Miocene winged fruits of *Loxopterygium* (Anacardiaceae) from the Ecuadorian Andes[1]

Robyn J. Burnham[2] and Nina L. Carranco

Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109-1079 USA

A new species of asymmetrically winged fruit is described from Miocene sediments of Andean Ecuador. The new fruit is readily placed in the genus *Loxopterygium* of the Anacardiaceae based on the size, position of the stigma, wing venation, and serration of the wing tip. The new fossil species is very similar to extant species of *Loxopterygium* now distributed in dry habitats of coastal Ecuador and Peru, as well as dry interior forests of Bolivia and northern Argentina. We use the fossil to calibrate a molecular-based phylogeny of some members of the Anacardiaceae, showing that dry forest habitats may have been present in South America for more than 10 million years.

Key words: anemochory; dry tropical forest; Ecuador; *Loxopterygium*; paleobotany; Tertiary; winged diaspores.

Winged fruits frequently are produced in bulk quantities by large- and moderate-sized trees. Their movement via wind currents and gravity creates an ideal situation for dispersal to depositional basins: lakes, slow-moving rivers, swamps, and coastal deltas. Thus, winged fruits are common in the fossil record (e.g., Magallon-Puebla and Cevallos-Ferriz, 1994; Manchester and Hably, 1997; Wang and Manchester, 2000; McClain and Manchester, 2003). Angiosperm fruits are ideal sources of phylogenetic information from the fossil record because angiosperm morphological taxonomy is frequently based on the reproductive features of plants and their fruits often reveal critical reproductive details (e.g., ovary position, style, locule number, etc.). Documentation of the occurrence of a genus or family at a particular time-period can be established because the critical features of specific clades are well known for reproductive organs of plants.

Asymmetrically winged fruits, or samaras, have been reported from 11 extant families and 39 extant genera in the Western Hemisphere alone (Mirle and Burnham, 1999). Fossils of these extant genera and families are to be expected in younger Tertiary sediments of the Western Hemisphere, but to date few determinations of asymmetrically winged fruits from South America have been made (Engelhardt, 1895; Burnham, 1995). To our knowledge, no similar compilation of other types of extant winged fruits (symmetrically winged samaras, helicopters, etc.) of the Western Hemisphere has yet been published. Because of the importance and abundance of winged fruits in the fossil record, such a compilation would be useful.

During fieldwork in the Ecuadorian valleys of Cuenca, Nabon, and Loja, fossil fruits belonging to the angiosperm family Anacardiaceae were recovered. A sufficient quantity of fruits now has been collected to adequately characterize the fruits, and the material is described here.

The Anacardiaceae (poison ivy, cashew, or sumac family) is a member of the order Sapindales, closest to Burseraceae, but also allied to Rutaceae, Meliaceae, and Sapindaceae (Zomlefer, 1994; Gadek et al., 1996; Pell and Urbatsch, 2001; Judd et al., 2002). The Anacardiaceae are characterized by usually alternate, often pinnately compound leaves, resin canals in the bark and larger veins, and three-carpellate ovaries, which are often reduced to a single locule with a single seed. In spite of the frequently irritant resin (Mitchell, 1990), the family is probably best known for its production of the edible fruits or seeds of pistachios, mangos, and cashews. Anacardiaceae are pantropical in distribution, with well known *Rhus* and *Toxicodendron* extending into temperate areas (Zomlefer, 1994).

Here we describe a new fossil species of asymmetrically winged fruit assigned to the genus *Loxopterygium* (Anacardiaceae) from Ecuador, whose distribution is known only from two small geographic areas in the basins of Cuenca and Loja, Ecuador. The species is the first known record of the genus from the fossil record and contributes to a reconstruction of the vegetation of the Andes Mountains during a critical time of uplift and physiographic change. The new species has also contributed to constraining the temporal relationships among extant members of the genus (Pell and Urbatsch, 2001; Pennington et al., 2004).

