllotaxy are consistent with some extant genera of Myrtaceae, the flowers and fruits indicate that it does not belong to any known living genus of Myrtaceae. It represents a new genus for which we propose the name *Syzygioides*.

2. Materials and methods

Specimens cited in this paper are from collections of the Buffalo Museum of Science, New York (BMS), Cornell University, Ithaca (CUPC), University of Colorado Museum (UCM), the U.S. National Museum, Washington, D.C. (USNM), and the Denver Museum of Natural History (DMNH). The most informative specimens, including branches with attached leaves and fruits, are preserved in shale of the Green River Formation from localities near Douglas Pass, Colorado. Isolated leaves also occur as rare elements in shale exposed near Bonanza, Utah. These localities in eastern Utah and adjacent western Colorado were deposited in the large extinct lake Uinta and are considered to be Middle Eocene (Grande, 1984). Other occurrences, based upon leaf remains from other geologic formations, were identified through field work and study of collections at USNM to give a broader understanding of the geographic and stratigraphic distribution of the species.

Modern herbarium collections were examined at the Field Museum, Missouri Botanical Garden, Harvard University and Leiden.

3. Systematics

Order MYRTALES
Family MYRTACEAE

SYZYGIOIDES *Manchester, Dilcher et Wing, gen. nov.*

Type: Syzygioides americana (Lesquereux, 1872) Manchester, Dilcher et Wing, comb. nov.

Diagnosis: Leaves opposite and decussate, narrow-elliptical, broadest near the middle. Base acute, apex attenuate, lamina decurrent on thick petiole. Margin entire. Venation pinnate, eucamptodromous; midvein stout; secondary veins thin, closely spaced, arising decurrently from midvein and joining into prominent intramarginal vein. Intersecondary veins common, diverging from midrib at a wider angle than the secondary veins, also joining into the intramarginal vein. Tertiary veins approximately perpendicular to midvein, irregularly percurrent, somewhat sinuous, connecting with intramarginal vein and delimiting elongate areas.

Inflorescences axillary, dichotomously branched panicles, forming terminal pseudomonochasia, each with an enlarged terminal fruit and a small, shortly pedicellate lateral fruit. Branches thickened at nodes and at attachments with flowers or fruits. Flowers perigynous to epigynous with floral remnants, possibly stamen filaments arising from hypanthial rim and with persistent style terminated by a thick capitate stigma. Fruits ellipsoidal, with about 5 tepals that are closely appressed; style persistent with a capitate stigma.

Etymology: The generic name refers to the similarity of the leaves to those of some extant species of *Syzygium*. This name refers to the gross similarity and is not meant to imply that the fossil is closely related to *Syzygium*.

Syzygioides americana (Lesquereux, 1872) Manchester, Dilcher et Wing, comb. nov. (Figs. 1 and 2; Plates I–III)

Lectotype: We designate USNM 489, figured by Lesquereux, 1878, pl. 59, fig. 11, and here in Plate II, 1, as the lectotype.

Basionym: Eucalyptus americana Lesquereux, 1872, U.S. Geol. Geogr. Surv. Territ. Ann. Rep. for 1871, Suppl. 7 (not figured). Subsequently published with illustration as *Eucalyptus? americana* Lesquereux, 1878, U.S. Geol. Surv. Territ. Rep. 7, 296, pl. 59, figs. 11, 12.

Synonyms:

1878 *Eucalyptus? americana* Lesquereux, p. 296, pl. 59, figs. 11, 12.
1923 *Eucalyptus? americana* Lesquereux, Knowlton, p. 171, pl. 39, figs. 1–3.
1929 *Ficus omballi* Brown, p. 285, pl. 72, fig. 2.
1969 *Eugenia americana* (Lesquereux) MacGinitie, pp. 122–123, pl. 18, figs. 2, 3; pl. 19, fig. 1; pl. 23, fig. 1.

Fig. 1. Reconstruction of *Syzygioides americana* (Lesquereux, 1872) Manchester, Dilcher et Wing, comb. nov.

