FRUIT MORPHOLOGY, FOSSIL HISTORY, AND BIOGEOGRAPHY OF *PALIURUS* (RHAMNACEAE)

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The genus *Paliurus*, recognized by its distinctive orbicular-winged fruit, is well represented in the fossil record of the Northern Hemisphere. Fruits assignable to *Paliurus* are known from the Tertiary of North America, Europe, and Asia, while extant species are limited to Eurasia. We examined variation in fruit morphology among extant species as a basis for interpreting fossil fruits. Although *Paliurus* fruits are diverse in size, shape, and sculpture, there are few consistent criteria for demarcating species. On the basis of morphometric analysis, we recommend synonymy of most fossil fruits under the name *Paliurus favonii*. New records for this species are reported from the Eocene and Miocene of North America, and a distinctive new species from the Middle Eocene of North America, *Paliurus clarnensis*, is introduced. The genus ranges from the Middle Eocene to Late Miocene in North America, the Late Eocene to Pleistocene in Asia, and from the Oligocene to Pliocene in Europe. The fossil record indicates range expansion over the Northern Hemisphere during the Eocene and Miocene, possibly via high latitude migratory routes, followed by dramatic range contraction near the close of the Miocene, including extinction from central Asia and North America.

Keywords: *Paliurus*, fossil fruits, Rhamnaceae, *Ziziphus*, *Cyclocarya*, biogeography.

Online enhancements: tables.

Introduction

The genus *Paliurus* Mill. contains five species of predominantly evergreen shrubs and small trees that are naturally distributed in the southern portions of Europe and Asia (Schirarend and Olabi 1994). *Paliurus spina-christi* Mill. occurs natively in southern Europe and western Asia (fig. 1) but is naturalized in other regions, such as North Africa, where it has a history of cultivation as a protecting hedge and medicinal plant (Horvat et al. 1974). The remaining four species are eastern Asian in distribution, limited to China, Korea, Japan, Vietnam, and Taiwan (fig. 1). Thus, the present distribution of the genus is disjunct across southern central Asia, with a gap of more than 4500 km separating the predominantly European species *P. spina-christi* from the nearest eastern Asian species (Schirarend and Olabi 1994). The fossil record, by contrast, indicates a broader distribution for the genus in the Northern Hemisphere during the Tertiary, including records from North America and northern portions of Europe and Asia (Berry 1928; Kirchheimer 1957; Manchester 1999).

Paliurus is a member of the family Rhamnaceae. As a group, the 50 genera and ~900 species of Rhamnaceae are cosmopolitan in distribution, although most diversity is found in the Southern Hemisphere (Richardson et al. 2000*b*). The family is characterized by simple leaves, small flowers with petal-opposed stamens (obhaplostemony), a tendency toward xeromorphism, and a predominantly shrubby habit (Suessenguth 1953; Richardson et al. 2000*b*). Past classifications (Cronquist

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1981) have allied Rhamnaceae with Vitaceae and Cornaceae, the former sharing with Rhamnaceae the relatively rare characteristic of obhaplostemony. However, molecular phylogenetic results using the plastid gene *rbcL* (Chase et al. 1993; Soltis et al. 1995), 18S nuclear ribosomal DNA (Soltis et al. 1997), *rbcL* combined with *atpB* (Savolainen et al. 2000), and a combined analysis of all three genes (Soltis et al. 2000) recover a close relationship with Rosaceae, Eleagnaceae, and the former Urticales, within the newly circumscribed Rosales (APG II 2003).

Although *Paliurus* has consistently been treated within the Rhamnaceae since its first recognition (de Jussieu 1789; Endlicher 1840; Hooker 1862; Suessenguth 1953), it has been grouped with different members of the family. Most treatments, however, have allied *Paliurus* to *Ziziphus* Mill., a large (~170 spp.) genus of predominantly tropical to subtropical trees and shrubs (Hooker 1862; Suessenguth 1953; Liu and Cheng 1995; Richardson et al. 2000*b*). Molecular phylogenetic analyses using the chloroplast regions *rbcL* and *trnL-F* strongly support a group containing *Ziziphus*, *Paliurus*, and the east Asian genus *Hovenia* Thunb. (Richardson et al. 2000*a*), a result also supported by morphological cladistic analyses (Richardson et al. 2000*b*). While support obtained for this group is strong, relationships within it were recently called into question by Islam and Simmons (2006), who found that *Paliurus* is nested within *Ziziphus*. Thus, an analysis of the fossil record of *Paliurus* may provide information relevant to the evolutionary origin of *Paliurus* from within *Ziziphus*.

The paleobotanical record contains isolated but characteristic fruits of *Paliurus* as well as abundant leaves with possible affinities to the genus. Fruits of *Paliurus* are distinguished
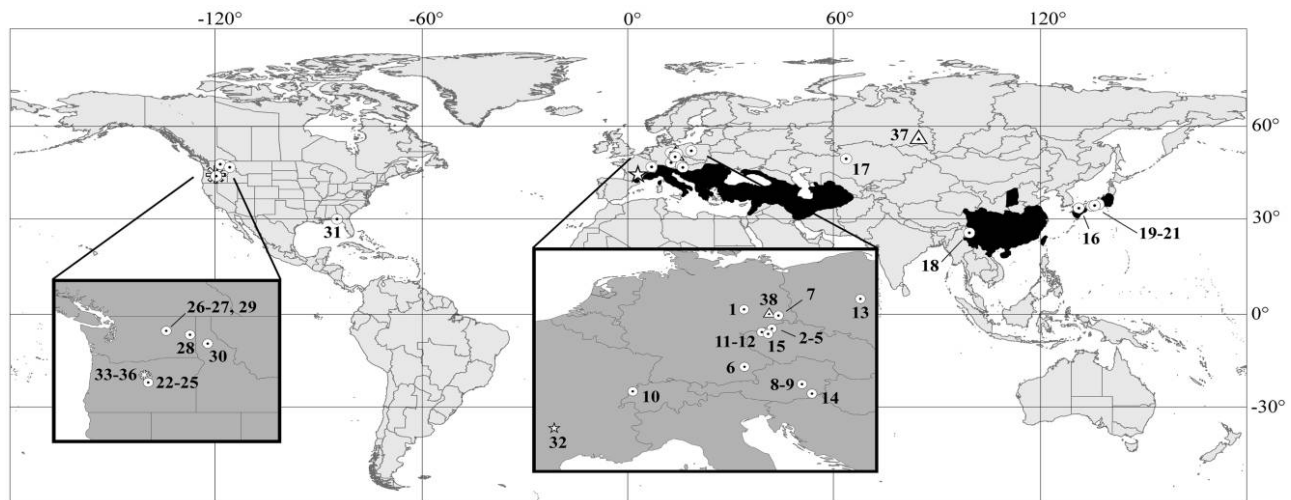
Fig. 1 Geographic distribution of extant and fossil *Paliurus*. Black shading indicates extant distribution, based on Schirarend and Olabi (1994). Fossil taxa: *Paliurus favonii* (circles, 1–31; table B1 in the online edition of the *International Journal of Plant Sciences*), *Paliurus* sp. aff. *hemsleyanus* (star, 32), *Paliurus clarnensis* (asterisk, 33–36), and *Paliurus sibirica* (triangles, 37, 38). See text for details on fossil occurrences for 32–38.

from those of other taxa with disk-shaped wings, such as *Cyclocarya* Iljinsk. (Juglandaceae) and *Dioncophyllum* Baill. (Dioncophyllaceae), by their trilocular endocarp and persistent receptacular rim (fig. 3). Because of these characteristics, well-preserved fossil fruits of *Paliurus* are easily recognizable and should provide a reliable means of documenting the phytogeographic history of the genus during the Tertiary. Nevertheless, the specific taxonomy applied to these fruits has emphasized geography and stratigraphic age rather than explicit morphological differences and thus may not reflect the species-level biogeographic history. In addition, the description of fossil *Paliurus* species on the basis of leaves may have confused the history of the group. Serrate-to undulate-margined leaves with a prominent pair of strongly ascending basal secondary veins resembling those of modern *Paliurus* (fig. 4A) are frequently found associated with the fruits, although never in direct physical connection. While leaf fossils assigned to *Paliurus* may represent this genus, the leaf morphology of *Paliurus* overlaps with that of other rhamnaceous genera such as *Ziziphus* and *Ceanothus* L. (fig. 4B–4D). Thus, we emphasize records based on the characteristic fruits of *Paliurus*.

The aims of this contribution are (1) to provide an updated synonymy for the widespread fossil species *Paliurus favonii* Unger and describe a new species of *Paliurus* from the Middle Eocene of North America; (2) to review the fossil history of *Paliurus* fruits, with attention to characteristics that are diagnostic at the generic and specific levels, and to suggest taxonomic changes; (3) to introduce new fruit records of the genus from the Late Eocene and Middle Miocene of North America; and (4) to discuss the geographic and systematic relationships among fossil and extant *Paliurus*.

Material and Methods

Fossil material was examined from museum collections, including previously unpublished material from North America.

Records from the literature were considered for the summary of the *Paliurus* fossil record only if photographs or figures were provided showing the diagnostic morphological features of *Paliurus* fruits. Specimens were examined and photographed from the following institutions: Florida Museum of Natural History, University of Florida, Gainesville (UF); University of California Museum of Paleontology, Berkeley (UCMP); Smithsonian Institution, Washington, DC (USNM); Denver Museum of Nature and Science (DMNH); National Museum, Prague (NMPC); Staatliches Museum für Naturkunde, Stuttgart (SMNS); personal collection of Richard M. Dillhoff. Fossil specimens were examined at ×6–64 magnification using Wild dissecting microscopes (MS-84581 and Photomakroskop M400), with reflected light provided from the side by gooseneck fiber-optic lamps. Photographs of fossils were taken with a Nikon CoolPix 995 camera in macrophotography mode or in connection with the photomacroscope under similar lighting conditions. Measurements were taken under the MS-84581 dissecting microscope using a 0.1-mm scale (Metric Mini Scale 3, Electron Microscopy Sciences, Hatfield, PA). In order to examine otherwise hidden or subtle features of the fossils, silicone rubber casts were prepared from selected specimens. These casts were then palladium coated using a sputter-coater to provide an opaque surface for improved contrast in light photomacroscopy.