Fossil representatives of Anacardiaceae in Central and South America—Fossil representatives of the Anacardiaceae are frequently listed in paleobotanical literature, but few recently confirmed members of the family can be cited. It is beyond the scope of this report of a new species of fossil fruit to revise the fossil representatives of the entire family. However, we briefly review here citations of various plant organs assigned to the family that have been previously reported from South America, Central America, and the Caribbean region. In South America there are numerous unrevised citations of *Anacardium* fruits by E. W. Berry (1924a, b, 1927a, 1929a, b). These fruits and seed casts are generally reniform, calcified specimens with a thick ligneous endocarp (''shell'' of Berry), and are attributed to Eocene and Oligocene sediments. In addition, Reid (1933) described a new genus, *Colombicarpum*, a biloculate endocarp similar to the modern drupaceous *Tapirira* from the Tertiary of Colombia.

With respect to leaves, in 1927 Berry stated, ''The genus *Anacardites* of Saporta affords a convenient resting place for

fossil leaves of the Anacardiaceae of doubtful generic identity'' (Berry, 1927b). In fact, much of the foliage attributed to the Anacardiaceae may not belong in the family at all and a thorough revision of the fossil members of the family is in order. Between 1895 and 1939 descriptions were published by various authors of leaves or leaflets of about 15 species placed in the genera *Anacardites*, *Duvaua* (= *Schinus*), *Metopium*, *Roophyllum*, *Spondias*, *Schinus*, *Schinopsis*, and *Tapirira* from Colombia, Ecuador, Brasil, Peru, Bolivia, and Argentina (largely by E. W. Berry but also by Engelhardt [1895] and Hoffman [1931]). *Schinopsis patagonica*, *S. morongifolia* and *S. balansiformis* were reported from Eocene deposits of Argentina, and may be the oldest record of this genus, although those records (Berry, 1925, 1938) have not been confirmed as valid records of that genus (which bears asymmetrically winged fruits) and are simply relisted by Romero (1986). Recently, a reliable reference to leaves of two species of *Pseudosmodingium* from Puebla, Mexico was published (Ramirez et al., 2000). Gregory-Wodzicki (2002) reported that two species of undescribed Anacardiaceae make up 48% of foliage specimens from the Miocene Jakokkota flora of Bolivia.

Various genera of fossil wood have been described in the literature on South and Central America (*Anacardioxylon* from the West Indies: Hollick, 1924; *Schinopsixylon* from the Pleistocene of Argentina: Brea, 1999), but nothing has been reported as far as we are aware from northern South America.

Form genera used in the palynological literature (especially those used for purely stratigraphic purposes) make searching for family-level pollen records more difficult than a standard taxonomic search. Records of pollen assignable to Anacardiaceae are certainly present in the oil company literature, however there are two common taxonomic form names for pollen types of the Anacardiaceae: *Tricolporopollenites pseudocingulum* and *Striatricolporites gamerroi* (Muller, 1981; Romero and Castro, 1986). In Southern Argentina (Chubut and Santa Cruz Provinces) *S. gamerroi* appears as some of the earliest records of presumed Anacardiaceae pollen in Eocene and Paleocene sediments (Archangelsky, 1973; Romero and Castro, 1986; Romero, 1993). The apparently oldest confirmed record of pollen assigned to an extant Anacardiaceous genus is that of *Metopium* from the Miocene of Cuba (Graham, 2003), while *Tapirira* pollen is reported from the late Miocene of the Cordillera Oriental by Wijninga (1996).