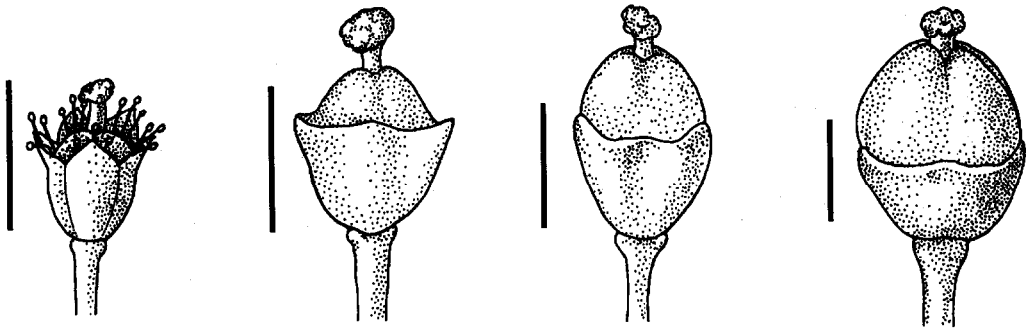
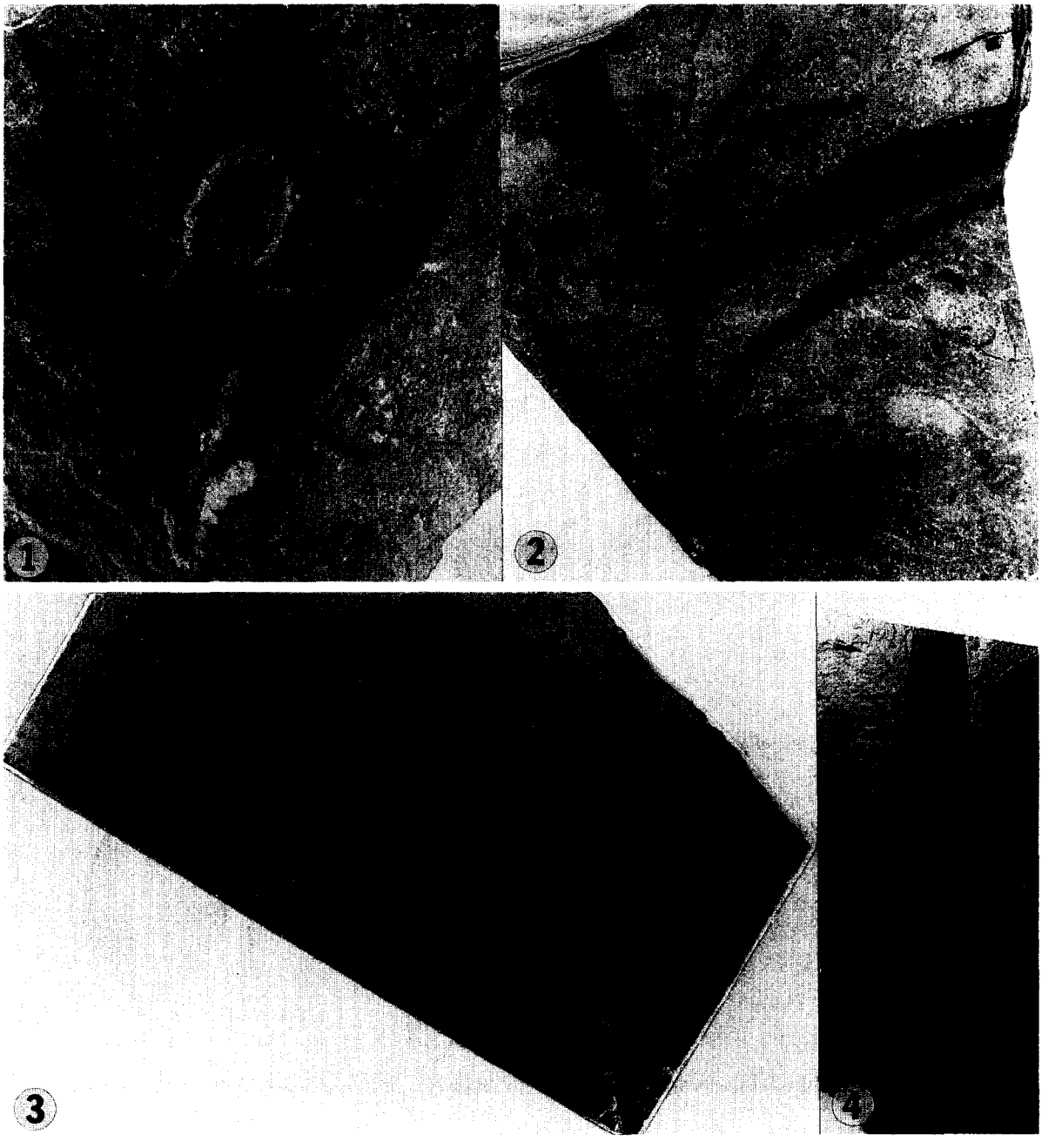


Fig. 2. Successive stages of fruit maturation in *Syzygioides americana* (Lesquereux, 1872) Manchester, Dilcher et Wing, comb. nov. Scale bars = 2 mm.