In order to determine morphological characteristics useful in identifying fossil fruits of *Paliurus* and discerning possible relationships among extant and fossil species, we studied the fruit morphology of all five extant species: *Paliurus spina-christi*, *Paliurus orientalis* (Franch.) Hemsl., *Paliurus hemsleyanus* Rehder ex. Schirarend & Olabi, *Paliurus ramosissimus* (Lour.) Poir., and *Paliurus hirsutus* Hemsl. We examined herbarium material from China, Italy, Greece, Albania, and Iran (table A1 in the online edition of the *International Journal of Plant Sciences*) at the California Academy of Sciences (CAS) and the Smithsonian Institution, Washington, DC (USNM). Fruiting specimens of *P. hirsutus*
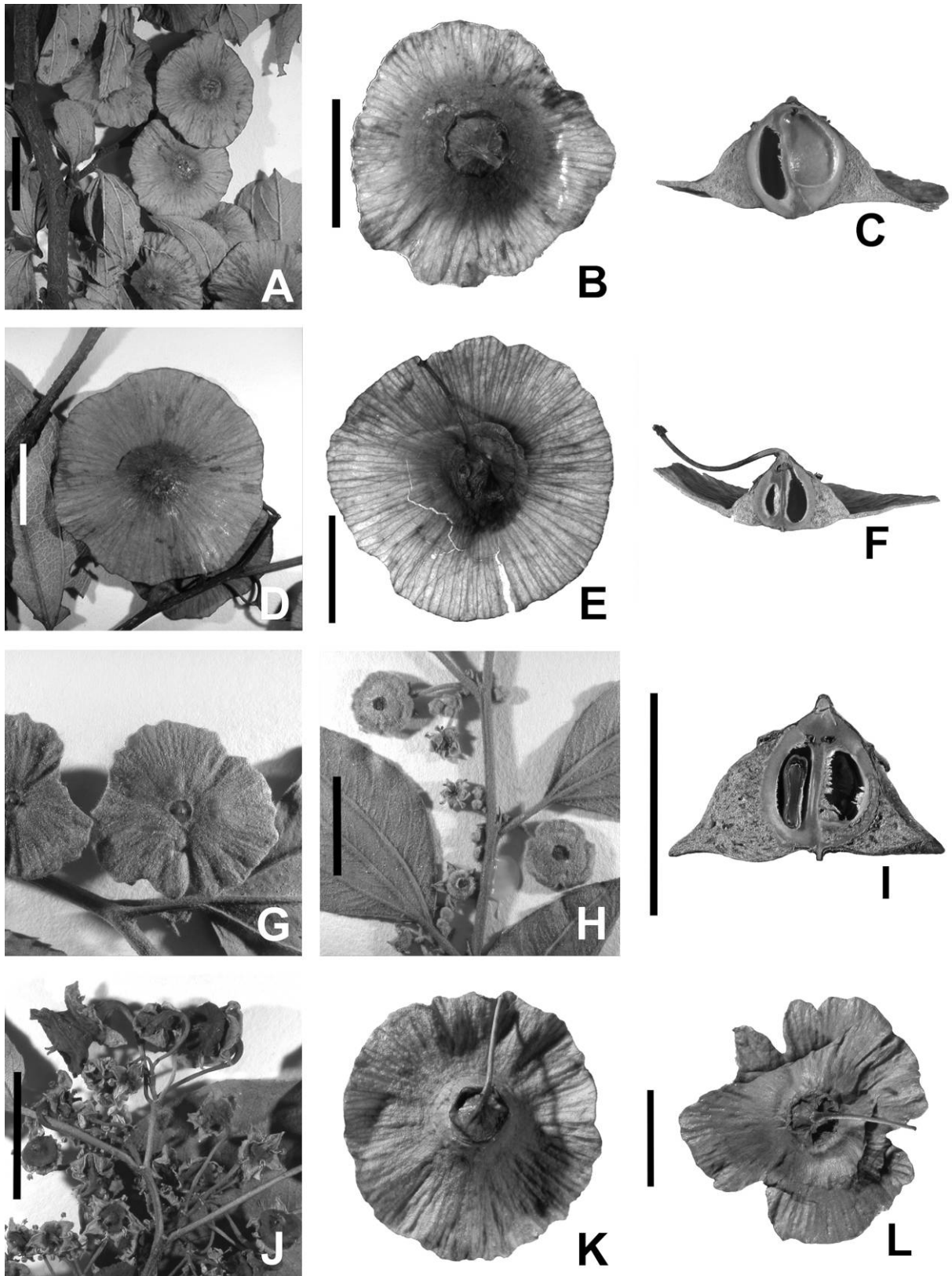
Fig. 2 Extant species of *Paliurus*. *A–C, Paliurus orientalis*, Dali Xian, Yunnan Province, China, CAS 724952. *D–F, Paliurus hemsleyanus*, Dabu, Guilin Province, China, CAS 724106. *A, D*, Apical views of fruits. *B, E*, Basal views of fruits. *C, F*, Longitudinal sections of fruits. *G*, Fruits of *Paliurus ramosissimus*, tip view, Shunhuangshan, Hunan Province, China, CAS 1056359. *H*, Flowers and developing fruits of *P. ramosissimus*,
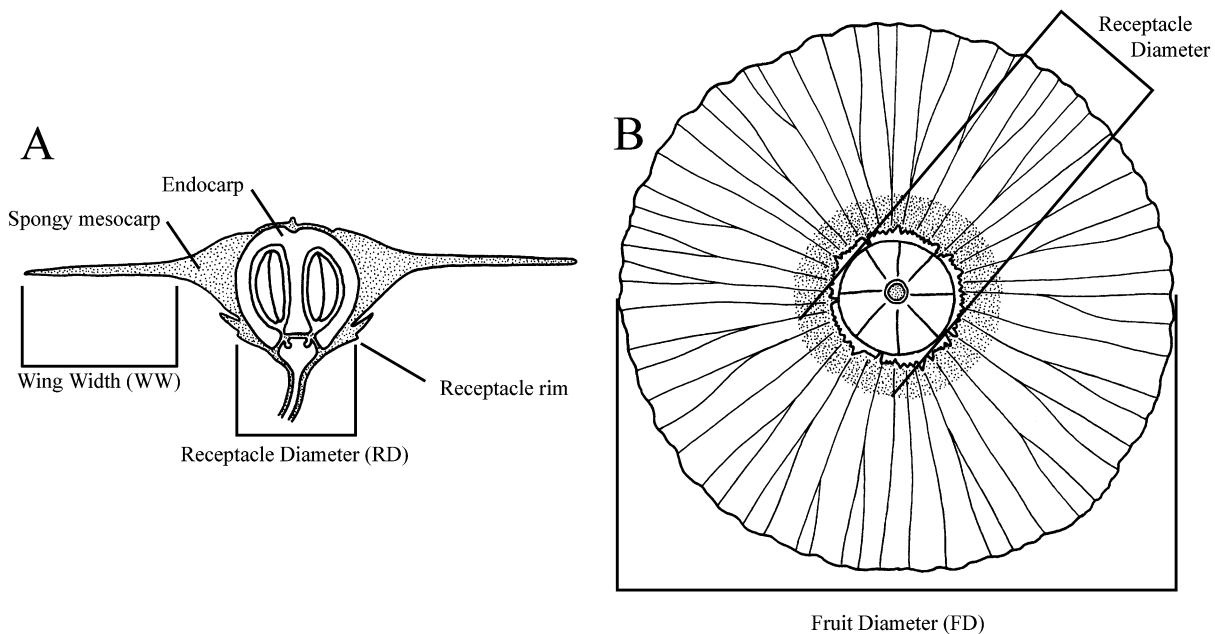
Fig. 3 Diagrammatic representation of *Paliurus* fruit showing key morphological features and measurements taken for morphometric analyses. *A*, Longitudinal section of fruit showing receptacle diameter (*RD*) and wing width (*WW*) measurements. *B*, Basal (receptacle end) view of whole fruit showing fruit diameter (*FD*) and RD measurements.

were studied on the basis of photographs of herbarium sheets held at the Kunming Institute of Botany (KUN). Fruit morphology was examined, and photographs of fruit details were obtained under the same conditions as the fossils. Anatomical details were examined on transverse and longitudinal sections of fruits from three species of *Paliurus* (CAS and the modern fruit collection of the Florida Museum of Natural History paleobotanical laboratory), prepared using a Microslice 2 Precision Slicing Machine (Malvern Instruments, Malvern), fitted with an annular diamond blade.

Morphometric analysis was used to identify potential quantitative differences among fruits of fossil and extant species. Measurements were taken only from material representing mature fruits. Fruits were considered mature if the wing was fully expanded. In immature fruits, the wing will shrink and collapse upon drying. Measurements included (1) fruit diameter (FD; fig. 3*B*; the average distance across the fruit wing based on two perpendicular measurements); (2) wing width (WW; fig. 3*A*; the average width of the wing measured at four points 90° apart on the bottom [pedicel] side of the fruit); and (3) receptacle diameter (RD; fig. 3; the average distance across the receptacle based on two perpendicular measurements). These measurements were chosen for their utility in separating some modern species (table 1) and because they are easily measured on most fossil material. Using these measurements, several morphometric indices were calculated for each fruit. The indices that proved

most useful were receptacle index (RD/FD) and wing index (WW/FD). Measurements were taken from 75 fruits of extant species, representing 18 herbarium sheets, and from 41 fossil fruits (tables 1, A1; data available from the first author on request). Not all measurements were obtained from all fruits as a result of differences in preservation of fossil material and orientation of fruits on herbarium sheets. For all European and Asian fossils, measurements were taken from published figures or photographs. Significance levels for morphological differences among species were calculated using one-way ANOVA and Tukey's HSD in R (ver. 2.6.0; R Development Core Team 2007).

The geographic distribution of fossil localities for *Paliurus* was plotted using ArcGIS software (ver. 9.1; ESRI, Redlands, CA) and georeference data for individual fossil sites (fig. 1). In most cases, descriptive locality data from the literature was converted into latitude and longitude using maps supplemented with information from geographic databases. For the extant species, distributions were interpreted from Schirarend and Olabi (1994) and plotted by hand.

Systematic Descriptions

Species—Paliurus favonii *Unger (Figs. 7, 8)*

Basionym. Paliurus favonii Unger, 1847, Chloris Protogaea, VIII–X, p. 147, pl. 50, fig. 6.

Sichuan Province, China, CAS 827770. *I*, Longitudinal section of *P. ramosissimus* fruit, Jiangxi Province, China, CAS 51639. *J*, Flowers and developing fruits of *Paliurus spina-christi*, Iran, DH 399714. *K*, Basal view of *P. spina-christi* fruit, Gilan, Iran, MO 1983529. *L*, Basal view of *P. spina-christi* fruit, showing three lobes of the wing (top left lobe partially broken), Armenia, US 2061589. Scale bars = 1 cm in *A*, *B* (applies also to *C*), *D*, *E* (applies also to *F*), *H* (applies also to *G*), *I*, *J*, *L* (applies also to *K*).
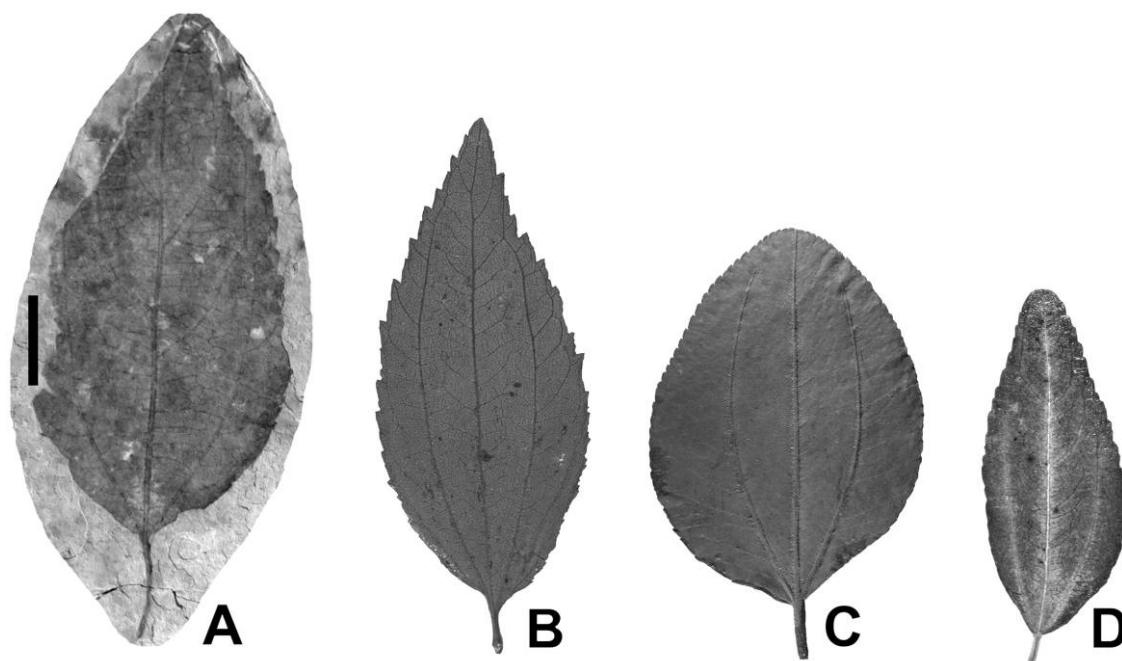
Fig. 4 Fossil and modern leaves of *Paliurus* and related genera. *A*, Ziziphoid leaf fossil, Miocene, UF 242-19660. *B–D*, Leaves of modern ziziphoid Rhamnaceae. *B*, *Ceanothus americanus* L., UF modern collection 2372 (MO 831107). *C*, *Paliurus orientalis*, CAS 724952. *D*, *Ziziphus jujuba* Mill., UF modern collection 2414 (MO 1920411). Scale bar = 1 cm (applies to all leaves).

Synonymy. *Paliurus hesperius* E.W. Berry, 1928, Am. J. Sci. Series 5, p. 40, figs. 1–3—holotype USNM 43720: Grand Coulee, Washington; Miocene Latah Formation Berry, 1931, U.S. Geol. Surv. Prof. Pap. 170, p. 170, pl. 13, figs. 4, 5: Grand Coulee, Washington; Miocene Latah Formation Brown, 1937, U.S. Geol. Surv. Prof. Pap. 186-J, pl. 56, figs. 8, 9: Spokane, Washington; Miocene Latah Formation.

Lectotype. LMJ (Landesmuseum Joanneum, Graz) 76518, designated by Kovar-Eder et al. (2004), pl. 11, fig. 7. Same specimen figured by Unger (1847), p. 147, pl. 50, fig. 6.

Revised assignments. Specimens previously illustrated in the literature under other binomials are now transferred to *P. favonii* (table B1 in the online edition of the *International Journal of Plant Sciences*, underlined data). Although these specimens are transferred, the indicated binomials may remain in effect for other specimens. These are not formally trans-

ferred to *P. favonii* because the original species were based on both leaf and fruit material, and holotypes were not designated by the original authors (table B1).

Supplementary description. Fruit an indehiscent winged drupe; FD 5.7–20.0 mm; receptacle flat with pronounced rim; receptacle 1.9–5.7 mm in diameter; endocarp 2.4–13.5 mm in diameter and 1.0–5.6 mm deep, sometimes with strong, straight ridges radiating from base of pedicel to edge of receptacle (fig. 8K, left); wing usually thin and more or less circular, 1.1–5.5 mm wide, oriented perpendicular to main axis of fruit, with fine radiating, dichotomizing, and anastomosing venation (fig. 7E; fig. 8I, 8J); edges of wing mostly irregular, occasionally with prominent clefts (fig. 8A, 8H) or obvious lobes (fig. 7B, 7C).