The fossil record of asymmetric samaras in northern South America—Although many winged fruits can be found in museum collections of fossils from various localities in northern South America, a surprising lack of information in published literature exists. Only two species of asymmetrically winged samaras from Bolivia, Peru, Ecuador, and Colombia are known to have been published since 1895 (*Banisteria aceroides* Engelhardt and *Tipuana ecuatoriana* Burnham). There are no known reports of fossils of the genus *Loxopterygium*. The species of ''*Banisteria*'' described by Engelhardt (1895) was reconfirmed by Berry (1929c). Unfortunately the plate figuring this specimen published by Engelhardt in 1895 apparently reversed the figure numbers of two genera and four figures, so text reference to *Banisteria* cites the two figures of *Hiraea* instead of *Banisteria*, and vice versa. Careful reading of the German text certainly indicates the error. Extant species of the genus ''*Banisteria*'' were reassigned to the genera *Heteropterys* and *Banisteriopsis* (Gates, 1982; Mabberley, 1997) subsequent to Engelhardt's work, and the species of extant

Banisteria to which Engelhardt compared his fossil specimen, *Banisteria adamantium*, is now known as *Banisteriopsis schizoptera* (Gates, 1982). We believe this specimen is appropriately placed in the Malpighiaceae based on inspection of the drawing in Engelhardt's monograph.

MATERIALS AND METHODS

Asymmetrically winged fossil fruits were recovered from six localities in the valley of Cuenca (2°45′25″ S, 78°51′00″ W), near the town of Azogues, Ecuador. Azogues lies at approximately 2500 m elevation in a large north-south trending inter-Andean valley (the Cuenca Basin) that is centered on the city of Cuenca. The 19 fossil specimens were found in deposits of the Azogues or Guapán Members of the Azogues Formation, whose sediments have been dated at 13.0–10.2 Ma (Hungerbühler et al., 2002). Sediments enclosing the fossils are fine clays and silts, indicative of quiet water, lacustrine deposition, but at most outcrops small-scale soft sediment deformation indicates that sedimentation rate was fairly high (estimated at 1 mm/year by Steinmann, 1997; reported in Hungerbühler et al., 2002).

One additional specimen was recovered from very fine lacustrine diatomitic shales in the San Cayetano Formation in the Loja Basin (3°59′27.8″ S, 79°11′25.5″ W), about 140 km to the south of the localities in Azogues. The Loja locality lies at approximately 2160 m. Hungerbühler et al. (2002) also interpreted the quiet water facies of the San Cayetano Formation as a ''freshwater lake situated in a tropical environment at low elevation.'' The fossils are derived from the Siltstone Member, dated at 10.7 ± 1.6 to 10.0 ± 1.4 Ma (Hungerbühler et al., 2002). Thus the fossil leaf bearing deposits from the two basins are roughly contemporary, as far as we can determine, and assignable to the Middle Miocene.

Specimens of three extant species of *Loxopterygium* (Figs. 1–3) were examined at the University of Michigan herbarium (MICH), as well as specimens on loan from the Field Museum of Natural History in Chicago (F), New York Botanical Garden (NYBG), and Missouri Botanical Garden (MO). Specimens bearing mature and immature fruits were examined for the extant species *L. grisebachii*, *L. huasango*, and *L. sagotii*. Representative fruiting specimens of species of *Schinopsis* (Anacardiaceae), *Banisteriopsis*, *Heteropterys*, *Stigmaphyllon* (Malpighiaceae), *Tipuana*, *Machaerium*, *Nissolia* (Fabaceae), *Securidaca* (Polygalaceae), *Seguieria* (Phytolaccaceae), *Phyllostylon* (Ulmaceae), *Acer*, *Serjania*, *Thouinia*, *Thinouia*, *Thouindium* (Sapindaceae), as well as winged seeds of *Anthodon* (Celastraceae) and *Cedrela* (Meliaceae) are compared to the fossil.

RESULTS

Systematics—*Loxopterygium laplayense* Burnham and Carranco, sp. nov., Figs. 4–6.