Description: Leaves opposite and decussate, lamina 3.2–12.5 (avg. 8.3) cm long, 0.6–3.0 (avg. 1.6) cm wide; narrow-elliptical, broadest near the middle, length/width ratio 3.1–8.9 (avg. 5.8); base acute; apex attenuate, stipules not observed; petiole stout, ca 2 mm wide, and 2–8 mm long, lamina decurrent on petiole. Margin entire. Venation pinnate, eucamptodromous; midvein stout, prominent, straight

PLATE I



to curved; secondary veins thin, closely spaced, arising decurrently from the midvein at angles of 35–65° joining into a prominent intramarginal vein situated 0.5 to 1.0 mm inside the margin. Intersecondary veins common, diverging from the midrib at wider angles than the secondary veins, joining into the intramarginal vein. Tertiary veins approximately perpendicular to the midvein, irregularly percurrent, somewhat sinuous, connecting with intramarginal vein and delimiting elongate areas. Higher order veins not well preserved. Occasional concave veins of intersecondary to tertiary thickness connect between the intramarginal vein and the lamina margin.

Fruits borne in axillary panicles that are branched dichotomously about 5 times, forming terminal pseudomonochasia, each with an enlarged terminal fruit and one small shortly pedicellate lateral fruit. Branches thickened at the nodes. Inflorescence internode length 2 mm (proximal branch), 4.5–10 mm (2–4 order branches), 1–4 mm (ultimate branches). Width of inflorescence axis 0.6 mm near the base to 0.3 mm at ultimate node.

Flowers rhomboid in lateral view, 1.8–2.3 mm wide, 2.5 mm long (or up to 4 mm long including style). Poorly preserved floral remnants, possibly stamen filaments and petals; perigynous to epigynous. Apex conical, style about 0.5 mm thick, terminated by a thick and carbonaceous capitate stigma about 1 mm in diameter and 0.5 mm thick.

Fruits ellipsoidal, 4.0–4.7, avg. 4.3 mm long; 2.5–3.2, avg. 2.9 mm wide, with about 5 (2.5–3 in face view of compression) tepals that are *closely* appressed and divided 1/3 to 1/2 of the length from the apex to the base of the fruit. Persistent style extending about 1 mm beyond the top of the fruit with a capitate stigma.

Other specimens studied: In addition to the lectotype cited above, we studied BMS E25188 (and counterpart CUPC 1001) (attached fruits and leaves), DMNH 6332 (twig with four pairs of leaves), USNM 336317 (twig with two pairs of leaves); DMNH 6328, 6329 (isolated leaves). Number of leaves examined ca. 25; number of fruits examined (all on the same infructescence specimen) 17.

4. Discussion

The above description is based on the lectotype leaf impression of Lesquereux (Plate II, 1) supplemented with information provided by new specimens showing the attachment of leaves to the twigs (Plate I, 1–2), and by a rare specimen with attached leaves, flowers and fruits (Plate I, 3). Size range for the leaves is based on examination of many isolated leaves from several localities of the Green River Formation. Although leaves with similar venation occur in the Eocene Clarno Formation of Oregon and Claiborne Formation of Kentucky, Tennessee and Mississippi, we excluded them from this study of *Syzygioides americana* because we were unable to find associated fruits similar to those attached with the leaves from Colorado.