Comments. We discuss this widely distributed fossil species in more detail following our review of the extant species. Our concept of the species includes occurrences from Europe,

Table 1

Morphological Characteristics of Extant and Fossil *Paliurus* Species

Species	Fruit diameter (mm)	Mean	Fruits measured	Wing index	Receptacle index	Fruit pubescence	No. and form of spines
Extant species:							
P. hirsutus	9–17	14.7	5	.2	.3	Yes	1; hooklike
P. ramosissimus	11–18	14.0	20	.1	.3–.4	Yes	2; both erect
P. orientalis	11–20	14.2	25	.2–.3	.2–.3	No	2; both erect
P. hemsleyanus	19–35	25.4	21	.3–.4	.2	No	2; both erect
P. spina-christi	15–35	21.5	4	.2–.3	.2–.4	No	2; 1 erect and 1 hooklike
Fossil species:							
P. favonii	6–20	13.0	37	.1–.3	.2–.5	Unknown	na
P. clarnensis	19–24	20.8	4	.3–.4	.1	Unknown	na

Note. na = not applicable.

where it was first described, as well as from North America and Asia. Taken together, these fossils comprise a morphologically intergrading set with no quantitative discontinuities for several key fruit dimensions. Thus, we have emended the diagnosis of *P. favonii* to include the full range of dimensions observed in this study (table 1) and transferred fruits previously described as different species to *P. favonii* (table B1). As discussed below, *P. favonii* may encompass more than one biological species having indistinguishable fruits.

Species—Paliurus clarnensis, Burge & Manchester sp. nov. (Fig. 9)

Supplementary description. Fruit an indehiscent, winged drupe; FD 18.5–23.5 mm; pedicel slender to relatively robust, broadening slightly at junction with base of fruit, forming flat receptacle with pronounced rim; RD 1.2–1.8 mm; endocarp 6.0–7.3 mm in diameter and 1.0–1.6 mm deep, sometimes with strong, straight ridges radiating from receptacle on basal surface of fruit (fig. 9*E*) or on both apical and basal surfaces (fig. 9*E*, 9*F*); wing thin, more or less circular, 6.3–8.0 mm wide, oriented perpendicular to main axis of fruit, with fine radiating, dichotomizing, and anastomosing venation (fig. 9*A*, 9*G*); edges of wing mostly irregular, sometimes cleft (fig. 9*B*).

Holotype. UF 46876, fig. 9*K*, 9*L*, Middle Eocene (~44 Ma) of Red Gap, Jefferson County, Oregon (UF locality 251A).

Other specimens. Gosner Road, OR: UF 00238-19822, pt. & ctpt. (fig. 9*A*–9*C*); White Cliffs, OR: UF 00262-17703, pt & ctpt. (fig. 9*D*–9*F*); West Branch of Bridge Creek, OR: UF 00230-18356, pt. & ctpt. (fig 9*G*–9*I*); Red Gap, OR: UF 251A-51200, pt. & ctpt. (fig. 9*J*).

Etymology. The epithet refers to the name of the geologic horizon in which all confirmed specimens occur, the Clarno Formation of Oregon.

Discussion of Paliurus clarnensis *sp. nov.* Fruits of *P. clarnensis* differ from those of *P. favonii* by their narrow receptacle in comparison to FD and their wide wing. Although *P. clarnensis* overlaps with *P. favonii* for FD (fig. 5*C*, 5*D*; *P. favonii* FD: 5.7–20.0 mm; *P. clarnensis* FD: 18.5–23.5 mm; Tukey's HSD: $P \ll 0.05$), the two species do not overlap with respect to RD (fig. 5*D*; *P. favonii* RD: 1.9–5.7 mm; *P. clarnensis* RD: 1.2–1.8 mm; Tukey's HSD: $P \ll 0.05$) or WW (fig. 5*C*; *P. favonii* WW: 1.1–5.5 mm; *P. clarnensis* WW: 6.3–8.0 mm; Tukey's HSD: $P \ll 0.05$). The difference between the species is most obvious in a bivariate plot of FD against RD (fig. 5*D*), in which *P. clarnensis* and *P. favonii* each form discrete clouds of points with different allometric trends. The isolation of *P. clarnensis* is also summarized by the receptacle index (RD/FD), which is 0.1 for all known fossils of *P. clarnensis* but no less than 0.2 for other *Paliurus* fossils measured during this study. Differences in wing venation are also discernible. The veins of *P. clarnensis* are typically finer, more closely spaced, and somewhat less branched than those of other *Paliurus* fossils (fig. 7*G*, 7*E* vs. fig. 9*A*, 9*G*).

Because there are so few known fossils of *P. clarnensis*—a total of five fruits from four localities—it is difficult to determine levels of local variation. One of the fruits (UF 00230-18356; fig. 9*G*–9*I*), despite corresponding to the other specimens in terms of overall size, WW, and shape, does not clearly display a receptacular rim (fig. 9*I*). Because of its similarity to confirmed specimens and the geographic proximity of

localities, we have concluded that the missing character is probably due to differences in preservation and have thus included this specimen within the new species. As a species, *P. clarnensis* is variable with respect to the qualitative characters of sculpture and wing margin shape. However, the species is relatively uniform for key fruit dimensions, including FD (18.5–23.5 mm) and RD (1.2–1.8 mm).

Paliurus clarnensis is an unusual, geographically localized species and the oldest known member of *Paliurus*. The morphology of the fruit, including its RD allometry, which differs from that of other known fossil forms (fig. 5*D*), indicates that this species may represent an ancestral or early diverging lineage of the genus. Furthermore, the fruits of *P. clarnensis* possess all of the diagnostic characters for the genus, which demonstrates that *Paliurus* had already attained its distinctive form by the Middle Eocene. The early occurrence of *P. clarnensis* in North America also points toward the possibility of a North American origin for the genus.

Results and Discussion

Morphology

Extant species. At anthesis the small, perigynous, tricarpellate flowers of *Paliurus* are similar to those of *Ziziphus*, which does not have winged fruits. In *Paliurus*, however, the base of the gynoecium begins to swell laterally following fertilization (fig. 2*J*), forming a circular, disk-shaped (orbicular) wing of varying thickness (fig. 2*C*, 2*F*, 2*I*). In mature fruits, the receptacle is persistent and hemisphere- or disk-shaped. The edge of the receptacle forms a continuous rim around the base of the ovary. This receptacular rim represents the remains of the nectary disk and perianth as well as the attachment region for the corolla. The receptacular rim, or its persistent scar, is diagnostic of *Paliurus* in comparison to superficially similar fruits belonging to other taxa.

Extant species of *Paliurus* can be divided into two groups on the basis of fruit morphology. In the first group, comprising *Paliurus spina-christi*, *Paliurus orientalis*, and *Paliurus hemsleyanus*, the wing of the mature fruit is thin, papery (chartaceous), relatively wide, and equatorially extended, with limited development of spongy parenchyma in the mesocarp (fig. 2*A*–2*F*, 2*K*, 2*L*). This set of species will be referred to as the *P. spina-christi* group. In the second group, containing *Paliurus ramosissimus* and *Paliurus hirsutus*, the wing is thick, wedge-shaped in longitudinal section, and typically narrower than in the first group (fig. 2*G*, 2*I*). In these species, the thickening of the wing derives from greater development of spongy parenchyma in the mesocarp (fig. 2*I*). This pair of species will be referred to as the *P. ramosissimus* group.

While it is possible to separate extant species of *Paliurus* into groups on the basis of fruit morphology, variation in fruit shape and dimensions within each group is continuous. For example, the Chinese species *P. orientalis* and *P. hemsleyanus* are very similar (table 1; fig. 2*A*–2*C* vs. fig. 2*D*–2*F*), and are traditionally distinguished on the basis of FD or leaf length (Schirarend and Olabi 1994), both of which overlap between the species (table 1). Differences in presence, positioning, and morphology of spines, geographic distribution, and ecology seem to distinguish the Eurasian species *P. spina-christi* from the two Chinese
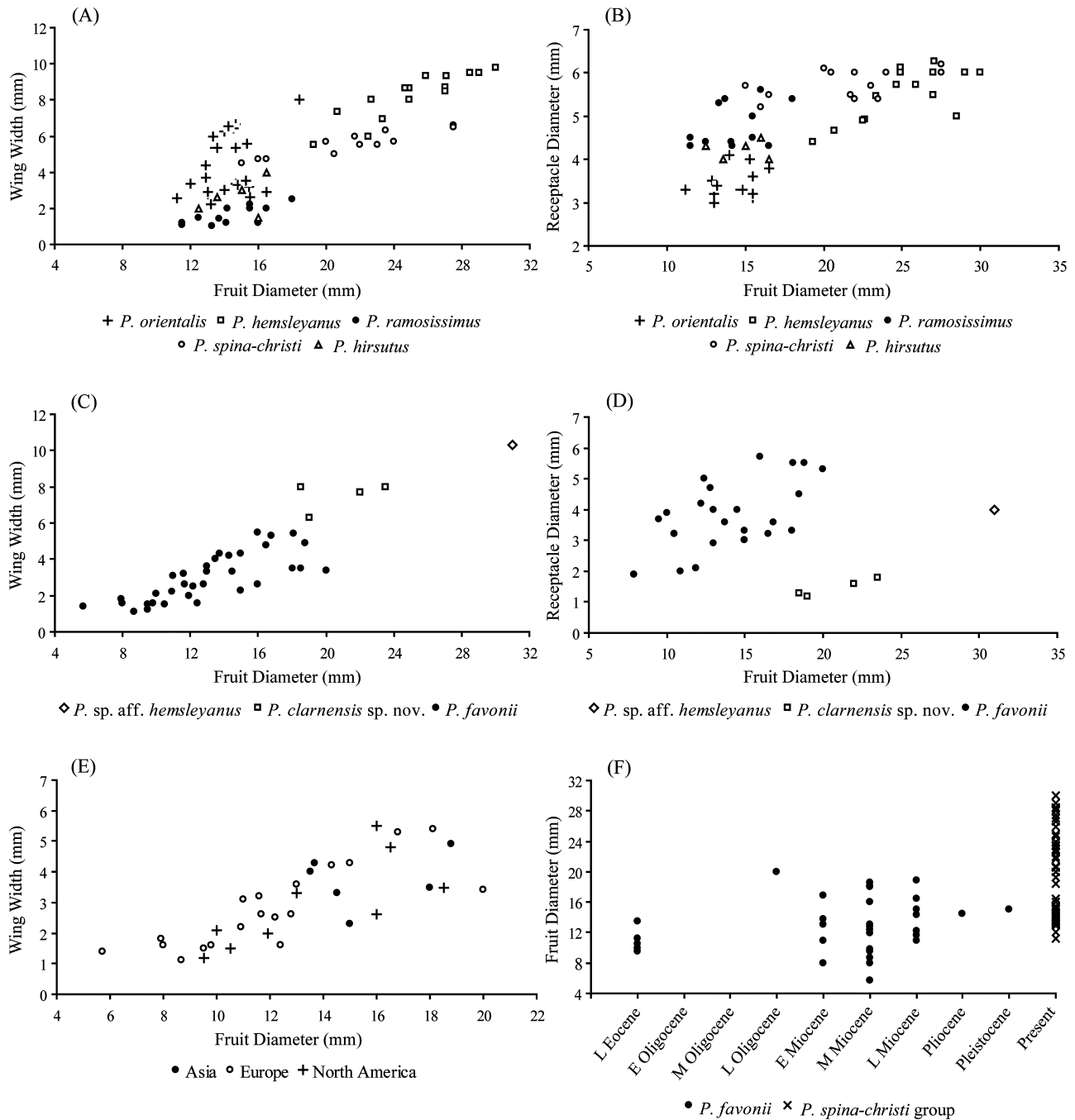
Fig. 5 Bivariate plots based on measurements taken from *Paliurus* fossil fruits and representative herbarium specimens (table 1; tables A1, B1 in the online edition of the *International Journal of Plant Sciences*). *A*, Plot of fruit diameter (FD) against wing width (WW) for five extant species of *Paliurus* (tables 1, A1). *B*, Plot of FD against receptacle diameter (RD) for five extant species of *Paliurus* (tables 1, A1). *C*, Plot of FD against WW for confirmed *Paliurus* fossil fruits. *Paliurus* sp. aff. *hemsleyanus* = *Paliurites martyi* (Langeron 1902), *Paliurus clarnensis* sp. nov. = all known records of new species from Eocene of Oregon, *Paliurus favonii* = *P. favonii* as interpreted in this article (table B1). *D*, Plot of FD against RD based on same records as *C*. *E*, Plot of FD against WW for all confirmed *Paliurus* fruit records conferred to *P. favonii* (table B1), segregated into Asian, European, and North American records. *F*, Plot of FD against time for *P. favonii* and allied extant species. For time category abbreviations, E = early, M = middle, L = late. Symbol for *P. favonii* as in *C* and *D*. *Paliurus spina-christi* group refers to pooled records of the modern species *P. spina-christi*, *P. hemsleyanus*, and *Paliurus orientalis* measured during this study (tables 1, A1).

species. However, *P. spina-christi* is difficult to consistently separate from its east Asian counterparts based on fruit morphology alone, as the range of morphological variation known for *P. spina-christi* encompasses nearly the entire range of fruit dimensions known for the Asian species, and overlaps with them morphometrically (table 1). The two species of the *P. ramosissimus* group are somewhat easier to separate on the basis of fruit shape. In *P. ramosissimus*, the wing is usually trilobed and strongly veined (fig. 2*G*), while in *P. hirsutus* the wing margin is usually entire, with less prominent venation (Schirarend and Olabi 1994, fig. 4). Nevertheless, some fruits of *P. ramosissimus* approach the condition of *P. hirsutus*, and variation in fruit size as well as allometric indices is continuous (table 1). In addition, supposedly diagnostic features of fruit morphology, such as form of wing lobes and degree of wing venation, vary within extant species and thus may not represent reliable characters for delineating species from fossil material. *Paliurus spina-christi*, for example, typically produces fruits with a continuous wing margin (fig. 2*K*), but is also capable of producing fruits with multilobed wings (fig. 2*L*).