The fossil specimens represent fruits with a single proximal locule and a distal wing, expanding from the side of the ovary wall. The remnant of the stigma is present medially on the backbone of the wing. In two specimens (EPN 885 and 1054) the stigma bears two minute lobes (Figs. 4–6). The pedicel of the fruit and calyx remnant are preserved at the proximal end of the locule, indicating orientation of the fruit, relative to the parent plant. The fruits range in length from 9.0 to 16.0 mm from pedicel attachment to wing tip. At their broadest point, the fruits are 2.6–5.5 mm wide. The locules are oblong in shape, rounded proximally and distally, ranging in length from 4.0 to 6.0 mm and in width from 2.0 to 4.0 mm. The boundary between the locule and the wing is clearly marked in most specimens due to crushing of the originally spherical, resistant endocarp. During fossilization, fracturing of the wall of the locule results in a quadrangular pattern over the locule wall in some specimens. This pattern is entirely absent from the wing of the fruit. Obliquely parallel venation is visible on the locule.
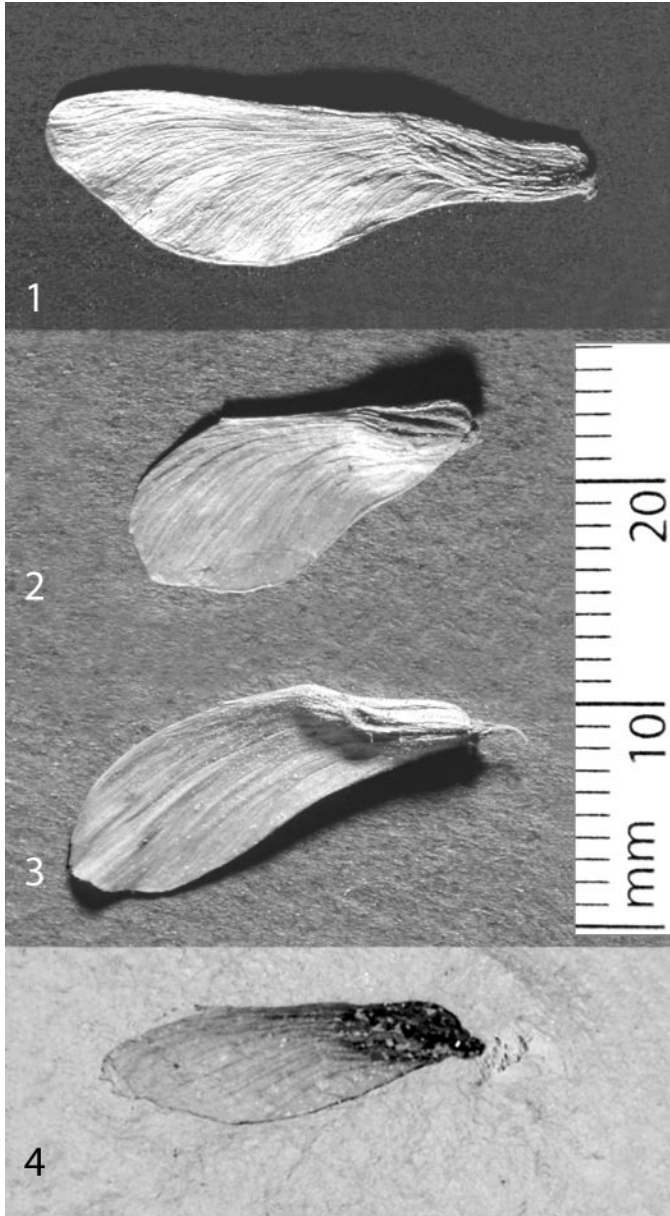
Figs. 1–4.   Modern and fossil species of *Loxopterygium*. **1.** *L. sagotii*. **2.** *L. huasango*. **3.** *L.grisebachii*. **4.** *L. laplayense* Burnham and Carranco n. sp., holotype, EPN 1054, Cuenca Basin.