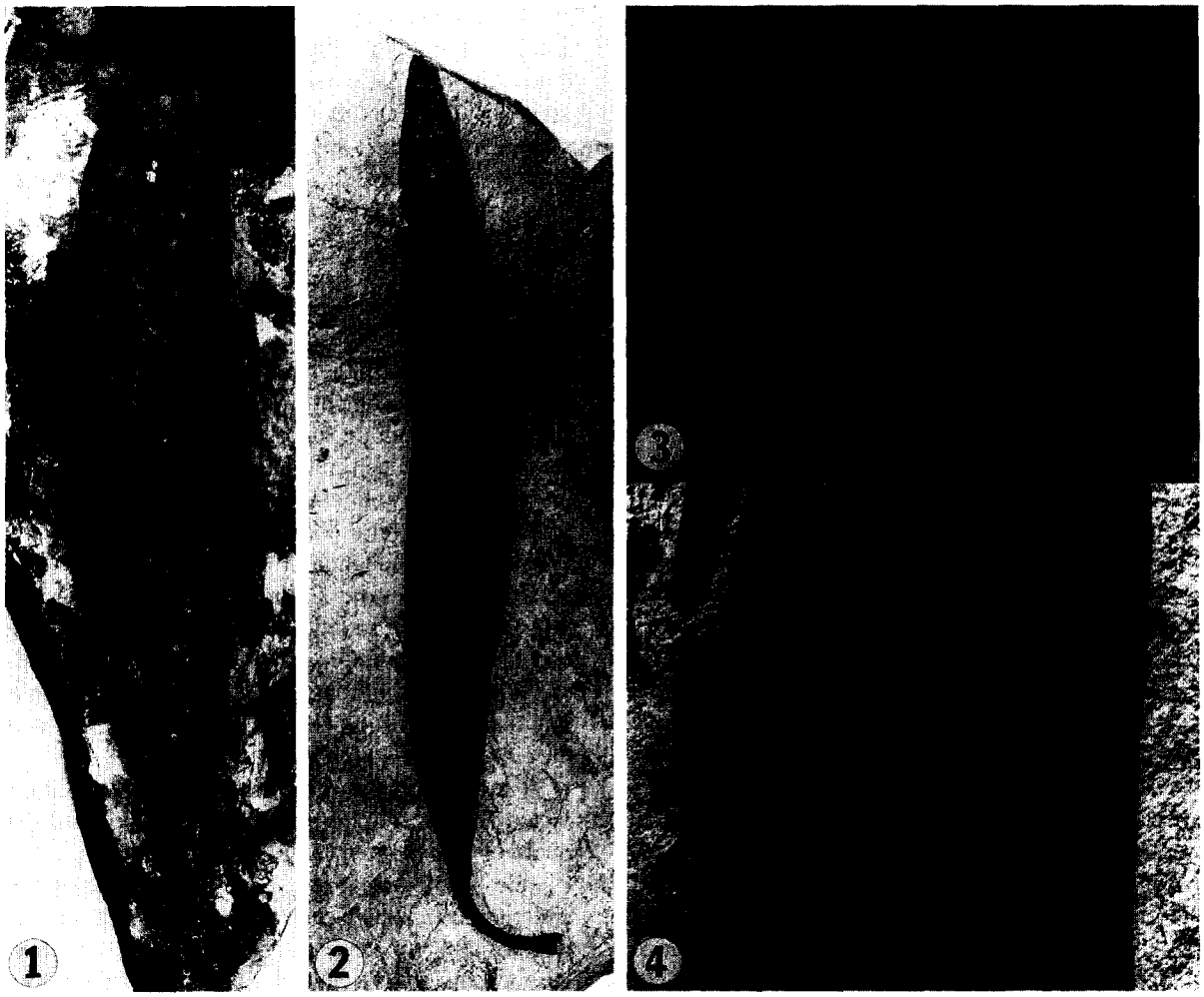
A reconstruction of the reproductive twig is depicted in Fig. 1. The vegetative and reproductive twigs of *Syzygioides americana* show opposite, decussate phyllotaxy (Plate I, 1–3), a condition that is common in the Myrtaceae. Other features consistent with Myrtaceae include entire-margined leaves with intramarginal veins, oblique, irregularly percurrent tertiary veins, cymose inflorescences, fruits and flowers that are epigynous to half epigynous with a hypanthium (Fig. 2; Plate III, 4–9), and numerous stamens borne on rim of hypanthium (Plate III, 9). An apparent difference from most extant Myrtaceae is that the calyx does not persist as a recurved rim on

PLATE I

Leaves and fruits of *Syzygioides americana* (Lesquereux, 1872) Manchester, Dilcher et Wing, comb. nov. from the Middle Eocene Parachute Creek Member of the Green River Formation, Colorado. ×1.

1. Vegetative branchlet showing four leaves arranged in two opposite pairs, USNM 336317. ×1.
2. Twig showing four decussate pairs of leaves, Denver Museum of Natural History locality 304, Rio Blanco County, Colorado, DMNH 6332.
3. Twig with opposite leaves and axillary infructescences, Douglas Pass area Colorado, BMS E25188.
4. A typical long elliptical leaf showing, prominent midvein and intramarginal vein, one mile E of Black Prince Mine dump; three miles northwest of the head of Ute trail, Garfield County, Colorado. UCM sn. ×1.

PLATE II



Syzygioides americana (Lesquereux, 1872) Manchester, Dilcher et Wing, comb. nov.

1. Lectotype of *Eucalyptus*? *americana* Lesquereux (1878, pl. 59, fig. 11), Green River, Wyoming, USNM 489. ×1.5.
2. Well preserved leaf from the same locality as Plate I, 4, showing similarity of venation to that of the lectotype. Note intramarginal vein, and angles of secondary and tertiary veins, UCM sn. ×1.5.
3. Detail of leaf venation from the specimen with attached fruits. Note the transverse orientation of intersecondary and tertiary veins, BMS-E25188. ×5.
4. Detail of venation from the well-preserved leaf in Plate I, 4. ×5.

the mature fruits. Instead, the apical part of the fruit curves smoothly inward. The latter feature might be taken as an argument against the placement of this genus within Myrtaceae, however, the other vegetative and reproductive characters support assignment to this family.