Fossil leaves. Fossil leaves with affinities to *Paliurus* (fig. 4*A*) are abundant in the Tertiary of the Northern Hemisphere. Because characters used to identify *Paliurus* leaves in the fossil record, such as "trinerved" (acrodromous) primary venation, crenate, minutely toothed leaf margins, and percurrent tertiary venation are shared with other Rhamnaceae such as *Ceanothus* and *Ziziphus* (fig. 4; Bůžek 1971; Meyer and Manchester 1997), many species of *Paliurus* described from leaf remains may not in fact represent this genus. Conversely, some fossil leaves identified as other genera may in fact represent *Paliurus*. The overlapping leaf architectural features of *Paliurus* and *Ziziphus* are not surprising in light of molecular results indicating that *Paliurus* is nested within *Ziziphus* (Islam and Simmons 2006). A comprehensive systematic treatment of putative leaf fossils for *Paliurus* and allied taxa does not yet exist and is beyond the scope of this paper. However, it appears unlikely that consistent differences exist. For example, Knobloch and Kvaček (1976) were able to show that even in cases where cuticle is preserved, it is not possible to identify fossil remains as *Paliurus* on the basis of leaf epidermal anatomy.

Fossil fruits. Fossil fruits identifiable as *Paliurus* are known from a wealth of Tertiary deposits in the Northern Hemisphere, including localities in North America, Europe, and Asia (fig. 1). In comparison to leaf remains ascribed to the genus, fossil fruits of *Paliurus* are more reliably assigned based on the characters discussed above. The present contribution does not attempt an exhaustive review of *Paliurus* fruit records but instead seeks to summarize the stratigraphic and geographic range of records (table B1).

Fossil *Paliurus* fruits are recognized by their distinctive winged morphology. Nevertheless, fruits of *Cyclocarya* (Juglandaceae; fig. 6*A*–6*C*), as well as some Lower Cretaceous fossil forms of unknown affinity (fig. 6*D*–6*F*), are convergently similar to those of *Paliurus*, which has led to confusion over the assignment of fossil remains. In well-preserved material, however, fruits of *Paliurus* show evidence of a receptacular rim on the basal side of the ovary, as described above. This character is missing in *Cyclocarya*, which instead has four apically positioned sepals that are sometimes visible on paleobotanical specimens (Manchester 1999). In anatomically preserved material, *Paliurus* fruits are dis-

tinguished by their typically trilocular endocarps. Those of *Cyclocarya* have a single locule, divided at the base by partial septa that are sometimes visible in fossils (Manchester and Dilcher 1982). In the absence of diagnostic characters, it is impossible to assign orbicular-winged fossils to either *Paliurus* or *Cyclocarya* due to striking convergence in wing form and venation (fig. 6*A* vs. fig. 9*B*). Likewise, identification of *Paliurus* fossils is not possible in the absence of a recognizable wing, because this organ may be lost during deposition, and wingless endocarps of *Paliurus* strongly resemble those of the closely related genus *Ziziphus* (Tcherepova 2001). In addition, only the basal counterpart of a compression fossil will show a receptacular rim impression. If the basal counterpart is missing and the carpel number cannot be determined, then identification of fossils as *Paliurus* is dubious.

Paliurus fruits exhibit a large amount of variation in size and shape, although little of this variation has been accounted for in the description of fossil species, many of which are based on leaves (Unger 1847; Heer 1859; Miki 1933*a*, 1933*b*, 1937; Bůžek 1971). Fossil fruits of *Paliurus* encompass nearly the entire range of dimensions known in fruits of extant species (table 1; fig. 5*A*, 5*B* vs. fig. 5*C*, 5*D*), have a comparable diversity of qualitative shape (fig. 2 vs. figs. 7–9), and exceed modern forms in terms of variability for some morphometric indices (table 1). Although the total amount of variation among fossil *Paliurus* fruits exceeds that of modern species, fruit dimensions vary continuously across geographic region (fig. 5*E*) and over time (fig. 5*F*), with few natural gaps. This continuum may represent multiple, closely related species that overlap broadly for fruit characteristics in the same fashion as do some modern species, which implies that fossil species may prove difficult to delineate on the basis of characters observable on isolated fruits. Furthermore, the sporadic occurrence of *Paliurus* fruits in the fossil record, with only small numbers of specimens typically recovered from a single deposit, makes it difficult to infer the variability of ancient species for comparison to modern ones.

Most fossil *Paliurus* fruits, including European, Asian, and North American records spanning Eocene through Pleistocene time, fall within a morphological continuum that contains Unger's (1847) original species, *Paliurus favonii*. This group may represent either a highly variable, long-lived, and widespread species or a set of allied but morphologically intergrading species, as in the modern *P. spina-christi* group. Although future studies on fossil *Paliurus* fruits may result in some objective criteria for segregating other species, at this time we propose synonymy of most fossils, with the notable exception of *Paliurus clarnensis*. Our species concept for *P. favonii* and potential segregates of the species are discussed further in the sections on European and North American records.

Europe. Fruits of *Paliurus* have been reported from the Czech Republic, Austria, Germany, France, and Poland (table B1; fig. 1). Oldest occurrences in Europe are from an Oligocene to Early Miocene locality in the Bitterfeld district of Germany (Mai and Walther 1991). Later occurrences are predominantly Miocene (Unger 1847; Heer 1859; Ettingshausen 1869; Brabenec 1904; Menzel 1933; Raniecka-Bobrowska 1959; Bůžek 1971; Bůžek et al. 1992; Krenn 1998; Kvaček and Hurník 2000; Kovar-Eder et al. 2004), followed by a handful of Pliocene occurrences (Langeron 1902; Gregor 1982).

While a majority of European records form a continuum based on fruit dimensions (fig. 5*E*), an occurrence from the
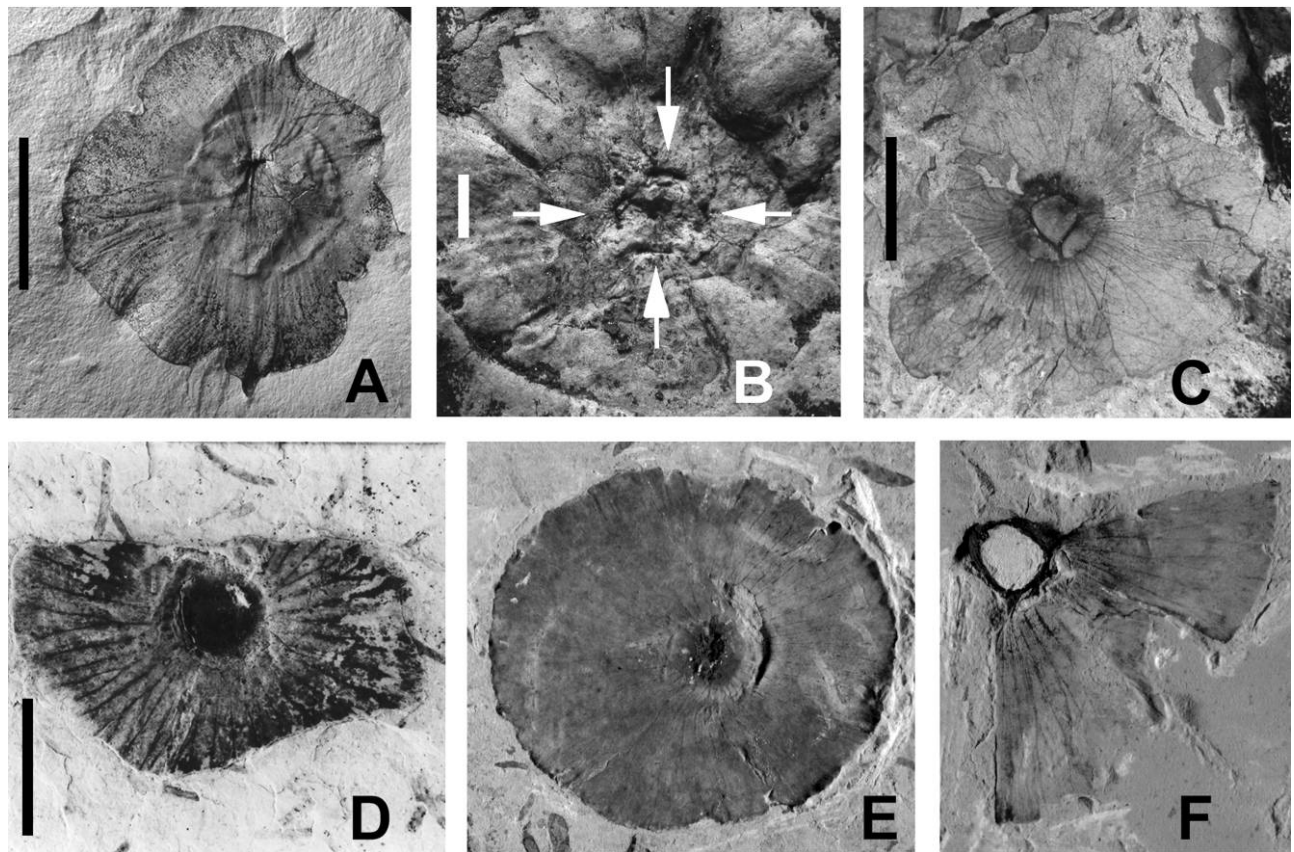
Fig. 6 Fossil fruits with superficial similarity to those of *Paliurus*. *A, B, Cyclocarya* sp., Early Eocene Wind River Formation, Wyoming. *A,* Basal surface of fruit, UCMP 168324A. *B,* Magnification of apical surface of fruit showing four perianth remnants (arrows), UCMP 168324B. *C,* Wing and fruit body, DMNH 16605. *D–F,* Fossil fruits of unknown taxonomic affinity, Lower Cretaceous Santana Formation of Brazil. *D,* Wing and central body of fruit, SMNS 5681. *E, F,* Two fruits from the personal collection of Richard M. Dillhoff. *E,* Apical surface of first fruit. *F,* Side view of second fruit, showing position of fruit body in relation to wing. Scale bars = 1 cm in *A, C, D* (applies also to *E, F*); 1 mm in *B*.

Pliocene of France, reported by Langeron (1902) from Pas de la Mougudo, near Cantal, is exceptional among fossil *Paliurus* for its size and falls outside the morphological range for other fossil *Paliurus* fruits (fig. 5C–5F, open diamond). Described as *Paliurites martyi* Langeron (Langeron 1902), this fruit corresponds in dimensions to the large-fruited modern species *P. spina-christi* and *P. hemsleyanus*. On the basis of the geographic occurrence of the fruit, this specimen may represent a relative of the modern European species *P. spina-christi*, as noted by Langeron (1902). However, the fruit is closest to *P. hemsleyanus* on the basis of bivariate plots of fruit dimensions for four of the modern species (fig. 5A vs. fig. 5C; fig. 5B vs. fig. 5D). Because of its similarity to the modern species *P. hemsleyanus*, this interesting fossil is provisionally referred to here as *Paliurus* sp. aff. *hemsleyanus*.