A strong vein, originating from the attachment point and running obliquely to the backbone, divides the locule into two parts (the side close to the backbone and the side away from the backbone). This vein, in well-preserved specimens, amplifies the difference in the spacing of the primary veins on the locule wall of these two sectors. On the side of the locule close to the backbone, the veins are typically more widely spaced (with the widest spacing up to ~0.5 mm) than on the side away from the backbone. The area between the veins of the locule on the side away from backbone is devoid of the quadrangular pattern.

The wing bears angled primary veins, which are parallel to the shape of the backbone and parallel to one another. These veins originate at the proximal portion of the locule and can extend to the wing margin. The veins are densely distributed
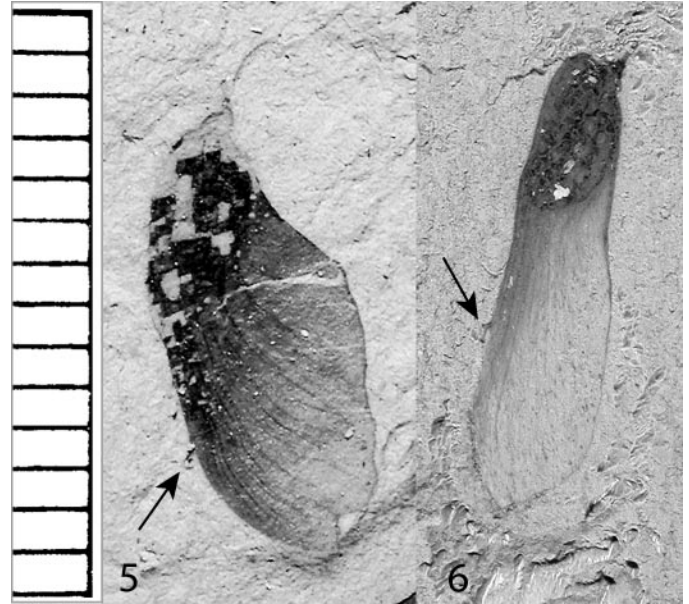
Figs. 5–6.   *Loxopterygium laplayense*, showing calyx remnant, short pedicel remnant, and stigma remnant (arrow). **5.** EPN 118, Cuenca Basin. **6.** EPN 885, Cuenca Basin.

near the backbone of the wing and spread laterally as they approach the distal edge of the wing. The primary veins terminate anywhere from two-thirds of the length to the wing tip up to the end of the wing tip. These veins spread out and diminish in thickness as they approach the wing margin. The veins are particularly faint on the side of the wing opposite the backbone. Only rarely do the main wing veins end in the occasional small serrations on the wing tip. The primary veins do not anastomose, and primary vein branching is rare in the fossil specimens (generally no more than 2–4 primary veins branch per specimen). The fossils have a smooth margin along the wing, with the exception of the wing tip. At the wing tip, the margin varies from erose to serrate.

Holotype—EPN 1054, Fig. 4, Locality RJB 9602 ("Azogues View"), Cuenca Basin, Departamento de Cuenca, Ecuador.

Other specimens—Accession numbers of Escuela Politecnica Nacional del Ecuador (EPN)—Cuenca Basin: 65, 67, 74, 118, 119, 120, 770, 776, 822, 884, 885, 938, 988, 989, 1005, 1238, 1254, 1264; Loja Basin: EPN 504. All specimens are permanently housed at the Escuela Politecnica Nacional del Ecuador in Quito, Ecuador.

Etymology—The epithet refers to the small neighborhood, Bolivia La Playa, near the town of Azogues, from which the majority of the fossil specimens were collected in the Cuenca Basin.

Discussion of Loxopterygium laplayense n. sp.—We have summarized the important fruit characters of similar-appearing modern genera bearing asymmetrically winged samaras (both fruits and seeds) from the western hemisphere in Table 1. The distinctive characters of the fossil are the medially placed stigma remnant on the backbone of the wing (Figs. 5, 6), the small size (<2 cm in total length), the remnant calyx at the proximal

TABLE 1. Comparison of morphological characters of extant and fossil asymmetric winged fruits of northern South America.