The leaves of *Syzygioides* are narrow and entire-margined with a relatively thick midvein, numerous pinnate secondaries, intersecondaries, and tertiary veins that join with prominent intramarginal veins (Plate II, 1–4). This distinctive pattern of venation occurs among several different genera of Myrtaceae, for example, in some species of *Eucalyptus* (e.g., *E. oleosa*, *E. rugosa*, *E. tereticornis*), *Eugenia* (e.g., *E. salicifolia*, *E. eucalyptoides*), *Syzygium* (e.g., *S. floribundum*, *S. pancheri*), and *Calyptranthes* (e.g.,

C. kleinii, *C. pallens*) (see Klucking, 1988, for these and other examples). Similar leaf architecture has been observed in species from the Tertiary of Australia (Christophel and Lys, 1986) and eastern Kazakhstan (Iljinskaja, 1986). Many extant genera of the Myrtaceae cannot reliably be distinguished on the basis of leaf characters (Christophel and Lys, 1986).

In attributing this fossil species to *Eugenia*, MacGinitie (1969) called attention to close similarities with the leaf architecture of extant *E. fluviatilis* Hemsley and *E. jambos* L. According to some authorities, most of the Asian species formerly classified as *Eugenia* should be placed in *Syzygium* on the basis of differences in fruit vasculature and floral histology (Schmid, 1972). Hence, the species that MacGinitie cited as *Eugenia* are now treated as *Syzygium fluviatile* (Hemsley) Merrill et Perry and *S. jambos* (L.) Alston. Leaf venation supports this transfer: most extant species of *Eugenia* have only weakly defined intramarginal veins that are more appropriately described as the successive arches of secondary veins inside the margin, but venation comparable to that of the fossil occurs in several other species of *Syzygium* as can be seen by reference to an atlas of cleared extant leaves (Klucking, 1988). Thus, if we were to assess the affinities of the fossil specimens based only on the isolated leaves, and on similarity to the living species that MacGinitie cited, it would seem appropriate to transfer the fossils from *Eugenia* to *Syzygium*. However, analysis of the attached fruits shows that assignment to *Syzygium* would also be incorrect.

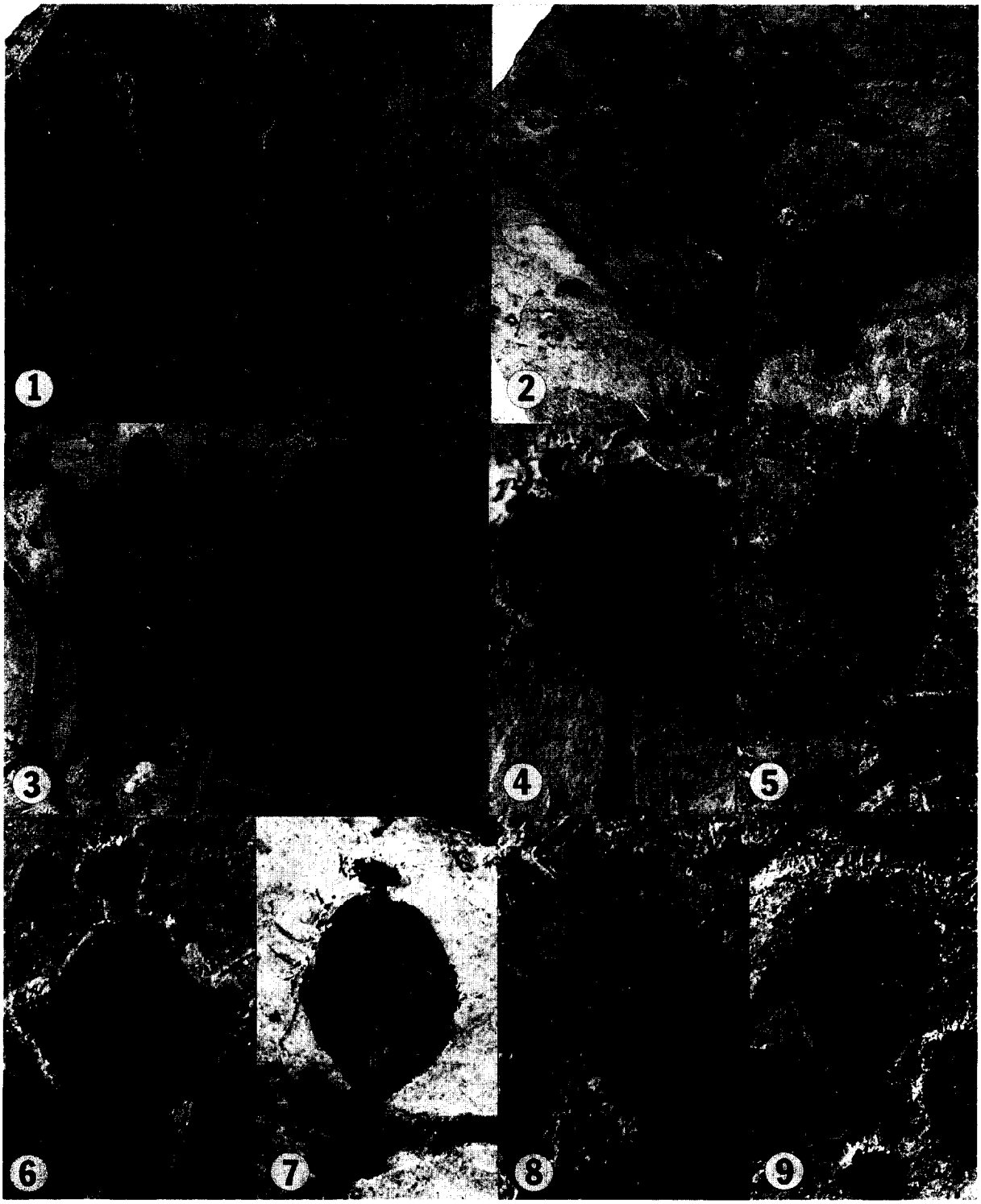
The infructescence is an axillary panicle with five successive nodes of branching, each with subtending bracts. Successive branches are arranged decussately. The distal nodes bear a sessile terminal fruit and a smaller, pedicellate lateral fruit (Plate III, 3). Symmetry suggests that an additional lateral flower may have been present at the same node, but was abortive (thus constituting a pseudomonochasial inflorescence; Briggs and Johnson, 1978). The proximal branches of the inflorescence are organized into three successive dichotomies, rather than successive trichotomies, considered the basic condition in Myrtaceae (Briggs and Johnson, 1978). However, this type of dichasial inflorescence occurs in extant Myrtaceae, and is formed by the abortion of median flowers (Briggs and Johnson, 1978, pp. 195–196).