Paliurus was first recognized in the fossil record by Unger (1847, p. 147, pl. 50, fig. 6), who described *P. favonii* on the basis of both fruits and leaves from Miocene deposits near Parschlug, Austria (fig. 1; table B1). The fruit diagrammed by Unger and refigured photographically by Kovar-Eder et al. (2004, pl. 11, fig. 7) is medium in size (FD 12.3 mm), with a narrow wing (WW 1.6 mm) and a wide receptacle (RD 5.0 mm). The wing appears

to be thin and was probably equatorially developed, as in the *P. spina-christi* group.

In 1859, Heer published *Paliurus thurmannii* Heer on the basis of fruits and leaves, without a designated holotype, from a Miocene deposit near Le Locle, Switzerland (fig. 1; table B1). Only one of the line drawings provided in this description appears to represent a *Paliurus* fruit (Heer 1859, pl. 122, fig. 28c). Although this fruit compares favorably with Unger's *P. favonii*, the dimensions of Heer's fruit are considerably smaller (FD 5.7 mm, WW 1.4 mm). If the illustration by Heer (1859) is taken as accurate, then this fruit is the smallest currently known.

Following Heer's 1859 description, Brabenec (1904) published the species *Paliurus fricii* Brabenec on the basis of a fruit from a Late Miocene deposit near Holedeč, Czech Republic (fig. 1; table B1). This fruit (Brabenec 1904, fig. 11a) is comparable with *P. favonii* but was synonymized with the leaf-based species *Paliurus tiliaefolius* Unger by Bůžek (1971), along with various leaf remains previously described as species of *Paliurus, Ziziphus, Ceanothus, Quercus* L., and *Ficus* L. (Bůžek 1971, p. 74). Assignment of *P. fricii* to the leaf-based species *P. tiliaefolius* requires the hypothesis that these fruits were actually borne by the same plants as the leaves. Later
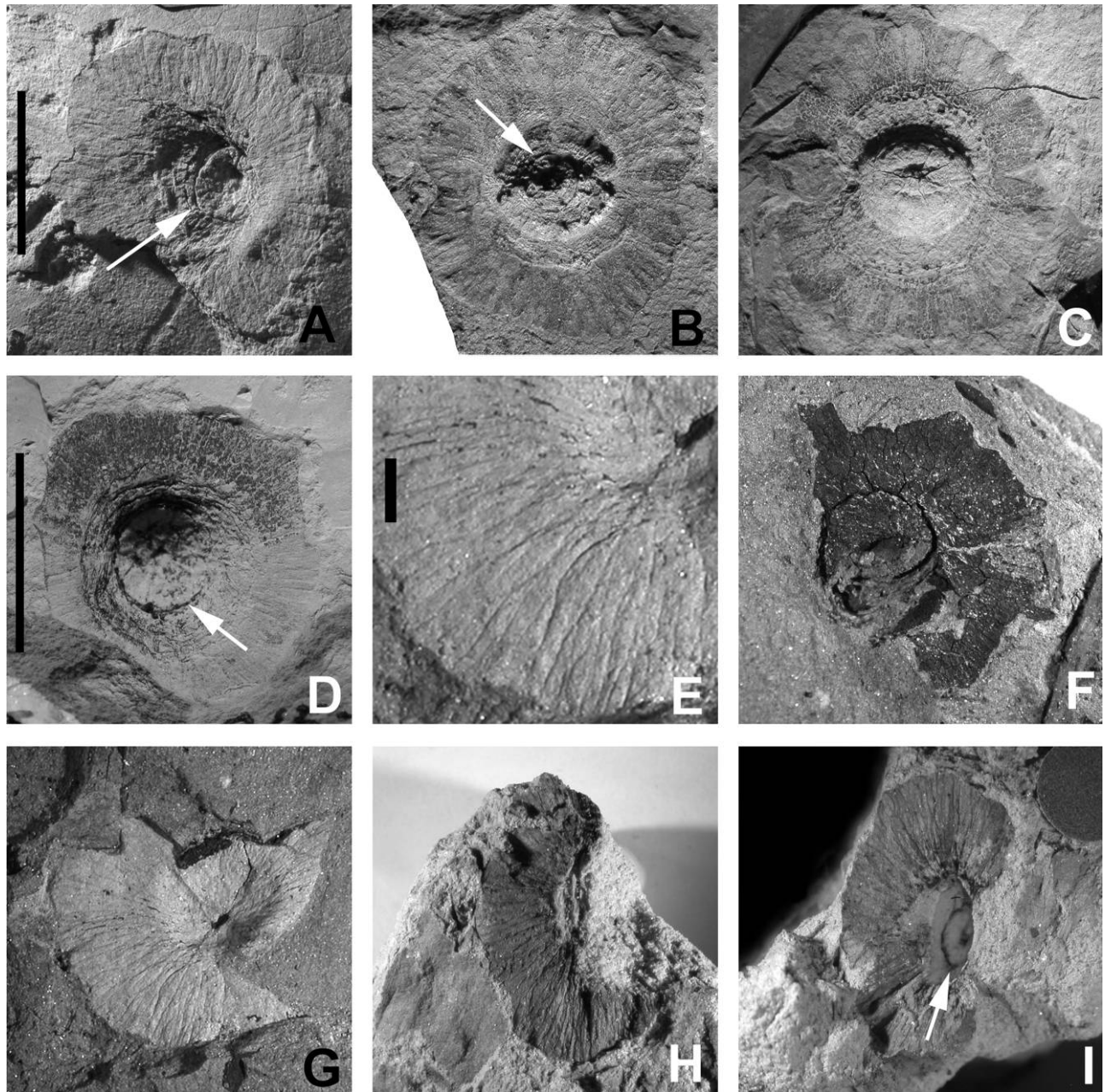
Fig. 7 North American *Paliurus favonii*. *A–C*, Grand Coulee, Washington; Miocene, Latah Formation. *A*, Holotype of *Paliurus hesperius*, basal surface of fruit, USNM 43720. *B*, Basal surface of fruit, USNM 38650 (=Berry 1931, pl. 13, fig. 4). *C*, Apical surface of fruit, USNM 316377 (Berry 1931, pl. 13, fig. 5). *D*, Basal surface of fruit, Spokane, Washington; Miocene, Latah Formation, USNM 315292 (=Brown 1937, pl. 56, figs. 8, 9). *E–G*, Clarkia Race Track, Shoshone County, Idaho; Miocene. *E*, Magnification of wing venation on apical surface of fruit, UF 15888-51202. *F*, basal view of fruit showing fragment of endocarp, UF 15888-51202′. *G*, Apical surface of fruit, UF 15888-51202. *H*, *I*, Alum Bluff, Liberty County, Florida; Miocene, Alum Bluff Group. *H*, Apical surface of fruit with fragmentary wing, UF 18049-26117. *I*, Counterpart showing basal surface of fruit with fragmentary wing surrounding central mold of fruit body, UF 18049-26117 (=Manchester 1999, fig. 9C). In all figures, arrow indicates the diagnostic receptacle rim. Scale bars = 1 cm in *A* (applies also to *B*, *C*), *D* (applies also to *F–I*); 1 mm in *E*.

authors noted this difficulty and advocated separate binomials for leaves and fruits (Mai and Walther 1991; Kvaček and Hurník 2000). We also advocate the use of separate binomials for fruits and leaves as well as the combination of *P. fricii* with *P. favonii* (table B1).

No additional species of *Paliurus* have been described from Europe since Brabenec's (1904) article. Subsequently, Kirchheimer (1957) provided the most comprehensive overview of European occurrences for *Paliurus* fossil fruits, combining most known records under *P. favonii*, *P. fricii*, and *P. thurmannii*.
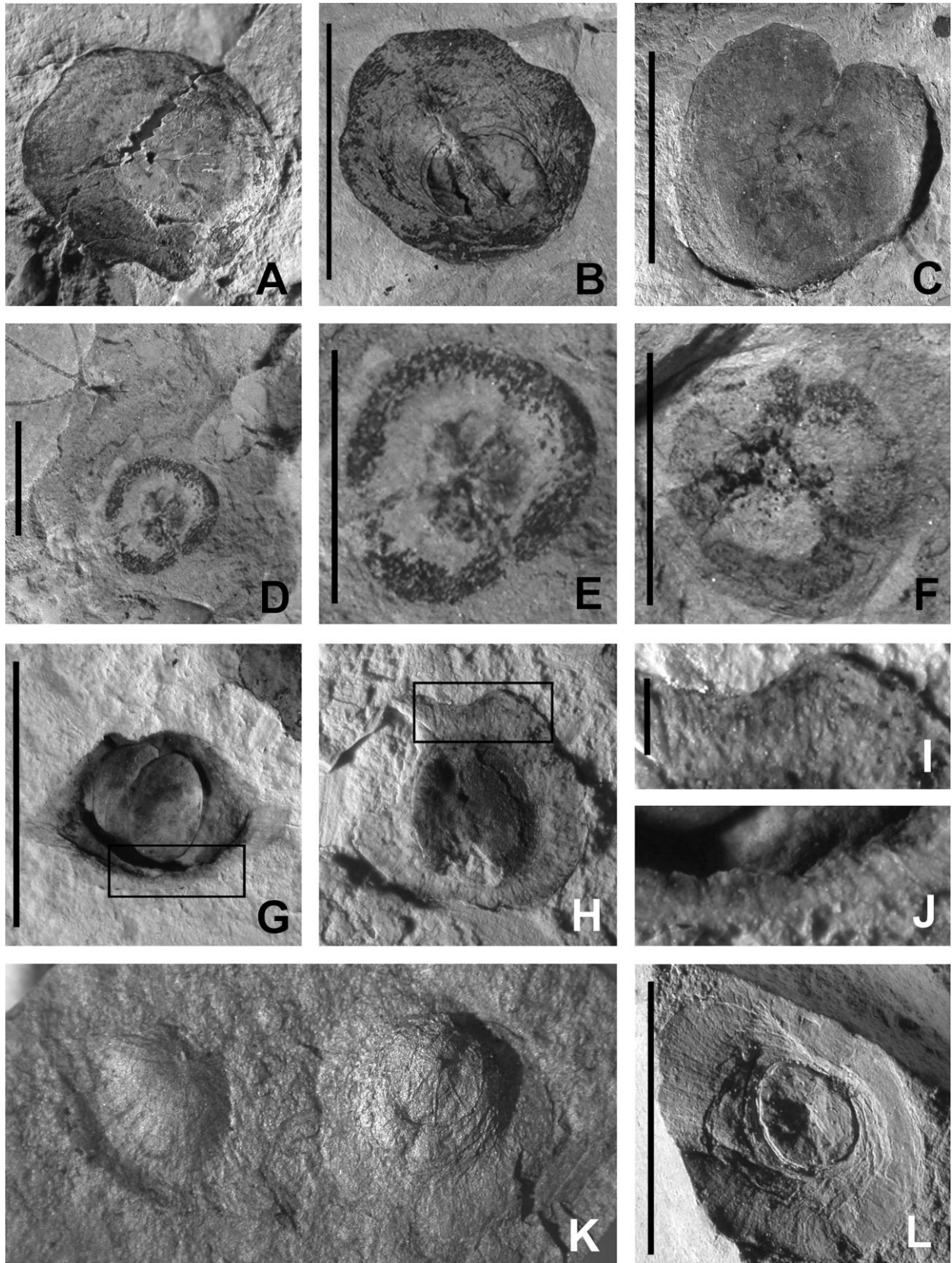
Fig. 8 Potential segregates of *Paliurus favonii*. *A–C*, Teater Road, Oregon; Late Eocene. *A*, Apical surface of fruit, UF 256-21060. *B*, Basal surface of fruit, UF 256-21060′. *C*, Apical surface of fruit, UF 256-20906. *D–F*, Čermníky, Czech Republic; Miocene. *D*, Basal surface of fruit,

Overall, the recent taxonomic trend has been toward synonymy of European fossils under *P. favonii* (Mai and Walther 1991; Kvaček and Hurník 2000; Kovar-Eder et al. 2004).

Taken as a group, the range of morphological diversity seen in European fruits is high, even at the level of a single fossil locality, as in the set of fruits reported by Bůžek (1971) that are highly variable with respect to FD and WW (table B1). Nevertheless, there are no diagnostic qualitative differences among European fossils, since the majority of confirmed records from this region form a continuum when compared using the fruit dimensions measured during this study (fig. 5E). The single exception is the Pliocene record from Cantal, France (Langeron 1902), referred to here as *Paliurus* sp. aff. *hemsleyanus* (fig. 5C, 5D, 5F). Overall, the European records form a morphological continuum with those from Asia and a portion of North American records (i.e., excluding *P. clarnensis*), although the Asian records tend toward the high end of the continuum for both FD and WW (fig. 5E).