Family	Genus and species examined	Style remnant position—dispersed	Relative diaspore size	Wing veins	Wing texture	Wing margin smooth or erose	Texture or veins on locule	Attachment surface present?	Calyx remnant visible usually?	Backbone course	Main vein ending	Wing with thick margin?
Anacardiaceae	*Loxopterygium laplayense*	BM	S	P	T	E	P	NO	YES	CX	WT	YES
Anacardiaceae	*Loxopterygium grisebachii, huasango, sagotii*	BM	S/M	P	T/M	E	P	NO	YES	CX	WT/WM	YES
Anacardiaceae	*Schinopsis* cf. *brasiliensis*	L	M	0	F	S	0	NO	YES	ST	0	YES
Celastraceae	*Anthodon* cf. *decusatum*	0	M	P	T	S	0	NO	NO	CX	WT	NO
Fabaceae	*Machaerium cuspidatum*	BT	L	R	F/M	S	R	NO	NO	CV	WM	YES
Fabaceae	*Nissolia fruticosa*	BT	M	PR	T	S	PR	NO	YES	CX	WT	YES
Fabaceae	*Sweetia fruticosa*	BT	L	RP	M	E/S	R	NO	NO	CV/CX	WM	NO
Fabaceae	*Tipuana tipu*	BT	L	P	F/M	S	P	NO	YES	ST	WM	YES
Malpighiaceae	*Banisteriopsis eriantha, muricata*	L	ML	P	F	E	*	YES	NO	CX	WM	NO
Malpighiaceae	*Heteropterys aureosericea, brachiata, laurifolia*	L	ML	P	M	E	0*	YES	NO	CX	WM	NO
Malpighiaceae	*Stigmaphyllon cardiophyllum, sinuatum*	L	M	P	M/F	E	*0	YES	NO	CX	WM	NO
Meliaceae	*Cedrela odorata*	0	SM	0	T	S	0	NO	NO	CX	0	NO
Phytolaccaceae	*Sequieria* cf. *aculeata*	0	M	PR	M	S	P	NO	YES	CX	WM	YES
Polygalaceae	*Securidaca virgata ovalifolia*	BM	M	PR	M	E	PR	NO	YES	CX	WM	NO
Sapindaceae	*Acer negundo, saccharum*	0	ML	PR	M/T	E/S	PR	YES	NO	CX	WM	NO
Sapindaceae	*Serjania* sp.	0	M	PR	M/F	S	R/0	YES	NO	ST	WM	YES
Sapindaceae	*Thouinia serrata*	0	S	P	M	E	P	YES	NO	CX	WM	YES
Sapindaceae	*Thinouia* cf. *oblique*	0	L	RP	M/T	S	R	YES	NO	ST	WM	YES
Sapindaceae	*Thouinidium decandrum*	0	M	R	M	E	0	YES	NO	CV	WM	YES
Ulmaceae	*Phyllostylon brasiliense*	L	M	PR	M/F	S	R	NO	YES	CV	WM	YES

Note: Style remnant position (dispersed): 0 = absent L = locule BM = backbone medial BT = backbone tip. Relative fruit size: S = small M = medium L = large. Wing venation: 0 = absent P = parallel R = reticulate RP = reticulate/parallel PR = parallel/reticulate. Wing texture: F = thick M = medium T = translucent. Wing margin: S = smooth E = erose. Texture or veins on locule: 0 = absent P = parallel R = reticulate * = ornamented. Attachment surface present?: YES or NO. Calyx remnant visible usually?: YES or NO. Backbone course: ST = straight CX = convex CV = concave. Where do the veins end?: 0 = no veins WM = all along wing margin WT = wing tip. Wing with thick margin?: YES or NO.

end of the locule, and the frequently erose to serrate wing tip (Figs. 4–6). This combination of characters placed the specimens in the genus *Loxopterygium* of the Anacardiaceae (Table 1).