The Myrtaceae are traditionally divided into two subfamilies, the Leptospermoideae, with dehiscent, usually dry and/or woody fruits, and the Myrtoideae, with indehiscent, typically fleshy fruits. The Leptospermoideae are distributed in southeastern Asia, Australia, and the Pacific with outliers in South Africa and Chile. The Myrtoideae are best developed in Central and South America, southeastern Asia, eastern Australia and the west Pacific, with *Eugenia* having a pantropical distribution and *Myrtus* extending into the Mediterranean region. The shape and texture of the fossil fruits indicate that *Syzygioides* conformed to the Myrtoideae in having leathery, berry-like fruits. They were not woody capsules as would be expected for *Eucalyptus* and other Leptospermoideae.

The fruits are of different sizes, 4 to 4.7 mm long, some more mature than others. Examination of successively larger fruits on the infructescence provides an ontogenetic series indicating that they matured from epigynous to perigynous (Fig. 2). The least mature fruits, situated most proximally on the inflorescence, retain some flower characters (Plate III, 8, 9). Neither internal fruit structure nor the seeds are preserved. This is unfortunate, because seed and embryo morphology provide important systematic characters within the Myrtoideae (Kausel, 1956; Landrum and Stevenson, 1986).

A conspicuous feature of the flowers and fruits of *Syzygioides* is the presence of a thick short style with a capitate, discoid persistent stigma (Plate III, 4–7). By contrast, *Eugenia*, *Syzygium*, and most other extant genera of the Myrtaceae have elongate, apically tapered styles without capitate stigmas. Similar short styles and peltate stigmas are described and figured for *Amomyrtella guili* (Spegazzini) Kausel (Kausel, 1956, p. 514) from Argentina. Capitate stigmas also occur in *Callistemon*. Although rare among extant Myrtaceae, the more common occurrence of capitate stigmas among other families of the Myrtales indicates that the capitate condition may be a primitive feature within the Myrtaceae. Because the combination of short, persistent capitate stigma, incurved persistent perianth, and leathery fruit have not been observed among extant genera of the Myrtaceae or related families, we consider *Syzygioides* to represent an extinct genus.

PLATE III



5. Geologic distribution

Leaves of *Syzygioides americana* are common in late Early and Middle Eocene floras over much of the northern Rocky Mountain region. The earliest record for the leaves is held by two specimens from the 621 m level of the Willwood Formation in the central Bighorn Basin, northern Wyoming (Bown et al., 1994). A minimum age for this laterally extensive carbonaceous shale deposit is provided by a date of 52.8 ± 0.3 million years obtained from a bentonitic tuff 13 m above. The lowest occurring Lostcabinian (Early Eocene) mammals in this section are at the 580 m level. *S. americana* leaves are abundant or even dominant in several compression fossil assemblages from the Lost Cabin Member of the Wind River Formation in the eastern Wind River Basin north of Moneta, Wyoming. One of these localities overlies by less than 10 m an earliest Middle Eocene (Gardnerbuttean) vertebrate locality (Stuckey et al., 1990). *S. americana* is also found in paludal volcaniclastic deposits of the Aycross Formation in the Absaroka Volcanic field (MacGinitie, 1974, p. 78, pl. 24, figs. 1, 2). Specimens from Parachute Creek Member of the Green River Formation of Colorado and Utah are regarded as probably later Middle Eocene, and may represent the younger end of the range of *S. americana*. At most localities of the Green River Formation, *S. americana* is only a rare or occasional element.