Asia. Fossil *Paliurus* fruits are known from Japan, China, Siberia, and Kazakhstan. Oldest occurrences are from the Late Eocene of southwest Honshu Province, Japan (Huzioka and Takahasi 1970), and most recent occurrences are from the Pleistocene of Yamashiro Province, Japan (Miki 1933a, 1933b). An Oligocene occurrence is known from western Siberia (Dorofeev 1963), and Miocene occurrences are from Kazakhstan (Zhilin 1989) and China (WGCPC 1978). All Asian fruit records appear to be referable to *P. favonii*, with the exception of an endocarp-based record from Siberia (Dorofeev 1963) and the records of Hu and Chaney (1940) and Huzioka (1963), which are not certainly identifiable as *Paliurus*.

Dorofeev (1963) described *Paliurus sibirica* P.I. Dorof. on the basis of trilocular endocarps recovered from Oligocene deposits near the Tym River in the Tomsk Region of Siberia (fig. 1; table B1). Most of the specimens are endocarps denuded of their wings, but two of the figured fruits (Dorofeev 1963, pl. 35, figs. 7, 9–11) clearly show the trilocular endocarp and remnants of a disk-shaped wing, justifying the generic assignment. However, because features such as FD and WW cannot be measured on specimens with only fragmentary wing preservation, it is impossible to determine their precise affinities with fossil fruits having intact wings. As other authors have done (Gregor 1978; Mai 2001, pl. 28, fig. 11), we maintain *P. sibirica* as a morphospecies to accommodate naked or nearly naked trilocular endocarps potentially assignable to *Paliurus*.

Paliurus nipponicus Miki (Miki 1933a, 1933b; see also Miki 1937) was described from fruits and leaves recovered in Pleistocene deposits at several localities in Yamashiro Province, Japan (fig. 1; table B1). The figured fruit (Miki 1933a, pl. 4, fig. I [= Miki 1933b, pl. I, figs. Q, R]) is well preserved and medium in size (FD 15.0 mm), with a relatively narrow wing (WW 2.3 mm). While the fruit falls within the continuum for *P. favonii* on the basis of these measurements (table 1; fig. 5C, 5E), this Pleis-

tocene fossil is similar to the extant species *P. orientalis*, which occurs today in China (fig. 1). Although Miki (1933b) discussed a potential affinity with the modern Japanese species *P. ramosissimus* (fig. 2G–2I), the fossil fruit lacks the distinct and robust wing lobes of *P. ramosissimus*. In fact, the dimensions of the fruit place it near the centroid of points for *P. orientalis* (fig. 5A, 5B), which raises the question of whether this Pleistocene fossil may represent a close relative of the modern Chinese species.

A second fossil species, *Paliurus akitanus* Huzioka, was described from Japan on the basis of leaves and winged organs from the Early Miocene Utto Formation, near Tsuchikumazawa in northern Honshu, Japan (Huzioka 1963). Nevertheless, the fruits figured for the description (Huzioka 1963, pl. 37, figs. 7, 7a) do not appear to possess the distinguishing characteristics of *Paliurus*. Thus, these fossils were not included in the morphometric analysis and are provisionally excluded from *Paliurus*.

A third species of *Paliurus* for Japan, *Paliurus ubensis* Huzioka & Takahasi, was described on the basis of leaves and fruits, with a leaf designated as holotype, from Late Eocene deposits of the Okinoyama Formation in the Ube Coal Field, southwest Honshu, Japan (Huzioka and Takahasi 1970). Although a receptacle rim is not clearly discernible in the fruit figured by Huzioka and Takahasi (1970, pl. 14, fig. 8; AKMG 3421, paratype) the size of the fruit (FD 13.5 mm) and the narrow wing (WW 4.0 mm) place it within the range of *P. favonii* (table 1; fig. 5C). Overall, this isolated Late Eocene fruit fossil may represent the earliest record in the Old World for *P. favonii*, an entity that appeared nearly simultaneously in North America.

Paliurus miosinicus Hu & R.W. Chaney was described from a winged fruit obtained in Miocene deposits near Shanwang, Shantung Province, China (Hu and Chaney 1940). While this record may represent *Paliurus*, we did not examine the fossil first hand, and the figure provided in the original description (Hu and Chaney 1940, p. 65, pl. 41, fig. 5) does not clearly display the distinguishing characteristics of *Paliurus*. If the fossil does represent *Paliurus*, its dimensions (FD 15.0 mm, WW 4.5 mm) place it within the range of variation for *P. favonii* (fig. 5E, fossil not plotted). Because distinguishing characteristics of *Paliurus* are not clearly discernible, however, we have excluded it from the current analysis. The only other *Paliurus* fruit fossil reported from China comes from Middle Miocene deposits near Jian Chuan, Yunnan Province, China (WGCPC 1978, pl. 131, fig. 3) and is clearly identifiable as *Paliurus*. The fruit is large (FD 18.0 mm) with a relatively narrow wing (WW 3.5 mm). This fruit falls within the morphometric continuum for *P. favonii* (fig. 5C–5E).

Paliurus zaporogensis Krysht. (Kryshtofovich 1914) and *P. sibirica* (Dorofeev 1963) are the only species of *Paliurus* that have been described from the central Asian region. *Paliurus zaporogensis* was described on the basis of fruit remains from a Miocene deposit near Orekhov (Volgogradskaya), Russia. How-

same as that figured by Bůžek (1971, fig. 9). E, Magnification of D. F, Apical surface of fruit, same as Bůžek (1971, fig. 14). G–L, Teater Road, Oregon; Late Eocene. G, Wing edge and endocarp with exposed seeds, first of two fruits, UF 10881. H, Apical surface, second of two fruits, UF 10881. I, Magnification of wing on H. J, Magnification of wing on G. K, Palladium-coated silicone rubber cast of UF 10881′ (counterpart of G, H), showing both apical (left) and basal (right) surfaces of fruits. L, Basal surface of fruit showing circular rim of receptacle and centrally positioned pedicel, UF 256-21573. Scale bars = 1 cm in B (applies also to A), C–F, G (applies also to H, K), L; 1 mm in I (applies also to J).
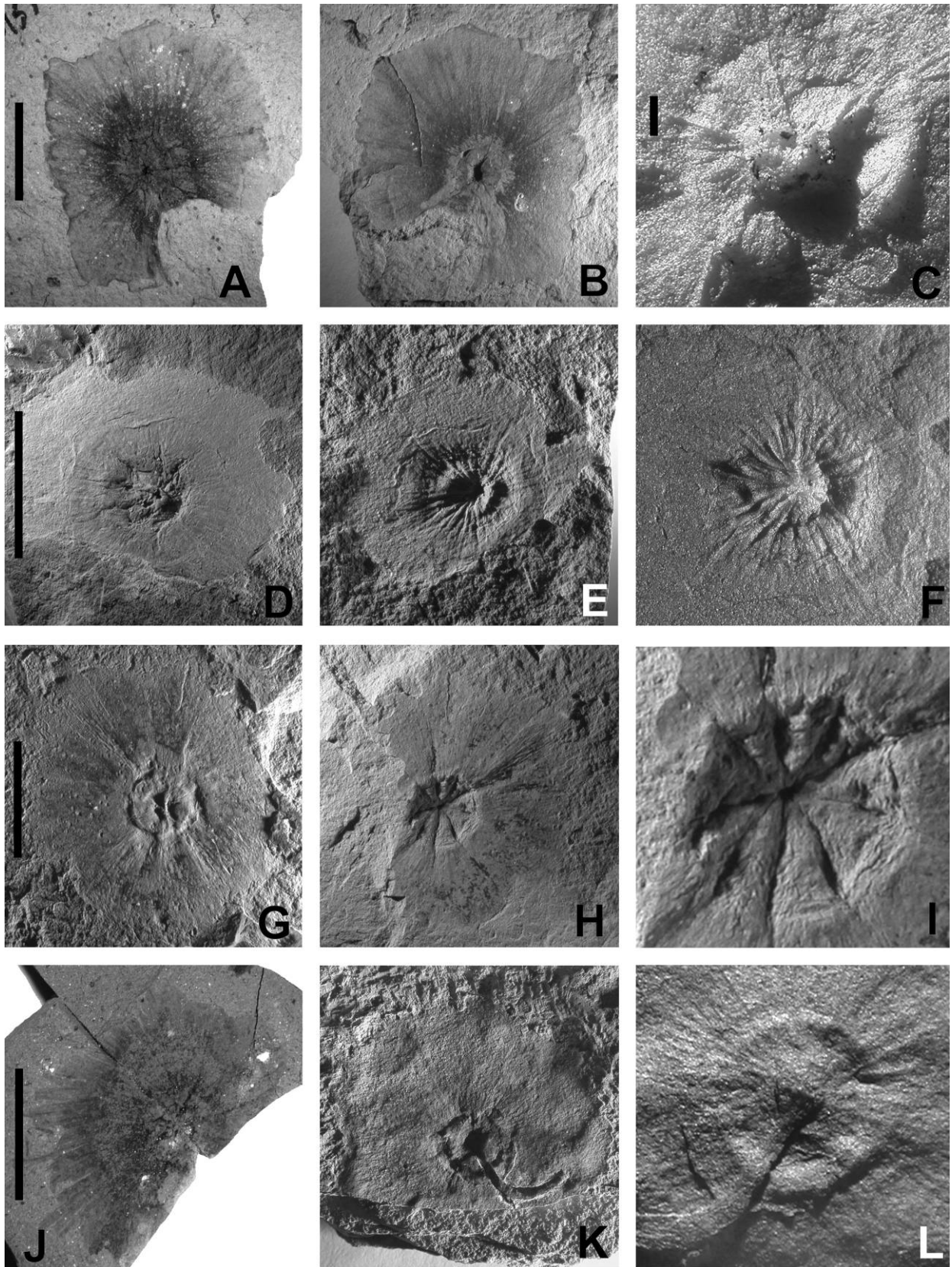
Fig. 9 Fruits of *Paliurus clarnensis*, Middle Eocene of Oregon. *A–C*, Gonser Road, Jefferson County, Oregon. *A*, Apical surface of fruit, UF 238-19822′. *B*, Basal surface of fruit, UF 238-19822. *C*, Magnification of silicon rubber cast, showing receptacle, UF 238-19822. *D–F*, White

ever, the holotype designated by Kryshtofovich (1914, pl. 1, fig. 1) does not clearly display a receptacle rim and thus cannot be confirmed as *Paliurus*. Nevertheless, a subsequent report of the species (Zhilin 1989) from Early Miocene deposits near Orzhilansay, Kazakhstan, is certainly *Paliurus*. The figured fruit (Zhilin 1989, fig. 3*B*) is medium in size (FD 13.7 mm) with a relatively wide wing (WW 4.3 mm), which places it within the range of *P. favonii* (table 1; fig. 5*C*, 5*E*) near the high end of WW for fruits of a similar diameter. This fruit represents an unequivocal record for the genus within the region over which modern *Paliurus* is disjunct (fig. 1), establishing that the genus formerly lived in at least parts of this region but also confirming the ancient nature of this geographic division.

North America. Within North America, fossil fruits assignable to *Paliurus* are known only from the western and southeastern United States (Manchester 1999). Oldest occurrences are from the Middle Eocene of Oregon, and youngest occurrences are from the Middle Miocene of Washington (Berry 1928, 1931; Brown 1937; Pigg and Wehr 2002), Idaho, and Florida (Manchester 1999). With the exception of *P. clarnensis*, North American fossils fall within the range of variation known for *P. favonii* in Europe and Asia. Several fossils from the Late Eocene of Oregon, however, represent a potential segregate of this species (fig. 8*A*–8*C*, 8*G*–8*K*).

Berry (1916*a*) described *Paliurus mississippiensis* E.W. Berry from fruits recovered in Early Eocene deposits of the Wilcox formation at and near Early Grove, Marshall County, Mississippi. However, examination of the holotype (USNM 3460) as well as other fossils referred to this species by Berry (1916*a*, pp. 279–280; USNM 36271 and 35847, USGS loc. 6462) revealed that these fossils do not represent *Paliurus*. The holotype consists of an impression and a disk-shaped fragment of lignitized tissue with bilateral rather than radial symmetry and veins running parallel to the margin. The remaining pair of fossils referred to this species (USNM 36271 and 35847, USGS loc. 6462) superficially resemble *Paliurus* fruits but probably represent organs of different plant taxa.

Later discoveries in North America proved to represent genuine *Paliurus* fruits. On the basis of a fossil fruit recovered from a Miocene deposit near Grand Coulee, Washington, Berry (1928) described *Paliurus hesperius* E.W. Berry (fig. 7*A*). This species was later redescribed on the basis of fruits and leaves found together at Grand Coulee (Berry 1931; fig. 7*B*, 7*C*). Subsequently, Brown (1937) reported *P. hesperius* from the Miocene Latah Formation near Spokane, Washington (fig. 7*D*). Taken together, the fossils previously conferred to *P. hesperius* (fig. 7*A*–7*D*) are large (FD 13–18.5 mm) and uniform in size, with a relatively narrow wing (WW 2.6–3.5 mm). One of the specimens (fig. 7*B*, 7*C*) is notable for having two locules and a bilobed wing. A bilocular condition is also known in some silici-

fied, anatomically preserved rhamnaceous fruits from the Miocene of Yakima Canyon, Washington (Tcherepova 2001; Pigg and Wehr 2002) that may be referable to *Paliurus* (K. Pigg, personal communication, 2007). Overall, species of *Paliurus* described from North America fall within the range of variation known for *P. favonii* from Europe and Asia (table B1; fig. 5*E*). Thus, we have conferred these fossils to *P. favonii*.