Three valid species of *Loxopterygium* are known today (Barkley, 1962; Rizzini, 1975; Mitchell and Daly, 1991; Pennington et al., 2004), the fruits of which have been compared to the fossil fruits from Ecuador. Measurements and characteristics of all three modern species based on study of herbarium specimens are summarized in Table 2. The fossil is easily distinguished from *L. sagotii* by a number of characteristics (particularly size and wing venation; Table 2, Fig. 1). Two modern species of *Loxopterygium* are very similar in fruit morphology to the fossil and we find it difficult to consistently distinguish between these two modern species (*L. huasango* and *L. grisebachii*) based on fruit characteristics alone (Figs. 2, 3). Although *L. huasango* has a tendency to have a lower length-to-width ratio, and a stigma placed further distally on the backbone than *L. grisebachii*, neither the length-to-width ratios of the two species nor the stigma position (as measured by the proportion of total fruit length) are statistically different among the specimens studied. However, *L. huasango* has a consistently and distinctly serrate wing tip, while specimens of *L. grisebachii* more often have an erose wing tip, rather than serrate. In addition, the pedicel is often dispersed with the fruit in *L. grisebachii*, whereas the pedicel remains attached to the parent plant in *L. huasango*. The number of specimens studied for these observations and measurements were limited by collections available (2–6 fruits/collection drawn from three to seven independent collections per species).

Of the 20 fossil specimens only eight were sufficiently complete to make all of the same measurements (complete wing and locule, wing venation detail), and those measurements are also reported in Table 2. Although the mean values of measurements of the fossils are generally smaller than the modern specimens, the ranges fall easily within the variation measured in the two modern dry forest species (*L. grisebachii* and *L. huasango*). The characters that most often distinguish the modern dry forest species, noted above, are variable among the fossil specimens, with specimens encompassing the range of variation seen in both modern species. Allying the fossil specimens more closely with one or the other of the two similar extant species would indicate greater knowledge than we have about the plants from which the fossil fruits were derived. We have therefore described the fossils as a new species of *Loxopterygium*.

Over 1200 specimens of leaves, flowers and fruits have been collected from deposits in the basins of Cuenca, Loja, and Nabon to date. Thus far no leaves that bear strong similarities to leaves of modern *Loxopterygium* have been recovered. A few partial leaves do seem to bear a resemblance to *Loxopterygium*, but these leaves are incomplete and without better material, it would not be possible to determine whether they are related to the fruits described here.

DISCUSSION

Biogeography, climatic distribution, and phylogeny—The extant distribution of the species of *Loxopterygium* based on herbarium records was mapped by Prado and Gibbs (1993). Two of the species they map are not currently recognized as distinct species of *Loxopterygium* (Pennington et al., 2004). However, at the continental scale, it is clear that there are two

TABLE 2. Comparison of modern and fossil species of *Loxopterygium*.

Loxopterygium	Length (mm)	Width (mm)	L/W Ratio	Length to stigma (mm)	% of fruit length to stigma	Locule shape	% Veins branching	Behavior and position of vein ending	Wing serration	Remnant stigma visibility	Pedicel ±
grisebachii N = 19											
Range	13–19	5.0–7.0	2.14–3.2	8–13	55–71	elongate	11–50	veins fade before margin; 0–4 end in teeth	usually erose, but some serrate	visible—rarely with lobes	Y (N)
Mean	15.3	5.8	2.63	9.8	64.5						
huasango N = 25											
Range	12.5–18	4.5–8	2.2–3.1	8.0–12.0	50–77	elongate	0–57	veins fade before margin; 0–4 end in teeth	serration strong, often on opposite side too	visible—rarely with lobes	N
Mean	14.8	5.8	2.58	9.9	67.3						
sagotii N = 14											
Range	23–31.5	6–10	3–4.5	12.5–18	41–60	elongate	100	veins bifurcate at margin	none	stub only remains	N
Mean	28.32	8.9	3.24	14.82	52.2						
laplayense N = 8											
Range	11–16	3–5.5	2–4.5	7–11	58–66	elongate	19–57	veins fade before margin; 0–6 end in teeth	erose to serrate	visible—rarely with lobes	N (Y)
Mean	11.94	3.9	3.17	8	59.3						

TABLE 3. Extant rainfall, elevation, and habitat distribution of species of *Loxopterygium* (Anacardiaceae).