Leaves of *Eugenia arenaceaeformis* (Cockerell) MacGinitie, from the latest Eocene Florissant flora of Colorado (MacGinitie, 1953), show the characteristic intramarginal veins and entire margin like those of *Syzygioides*; however, the fine venation of the Florissant leaves is poorly preserved and the fruits remain unknown, thus precluding a detailed comparison with *S. americana*.

The appearance of *Syzygioides americana* in the latter half of the Early Eocene coincides with the inferred warmest climates of the Cenozoic in this part of the world, and also with increasing sedimentological indications of seasonal aridity in the northern Rockies (Smoot, 1983; Wing, 1987). *S. americana* is typically found either in lacustrine sediments or in fine-grained, carbonaceous rocks that were probably deposited in fluvial backswamps. As pointed out by MacGinitie (1969, p. 123), the frequent association of this species with *Salix* and *Platanus* indicates that it was a component of streamside vegetation.

6. Implications for the fossil record of Myrtales

Because of the wide range of leaf architectural patterns observable even within the same extant genus of Myrtaceae (Klucking, 1988), it is dangerous to assign Tertiary myrtaceous foliage to modern genera in the absence of corroborative evidence from fruits or flowers. Although the leaves of *Syzygioides* are nearly identical to those in some modern genera, details of the infructescence and fruits indicate that it represents an extinct genus. With the knowledge that extinct genera of Myrtaceae were present in the early Tertiary of North America, it is inadvisable to accept reports of extant myrtaceous genera that are based

PLATE III

Infructescence and fruits of *Syzygioides americana* (Lesquereux, 1872) Manchester, Dilcher et Wing, comb. nov. from the Middle Eocene Parachute Creek Member of the Green River Formation, Colorado.

1. Specimen showing detail of dichotomously branched infructescences. CUPC 1001. ×2.
2. Counterpart of specimen in 1, image reversed for comparison. BMS-E25188. ×2.
3. Detail of infructescence from 2, showing bifurcating axis with bracts at each node, and oblong fruits with persistent capitate stigmas. ×4.
4. Fruit showing lobes of perianth and persistent stigma at the apex. A smaller, pedicellate fruit arises at right angles, apparently from the same node, BMS-E25188. ×8.
5. Fruit with the persistent stigma elevated slightly above the apex, CUPC 1001. ×8.
6. Flower with immature or abortive fruit with perianth extending only about half of the distance to the apex, and showing style with capitate stigma, BMS-E25188. ×15.
7. Immature or abortive fruit with perianth approximately equatorial, and with style and capitate stigma. BMS-E25188. ×10.
8. Immature or abortive fruit with faintly preserved petals (?) and stamen filaments surrounding the style. BMS-E25188. ×15.
9. Immature or abortive fruit showing stamen filaments surrounding the style, CUPC 1001. ×15.

on fossil leaves without clearly associated fruiting or flowering remains. Christophel and Lys (1986) surveyed the leaf venation and epidermal anatomy of eleven extant species in six genera of the Myrtaceae in an attempt to identify fossil leaves from the Eocene of Victoria, Australia. They concluded that their fossils should be placed in an organ genus, *Myrtaciphyllum*, which they described based upon excellently preserved leaves with details of cuticle and venation. Other organ genera that have been proposed for fossil myrtaceous leaves where epidermal anatomy is not preserved include *Myrtifolium* Unger, 1864 and *Myrtophyllum* Ettingshausen, 1886.

It follows from our findings that the assignment of early Tertiary fossils to extant myrtaceous genera should be questioned, especially when the generic assignment implies unusual biogeographic dispersal. For example, leaves attributed to *Eucalyptus borissovii* Iljinskaja, 1986 from the Eocene of Kiin Kerish, eastern Kazakhstan are similar to those of *Syzygioides*, and are unlikely to be true representatives of the Australian genus *Eucalyptus*. A particularly interesting specimen attributed to *Eucalyptus borissovii* by Iljinskaja (1986) is the impression of a twig showing an attached leaf and axillary fruits. However, the phyllotaxy appears to be alternate, rather than opposite, suggesting that the fruiting specimen might not belong to the Myrtaceae.

The myrtalean family Lythraceae is known from several extinct seed genera in the early and late Tertiary of Europe (Friis, 1985) and North America (reviewed by Tiffney, 1981). We considered the possibility that *Syzygioides* might represent a genus of the Lythraceae. However, the Lythraceae have an ovary that is fully superior both at anthesis and in fruit and the leaf venation of *Syzigioides* is unlike that in any of the extant genera of that family. Among the order Myrtales, both the Myrtaceae and Lythraceae were established by the Eocene and both families included extinct genera at that time.