Subsequent to the work of Berry (1916*a*, 1928, 1931), no new species of *Paliurus* have been described from North America, although a handful of new records have been reported (Manchester 1999; Pigg and Wehr 2002). A compression fossil from the Miocene Ellensburg Formation near Grand Coulee, Washington, reported by Pigg and Wehr (2002), is closely allied to the fruits from this area described as *P. hesperius* by Berry (1928, 1931; our fig. 7*A*–7*C*). The fossil reported by Manchester (1999) from the Late Miocene of Alum Bluff, Florida (UF 18049-26117; fig. 7*H*, 7*I*; FD 16.5 mm, WW 4.8 mm), is the only *Paliurus* fruit known from eastern North America. The fruit from the Early Eocene Wind River Formation of Wyoming (UCMP 168324), reported and illustrated in the same publication as the Alum Bluff fossil (Manchester 1999), was erroneously identified and should instead be placed in the genus *Cyclocarya* (Juglandaceae). *Paliurus* and *Cyclocarya* are convergent in wing morphology and venation, and the figured specimen (Manchester 1999, fig. 9*B*) is missing portions that would display the diagnostic receptacular rim of *Paliurus*. Another specimen from the same locality has four perianth remnants on its distal end (fig. 6*B*) that are positioned as in extant *Cyclocarya*, indicating that this unnamed species belongs to *Cyclocarya*. Although the Green River record (Manchester 1999) is not referable to *Paliurus*, both the Alum Bluff fossil (Manchester 1999) and the Miocene compression fossil from Grand Coulee, Washington (Pigg and Wehr 2002), fall within the range of variation known for *P. favonii* from Europe and Asia (table B1; fig. 5*E*), and so we confer them to this species.

Previously unreported North American fruits include remains from the Late Eocene of Oregon and the Miocene of Idaho. Fruits recovered from sediments of the John Day Formation near Teater Road, Crook County, Oregon (UF 256-21060, UF 256-20906, UF 10881, UF 256-21573; fig. 8*A*–8*C*, 8*G*–8*L*), are much smaller than other *Paliurus* fruits known for North America (table B1; FW 9.5–11.2 mm) and have a narrower wing (WW 1.2–2.1 mm). The new record from Idaho is a well-preserved compression (UF 15888; fig. 7*E*–7*G*; FD 16.0 mm, WW 5.5 mm) from the Miocene Clarkia fossil beds (table B1; Smiley and Rember 1985). This remarkably well-preserved fruit corresponds in dimensions to fossils recovered from the Miocene of Washington (table B1). Taken as a group, the new North American fossils reported here fall within the range of variation known for *P. favonii* from Europe and Asia (table B1; fig. 5*E*) and are thus conferred to this species.

Cliffs, Jefferson County, Oregon. *D*, Apical surface of fruit, UF 262-17703. *E*, Basal surface of fruit, UF 262-17703′. *F*, Magnification of silicon rubber cast showing receptacle, UF 262-17703′. *G*–*I*, West Branch Creek, Wheeler County, Oregon. *G*, Apical surface of fruit, UF 230-18356′. *H*, Basal surface of fruit, UF 230-18356. *I*, Magnification of receptacle region, UF 230-18356. *J*–*L*, Red Gap, Jefferson County, Oregon. *J*, UF 251A-51200. *K*, Holotype of *P. clarnensis*, basal surface of fruit and centrally attached curved pedicel (lower right), UF 251A-46876. *L*, Magnification of silicon rubber cast, showing receptacle, UF 251A-46876. Scale bars = 1 cm in *A* (applies also to *B*), *D* (applies also to *E*), *G* (applies also to *H*), *J* (applies also to *K*); 1 mm in *C*, *F*, *I*, *L*.

Although most North American fossil *Paliurus* fruits are referable to either *P. favonii* or *P. clarnensis*, the new records from the Late Eocene Teater Road locality of Oregon (UF 256-21060, UF 256-20906, UF 10881, UF 256-21573) represent a potential segregate of *P. favonii*. The small size of these fruits (table B1; FW 9.5–11.2 mm; fig. 8*A*–8*C*, 8*G*–8*L*) places them closer to some small European fruits, exemplified by those reported from the Miocene of Čermníky, Czech Republic (table B1), by Bůžek (1971, figs. 6, 7, 9, 14, 20, 21; FW 8.0–9.8 mm, WW 1.1–1.6 mm; our fig. 8*D*–8*F*). These European fruits also group closely with the North American fossils in bivariate plots (fig. 5*E*). One of these North American fossils (UF 10881; fig. 8*G*–8*K*) is particularly well preserved and clearly shows a narrow, thin wing (fig. 8*I*, 8*J*; WW 1.2–1.5 mm), consistent with our concept of *P. favonii*. The remaining fossils from the Teater Road locality (UF 256-21060, UF 256-20906, UF 256-21573) were collected from an outcrop adjacent to that of UF 10881. The specimen UF 256-21060 (FD 10.5 mm; fig. 8*A*, 8*B*) has a compact, wedge-shaped wing similar to that found in the extant *P. ramosissimus* group (fig. 2*I*). The absence of a thin, veined wing is also obvious on UF 256-20906 (FD 11.2 mm; fig. 8*C*). Although specimens UF 256-21060 and UF 256-20906 may represent a distinct species with affinities to the modern *P. ramosissimus* group, the presence of specimens more typical of *P. favonii* in the same (UF 256-21573; FD 10.0 mm, WW 2.1 mm; fig. 8*L*) and nearby deposits (UF 10881; fig. 8*G*–8*K*) indicates that these remains could represent immature fruits. In the absence of further fossil evidence, we confer all of the Teater Road fossils to *P. favonii*.

Comparison to modern species. In order to provide a context for the taxonomic interpretation of fossil remains, we examine the fruit morphology of extant *Paliurus* species. Because modern species are diagnosed on the basis of plant traits other than fruit dimensions (table 1), which are not available for the *Paliurus* fruit fossils, we rely on patterns seen in fruit size and shape among modern species to provide insight as to the level of variability expected among true species in the fossil record. Plots of fruit dimensions taken from herbarium sheets for four species of *Paliurus* show that several species display an allometric trend in fruit dimensions (fig. 5*A*, 5*B*). Indeed, some pairs of species are separable on this basis (e.g., *P. ramosissimus* and *P. hemsleyanus*). However, individual fruit dimensions form a continuum across all four extant species (table 1). Overall, the range of variability for each measured fruit dimension is much less within each of the modern species than within the set of fossils that we have referred to as *P. favonii* (table 1; fig. 5*A* vs. fig. 5*C* and fig. 5*B* vs. fig. 5*D*). Taken together, these fossils may represent (1) a single long-lived, highly variable, and widespread species or (2) a set of closely related and intergrading species, some of which may have overlapped both geographically and temporally. The large size range for these fruits (table 1) and the continua formed in bivariate plots for the four modern species favor the hypothesis that *P. favonii* represents more than one species.

Fruit dimensions through time. While conclusive taxonomic interpretation of *P. favonii* is not attempted here, it is informative to analyze the diversity of the group of fossils potentially assignable to *P. favonii* through the span of time that it encompassed and over the large geographic range that it occupied. As noted above, the group contains nearly an equal amount of variability in Asia, North America, and Europe (fig. 5*E*). However, variability in FD (fig. 5*F*) and WW (not figured) for the group does form a trend through time, beginning with a small amount of variability for these traits in the Eocene, when the species was represented only in Asia and North America, followed by an increase in variability starting in the Early Miocene that peaked near the Middle Miocene, when *P. favonii* was distributed in Asia, North America, and Europe, and finally decreasing during the Pliocene and Pleistocene, with records known only from Asia (table B1). Overall, a slight upward trend in fruit size occurs through time. On the basis of an interpretation of *P. favonii* corresponding to the modern *P. spina-christi* group, we plotted the variability in fruit size and WW for the three species included in this set as the most recent time category (fig. 5*F*). This plot shows a dramatic increase in variability from the latest fossil of *P. favonii* to the modern species as well as an increase in median fruit size.

Paleoecology

Most fossil *Paliurus* fruits have been obtained from sediments that were apparently deposited in lake or marsh environments (Miki 1937; Raniecka-Bobrowska 1959; Kvaček and Hurník 2000). Some fossils are also known from sediments that may have been laid down in alluvial or riparian environments (Bůžek et al. 1992; Kvaček and Hurník 2000) and in habitats with a strong maritime influence (Berry 1916*b*; Miki 1933*a*, 1933*b*, 1937; Manchester 1999; K. Uemura, personal communication). The fossil record for Japan, in particular, indicates that during the Neogene and Pleistocene, *Paliurus* inhabited maritime or coastal lowlands (Miki 1933*a*, 1933*b*, 1937; K. Uemura, personal communication). The Late Miocene record of *Paliurus* from Alum Bluff, Florida (Manchester 1999; table B1), also inhabited warm, lowland, marginal marine habitats (Berry 1916*b*). Although the maritime or riparian growing conditions inferred for some *Paliurus* in the fossil record are consistent with the ecology of several modern species with an affinity for coastal or riverine conditions (table 2), the fossil floras containing *Paliurus* are typically of a more inland situation without direct marine influence.

The majority of *Paliurus* records are from Miocene deposits of the middle northern latitudes and are typically associated with plants having a subtropical to warm-temperate affinity, particularly a deciduous component containing *Acer* L., *Alnus* Mill., *Betula* L., *Fagus* L., *Fraxinus* L., *Glyptostrobus* Endl., *Juglans* L., *Liquidambar* L., *Metasequoia* Miki ex Hu & W.C. Cheng, *Myrica* L., *Ostrya* Scop., *Platanus* L., *Pterocarya* Kunth, *Quercus*, *Sassafras* Nees & Eberm., and *Ulmus* L. (Unger 1847; Ettingshausen 1869; Miki 1933*a*, 1933*b*, 1937; Raniecka-Bobrowska 1959; Bůžek 1971; Ozaki 1991; Pigg and Wehr 2002; Kovar-Eder et al. 2004). Evergreen members of these associations include but are not limited to *Pinus* L. and *Berberis* L. (Ettingshausen 1869; Kovar-Eder et al. 2004). A component of wetland or riparian taxa is often associated, including *Cephalanthus* L., *Populus* L., *Potamogeton* L., *Salix* L., *Taxodium* Rich., and *Nelumbo* Adans. (Ettingshausen 1869; Miki 1933*a*, 1933*b*; Raniecka-Bobrowska 1959; Tcherepova 2001). Finally, some of the Eocene records of *Paliurus* are associated with subtropical to tropical elements such as *Sabal* Adans. and members of the Lauraceae, which formed mixed communities with the deciduous elements already described (Huzioka and Takahasi 1970; Bestland

Table 2

Distribution and Ecology of Extant and Fossil *Paliurus* Species

Species	Distribution	Ecology	Elevation (m)
Extant:			
P. hirsutus	Southeast China, Vietnam	Sandy soil along stream banks	<600
P. ramosissimus	Southeast Asia, Japan	Open woods near coast and streams	<1000
P. orientalis	Southern China	Mixed mesophytic forest	300–3500
P. hemsleyanus	Southern central China	Open woods or thicket, especially on limestone	1500–3300
P. spina-christi	Southern Europe, western Asia	Open woods or thicket, waste places	0–2300
Fossil:			
P. favonii	Europe, Asia, North America	Mixed mesophytic forest	na
P. clarnensis	North America	Mixed mesophytic forest	na

Note. na = not applicable.

et al. 1999). These mixed communities probably existed under a marginally tropical environment (Berry 1916*a*).

Paleoecological conditions for *Paliurus* imply that members of this genus occupied a greater diversity of environments in the past than they do today. The extant species *P. ramosissimus* and *P. hirsutus* are restricted to riparian and maritime environments, perhaps mirroring the coastal and riverine depositional environments inferred for some fossil floras in which *Paliurus* has been discovered (Miki 1933*a*, 1933*b*, 1937; Bůžek et al. 1992; Kvaček and Hurník 2000). By contrast, the widespread European and western Asian species *P. spina-christi* has an affinity for arid habitats that is not known for any fossil taxa. The remaining two species, *P. hemsleyanus* and *P. orientalis*, occur in thickets or open mixed mesophytic deciduous forest conditions in southern China (table 2; fig. 1). The habitats of these two species correspond to the warm-temperate to subtropical deciduous fossil floras that have yielded the majority of *Paliurus* records. Thus, of the five modern species of *Paliurus*, those with the closest ecological correspondence to fossil taxa are the most geographically restricted. However, it is possible that species of *Paliurus* occupied arid habitats in the past, in a similar fashion to the modern *P. spina-christi* (see below), but that this association has not been discovered as a result of a bias in the sedimentary record toward more mesic ecological settings.