Modern species	No. of collections	Countries of distribution	Known elevational range	Rainfall regime	Habitat
L. grisebachii	21	Bolivia, Argentina	200–2120 m	Dry	seasonally dry tropical forest
L. huasango	13	Ecuador, Peru	0–900 m	Dry	seasonally dry tropical forest
L. sagotii	4	Venezuela, Suriname, Guyana	0–400 m	Moist	evergreen primary forests

Andean species (*L. grisebachii* and *L. huasango*) and one Venezuelan-Guyanan species (*L. sagotii*). The known distributional data for these three species, as recorded in floras and from herbarium specimens is listed in Table 3. Two species are distributed in upland and lowland seasonally dry forests of the Andes and coastal regions of northern South America. A third species is found in moist primary forests of Venezuela, Suriname, and Guyana. Because the genus occurs in both wet and dry tropical forests, a generic determination alone is not definitive for inference of climatic distribution of the fossil species. However, because the fossil species reported here is clearly more similar to the two modern seasonally dry forest species and distinct from the modern rainforest species, it is proposed that the fossil species is representative of seasonally dry forest, rather than moist forest. In addition the ecological distributions of species of other recognizable genera in the Miocene flora from Ecuador (*Tipuana*, *Cedrela*, *Serjania*, *Ruprechtia*) are consistent with a tropical dry forest interpretation. The elevational range of *L. huasango* and *L. grisebachii* is from 0 to 2100 m, with *L. grisebachii* more commonly found above 1000 m than *L. huasango*.

A recently constructed molecular phylogeny of *Loxopterygium*, with selected Anacardiaceae outgroups (Pennington et al., 2004) allows these fossil representatives of *Loxopterygium* from Ecuador to serve as a calibration point. The fossils place a minimum age of about 10.2 ($\pm$1.5) Ma for the node that links the moist forest species (*L. sagotii*) to the stem lineage leading to the two dry forest species (*L. huasango* and *L. grisebachii*). Because the fossils cannot be placed with confidence in either of the two extant dry forest species, the presence of the fossils at ca. 10 Ma must only be used as a minimum age for this node. Documentation of morphological features of the fossils unique to the group (backbone stigma, distinctive venation on the locule, serrated wing, relative fruit size) is critical to the taxonomic placement of the fossils, as well as to placement of the fossils on the molecular phylogeny. Without such comparative detail, constraining nodes on a molecular phylogeny would be uncertain.

Today in some forested areas of Tumbes, Peru, *Loxopterygium* dominates a dry tropical forest woodland (Gentry, 1995). It is remarkable that the species of *Loxopterygium laplayense* represented by the fossils described here can be placed so readily within a small extant lineage of dry forest species. The lack of morphological change demonstrated by the modern dry forest species, at least in terms of fruit morphology, suggests that habitat similar to that in which these species are successful today has been in existence in the same area of the Andes for as much as 10 million years. The sedimentary deposits in the Loja Basin also bear fruits of *Tipuana ecuatoriana* (Fabaceae), which can scarcely be distinguished from the modern *Tipuana tipu* that occurs in the dry forests of Bolivia and Argentina today (Burnham, 1995). The record of *Tipuana*, as well as *Loxopterygium*, indicate that we still know very little about the rate of morphological change in South American plant gen-

era. The use of angiosperm fossils to calibrate well-constrained molecular phylogenies appears to be a fruitful means of constraining rates of morphological evolution in plants.

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