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References

Bown, T.M., Rose, K.D., Simons, E.L., Wing, S.L., 1994. Distribution and stratigraphic correlation of Upper Paleocene and Lower Eocene fossil mammal and plant localities of the Fort Union, Willwood, and Tatman Formations, southern Bighorn Basin Wyoming. 1994. U.S. Geol. Surv. Prof. Pap. 1540, 101.

Briggs, B.G., Johnson, L.A.S., 1978. Evolution in the Myrtaceae—Evidence from inflorescence structure. 1978. Proc. Linn. Soc. N.S.W. 102, 157–264.

Brown, R.W., Brown. Additions to the flora of the Green River Formation. Brown. U.S. Geol. Surv. Prof. Pap. 154J, 279–293.

Christophel, D.C., Lys, S.D., 1986. Mummified leaves of two new species of Myrtaceae from the Eocene of Victoria Australia. 1986. Aust. J. Bot. 34, 649–662.

Crane, P.R., Manchester, S.R., Dilcher, D.L., 1990. A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. 1990. Fieldiana Geol. Publ. 1418 (20), 63.

Ettingshausen, C., 1886. Beiträge zur Kenntniss der Tertiärflora australiens. 1886. K. Akad. Wiss. Wien Denkschr. 53, 143–192.

Friis, E.M., 1985. Angiosperm fruits and seeds from the Middle Miocene of Jutland (Denmark). Biol. Skr. 24 (3), 165 pp.

Grande, L., 1984. Paleontology of the Green River Formation, with a review of the fish fauna, 2nd ed. Geol. Surv. Wyo. Bull. 63, 333 pp.

Iljinskaja, I.A., 1986. Paleogene floras of Kiin-Kerish Mountain (eastern Kazakhstan) and their new species. 1986. Bot. Zh. 71, 1193–1199.

Kausel, E., 1956. Beitrag zur Systematic der Myrtaceen. 1956. Ark. Bot. Stockholm 3, 491–516.

Klucking, E.P., 1988. Leaf venation patterns, Vol. 3, Myrtaceae. Cramer, Berlin, 278 pp.

Knowlton, F.H., Knowlton. Revision of the flora of the Green River Formation with descriptions of new species. Knowlton. U.S. Geol. Surv. Prof. Pap. 131F, 133–182.

Landrum, L.R., Stevenson, D., 1986. Variability in the embryos in subtribe Myrtinae (Myrtaceae). 1986. Syst. Bot. 11, 155–162.

Lesquereux, L., 1872. An enumeration with descriptions of some Tertiary fossil plants from specimens procured in the explorations of Dr. F.V. Hayden in 1870. U.S. Geol. Geogr. Surv. Territ. Ann. Rep. for 1871 Vol. 5 (Suppl.), 22 pp.

Lesquereux, L., 1878. Contributions to the flora of the Western Territories II. The Tertiary flora. Rep. U.S. Geol. Surv. Territ. 7, 366 pp.

MacGinitie, H.D., 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Inst. Washington Publ. 599, 198 pp.

MacGinitie, H.D., 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. 1969. Univ. Calif. Publ. Geol. Sci. 83, 1–140.

MacGinitie, H.D., 1974. An early Middle Eocene flora from the Yellowstone–Absaroka volcanic province, northwestern Wind River Basin, Wyoming, Univ. Calif. Publ. Geol. Sci. 108, 103 pp.

Pigg, K.B., Stockey, R.A., Maxwell, S.L., 1992. *Paleomyrtinaea*, a new genus of permineralized fruits and seeds from the Eocene of British Columbia and Paleocene of North Dakota. 1992. Can. J. Bot. 71, 1–9.

Schmid, R., 1972. A resolution of the *Eugenia–Syzygium* controversy (Myrtaceae). 1972. Am. J. Bot. 59, 423–436.

Smoot, J.P., 1983. Depositional subenvironments in an arid closed basin, the Wilkins Peak Member of the Green River Formation (Eocene) Wyoming, U.S.A. 1983. Sedimentology 30, 801–827.

Stuckey, R.K., Krishtalka, L., Redline, A.D., 1990. Geology, vertebrate fauna, and paleoecology of the Buck Spring Quarries (Early Eocene, Wind River Formation) Wyoming. 1990. Geol. Soc. Am. Spec. Pap. 243, 169–186.

Tiffney, B.H., 1981. Fruits and seeds of the Brandon Lignite VI. *Microdiptera* (Lythraceae). 1981. J. Arnold Arbor. 62, 487–516.

Unger, F., 1864. Fossile Pflanzenreste aus Neu-Seeland Novarra Expedition. Geologischer Theil, Vol. 1 (2): Paläontologie. pp. 1–13.

Wing, S.L., 1987. Eocene and Oligocene floras and vegetation of the Rocky Mountains. 1987. Ann. Mo. Bot. Gard. 74, 748–784.