Phylogenetic Implications

Molecular phylogenetic work has helped to clarify the position of the Rhamnaceae (Soltis et al. 1995, 2000; Savolainen et al. 2000) and relationships both among and within its ~50 genera (Hardig et al. 2000; Richardson et al. 2000*a*; Aageson et al. 2005; Islam and Simmons 2006; Kellerman 2007). As phylogenetic resolution for the family and for lower-level taxa improves, fossil taxa should be included to obtain a complete picture of the evolution and distributional history of the family and its component taxa.

The Rhamnaceae is composed of two well-supported clades, dubbed the rhamnoids and the ziziphoids (Richardson et al. 2000*a*). Within these two clades, Richardson et al. (2000*a*) identified a number of well-supported monophyletic groups that were subsequently recognized in a revised tribe-level classification (Richardson et al. 2000*b*), including the tribe Paliureae,

containing *Paliurus*, *Hovenia*, and *Ziziphus*. The work of Islam and Simmons (2006) further refined the position of *Paliurus* based on ITS and 26S ribosomal DNA combined with the chloroplast region *trnL-trnF*. In addition to their finding that *Paliurus* is nested within the large (~170 spp.) and cosmopolitan genus *Ziziphus*, this work provided evidence for a close relationship between *Paliurus* and Old World *Ziziphus*, a result that is supported by wood anatomical studies (Schirarend 1991).

The results of Islam and Simmons (2006) indicate that *Paliurus* is a derived member of the Paliureae, emerging from within the larger and more widespread genus *Ziziphus*. However, because the fossil record for *Ziziphus* is not as complete or reliable as that of *Paliurus*, we cannot trace the evolution of characters separating these two genera. Instead, fossils with the diagnostic characteristics of modern *Paliurus* appear rather suddenly ~44 million years ago, with no apparent precursors. Thus, the minimum age for the origin of *Paliurus* is Middle Eocene. Such an age implies that the Paliureae and thus the ziziphoid Rhamnaceae are relatively old.

On the basis of the Rose Creek flower of Basinger and Dilcher (1984), Richardson et al. (2000*a*) originally estimated a minimum age for the Rhamnaceae of at least 94 million years. Although Richardson et al. (2000*a*) concluded that the Rose Creek flower belongs to Rhamnaceae, the fossil is among the oldest eudicot remains on record, and its characters indicate similarities with other rosids and Saxifragales (Basinger and Dilcher 1984). The assignment to Rhamnaceae might be supported by the condition of obhablostemony, but petal-opposed stamens also occur in Vitaceae, the apparent sister to all other rosids (Jansen et al. 2006), indicating that this condition might be expected in other early arising rosids. An estimate for the age of the Rhamnaceae based on the Rose Creek flower would imply that *Paliurus* is approximately half as old as the family itself. Recently, however, Richardson et al. (2004) reevaluated this hypothesis using an external calibration from a study on the Cucurbitales and Fagales (Wikström et al. 2004) rather than the Rose Creek flower and recovered an age of ~65 million years for the Rhamnaceae. This estimate implies a rapid radiation of the ziziphoid Rhamnaceae during its first 10–17 million years of evolution, near the Cretaceous-Tertiary boundary, in order to account for the great age of the relatively derived genus *Paliurus*.

At this time, *Paliurus* is one of only three extant genera of Rhamnaceae that have been reliably identified from occu-

rrences of fruits in the fossil record. Recently, Calvillo-Canadell and Cevallos-Ferriz (2007) reported a fruit of *Ventilago* Gaertner (Ventilagineae) from an Oligocene deposit in Puebla, Mexico. In addition, Grote (2007) recently described *Ziziphus khoksungensis* Grote from a Pleistocene deposit in northeastern Thailand. Taken together, these fossils represent an intriguing addition to the set of reliably identified material available for use in fossil-calibrated phylogenetic analysis of the Rhamnaceae. However, because known fossil fruits from the Rhamnaceae are rare and represent only a small fraction of the diversity found in the family, the resolution that they are likely to provide for divergence time estimates remains limited.

Fossil leaves could also provide calibration points or data for use in combined phylogenetic analyses of fossil and modern taxa. However, leaves have not previously yielded genus- or species-level resolution for this use. For example, entire-margined leaves with the distinctive transverse tertiary venation of *Berchemia* Necker ex DC., *Rhamnidium* Reisseck, and *Karwinskia* Zucc. are readily recognized in the fossil record. However, it is not possible to distinguish these genera from each other on the basis of leaf characters alone, which has led to the recognition of an organ morphogenus for such fossils, *Berhamniphyllum* Jones & Dilcher (Jones and Dilcher 1980). Similarly, some fossil leaves with serrate margins and basally actinodromous venation of the *Ziziphus* type are readily identified as belonging to the Rhamnaceae (fig. 4A), but assignments to particular genera are subject to question. For example, *Ceanothus blakei* R.W. Chaney (Chaney 1927) has been repeatedly cited as one of the earliest fossils for *Ceanothus* (Mason 1942; Jeong et al. 1997; Ackerly et al. 2006). However, it has been shown that this species has a venation pattern corresponding to that of *Hovenia* (Meyer and Manchester 1997). By contrast, a set of fossils from the Late Miocene through Pleistocene of western North America that have been referred to the *Cerastes* subgenus of *Ceanothus* (Mason 1942; Nobs 1963) on the basis of leaf shape and thickness appears to be reliably assignable to this genus on the basis of the apomorphic character of abaxial stomatal pits, which are visible on many of these fossils (personal observation). Thus, close anatomical study of other rhamnaceous leaf fossils in reference to modern taxa may allow for the reliable identification of lower-level taxa in the fossil record, which could lead to more informative analyses combining data from fossil and extant forms.

Biogeography

Earliest records of *Paliurus* are from the Middle Eocene of North America and the Late Eocene of Japan. By the Early Miocene, the genus had attained a circumboreal distribution, with occurrences in western and eastern North America, most of central Europe, and scattered localities in central and eastern Asia (fig. 1). Pliocene and Pleistocene records, by contrast, are limited to Europe and Asia (table B1), which corresponds with the distribution of modern species (fig. 1). The increase in geographic range and morphological diversity (fig. 5F) of *Paliurus* from the Middle Eocene into the Miocene is consistent with an origin for the genus during the Eocene. Nevertheless, winged fruits of an undescribed taxon from the Lower Cretaceous of Brazil (fig. 6D–6F; other elements of this flora described by Mohr and Friis [2000]) are similar to *Paliurus*,

although the specimens we have observed do not show the diagnostic receptacular rim.

Paliurus was distributed throughout the middle latitudes of the Northern Hemisphere during a large portion of its history, with conspicuous geographic gaps. Its absence from most of the central region of North America (fig. 1) may be due to a lack of appropriate depositional environments in the region during the Tertiary. Records of *Paliurus* are also scanty in central Asia, with just two confirmed reports from the region between Poland and western China (fig. 1). The scarcity of *Paliurus* in central Asia may reflect either a lack of appropriate depositional environments in this area during portions of the Tertiary or an ancient disjunction near the beginning of the Miocene, when the formerly continuous Old World distribution of the genus became fragmented into Eurasian and Asian regions in conjunction with the Himalayan orogeny (Wang et al. 2002).

Paliurus favonii, which includes the majority of fossil fruits confirmable as *Paliurus*, has a wide geographic spread and a history spanning most of the Tertiary. This entity appeared almost simultaneously in the Late Eocene of western North America and Japan (table B1) but did not become widespread (fig. 1) or morphologically diverse (fig. 5F) until the Miocene, when the species was distributed throughout the middle latitudes of the Northern Hemisphere, with occurrences in western and eastern North America, most of central Europe, and scattered localities in central and eastern Asia (fig. 1). Following the close of the Miocene, however, the range of this species appears to have contracted dramatically, with fossil occurrences for the Pliocene and Pleistocene limited to Japan. This range contraction may have been associated with global cooling toward the end of the Miocene as well as during the Pliocene and Pleistocene (Wolfe 1975).

In comparison to the dramatic range contraction implied by the paucity of Pliocene and Pleistocene fossils, modern members of the genus are more widespread, although limited to the Eastern Hemisphere (fig. 1). In reference to the modern taxa, *P. favonii* compares most favorably with members of the *P. spina-christi* group, which intergrade with respect to fruit dimensions (table 1; fig. 5A, 5B). If *P. favonii* represents a single species, then the extant species comprising the *P. spina-christi* group could be interpreted as recently diversified descendants of this lineage. Another possibility is that these modern species are descended from a set of cryptic taxa contained within the *P. favonii* fossil morphotype. Some fossils interpreted here as *P. favonii* display the narrow wing and compact form of extant species in the *P. ramosissimus* group (fig. 2G–2I vs. fig. 8A–8F). Because these fruits fall within the morphological continuum for *P. favonii*, we include them in this species. However, these more compact fossils may represent members of the same lineage that gave rise to the two members of the *P. ramosissimus* group.

On the basis of the Middle Eocene appearance of *P. clarnensis* in Oregon, *Paliurus* may have originated in North America, with subsequent spread to Asia, where it appears in the Late Eocene, followed by Europe, where it is first recorded from the Early Miocene. However, the close relationships between *Paliurus* and Old World *Ziziphus* (Islam and Simmons 2006) argues against the idea of a North American origin for *Paliurus*, since this hypothesis would require that *Ziziphus* of the Old World type once inhabited North America but subsequently became

extinct. Of the two species recognized in this article, *P. clarnensis* does not appear to have spread beyond North America, while *P. favonii*, which appeared during the Late Eocene in both North America and Japan, attained a circumboreal distribution by the beginning of the Miocene. The nearly simultaneous appearance of morphologically comparable *P. favonii* in the Late Eocene of Japan and Oregon makes it difficult to determine the geographic origin of this entity. However, we can infer that migration took place via the Bering land bridge, a path that was apparently followed by other plant groups during the Eocene (Manchester 1999). Subsequent migration of the species into Europe near the beginning of the Miocene might have occurred from North America via the North Atlantic land bridge or from the eastern Asian region (Japan) by migration north of the Turgai seaway. Although the species was well represented in both North America and Asia at the beginning of the Miocene, the more plausible source of the European immigration was Asia because the Turgai seaway had receded by this time and the North Atlantic migration route may not have been available after the end of the Eocene (Tiffney 1985; but see Manchester 1999). Those *Paliurus* records from the Oligocene and Early Miocene of central Asia (table B1; fig. 1) also support this view.

In reference to the past distribution and ecology of *Paliurus* implied by the fossil record, we draw some conclusions about the evolution of climatic tolerance in these plants. As previously discussed, molecular phylogenetic results indicate that *Paliurus* is derived from within the genus *Ziziphus*, an essentially tropical to subtropical group of plants with a modern distribution encompassing the New World and Old World tropics (Richardson et al. 2000b; Islam and Simmons 2006). *Ziziphus*, however, contains few representatives in the region of current or past distribution for *Paliurus*. Thus, *Paliurus* may represent a cold-tolerant derivative of the essentially tropical *Ziziphus* that was able to extend its distribution northward as subtropical to temperate mixed mesophytic forests became dominant in the Northern Hemisphere during portions of the Tertiary.

The consistent association of *Paliurus* with mesophytic forests indicates a limited range of climatic tolerance during most of the history of the genus. During the cool, dry period of the Oligocene to Early Miocene, the genus essentially disappears from the fossil record (fig. 5E), perhaps as a result of marginalization into suitable microclimates. Records from the Miocene

through Pliocene indicate little change in the climatic tolerance of *Paliurus*. In fact, the genus became extinct in North America and nearly disappeared from the fossil record during the Pliocene and Pleistocene. These changes may have been associated with the advent of a cooler, drier climate in the Northern Hemisphere (Tiffney 1985; Manchester 1999).

Similar to the apparently narrow climatic tolerances of their precursors, most modern species of *Paliurus* are limited to the moist, equable, temperate climate region of eastern Asia (fig. 1). In some cases, the modern species inhabit mixed mesophytic forests similar to those inferred for Miocene taxa. The notable exception is the deciduous *P. spina-christi*, which is native in summer-dry portions of Europe and Eurasia (Schirarend and Olabi 1994; fig. 1). Although the species has become naturalized in central Europe and northern Africa, where it tolerates a diversity of climatic conditions from subdesert to mesic temperate, the species may have evolved as a Mediterranean climate derivative of the mesophytic *P. favonii*. This contrasting climatic tolerance may be a product of the geographic isolation of European populations of *Paliurus* during or before the Middle Miocene.

Acknowledgments

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