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# NEITHER OAK NOR ALDER, BUT NEARLY: THE HISTORY OF TICODENDRACEAE<sup>1</sup>

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## ABSTRACT

The newly described monotypic family Ticodendraceae is endemic to Mesoamerica, where it ranges from southern Mexico to central Panama. Although locally common in some areas very close to old collecting sites (at least in Costa Rica), few collections from prior to 1985 are known. Recent funds for exploration and concentration on the arborescent flora may account for the "rediscovery" of *Ticodendron* during the 1980s. It may also have been overlooked by botanists because it looks so familiar, like an oak or an alder. Most evidence suggests that it can be placed comfortably in the Fagales. *Ticodendron* is most common in the narrow strip of wet montane Atlantic slope forests between 750 and 1,500 m, where it often grows in association with endemic taxa of *Alfaroa*, *Oreomunnoa*, *Nyssa*, and other remnants of the Tertiary Laurasian flora. Further study and survey of this area will surely provide insight into the composition of that ancient flora surviving in Mesoamerica.

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With the formal description of Ticodendraceae (Gómez-Laurito & Gómez P., 1991) in hand, this paper will present discussions of the history of discovery, distribution and habitat, biogeography, and a summary of relationships based on the following five papers, which present results of detailed studies of the wood anatomy (Carlquist), leaf anatomy (Hickey & Taylor), sieve-element characters (Behnke), floral anatomy and morphology (Tobe), and pollen morphology (Feuer).

## HISTORY OF DISCOVERY

In one sense, when *Ticodendron incognitum* Gómez-Laurito & Gómez P. (1989) was described, its epithet could be taken as ironic. The recent history of this plant attests to the fact that many people knew a lot about it even before the species was formally published; correspondence among specialists during the years immediately preceding this compendium is measured in reams. We now know *Ticodendron* to have a rather wide distribution; as recently as 1984 it was known only from Costa Rica, but now is known to be locally common, from southern Mexico to central Panama. The plant is also quite well known to woodsmen; in Costa Rica alone it has at least four common names—two of them referring to it as a kind of alder (Gómez-Laurito & Gómez P., 1989). Yet,

although *Ticodendron* was far from unknown at the time of publication, the Latin "incognitum" can have much the same meaning as the modern English usage of "incognito," and the fact that the family placement of this species has been such a puzzle makes the epithet appropriate. The plant has been famous in many ways, but its true identity has remained hidden (Fig. 1).

In spite of the fact that *Ticodendron* grows in relatively hospitable and accessible areas of moist to wet mid-elevation forests, some of which have been frequented by botanists for nearly a hundred years, we can cite only eight collections made prior to the 1980s. Four of those eight came to light recently, after the publication of the genus; *Ticodendron* has been hiding not only in the woods, but in the herbarium as well. Now that we know the tree we find it obvious and abundant, sometimes easily accessible at pasture edges and, at the right time of year, loaded with more or less conspicuous fruits (Fig. 2A) or littering the ground with the decaying fruits.

At first glance, especially when vegetative, this tree and its fallen leaves are easily mistaken for the common *Alnus* of the region, which often grows in the same areas as *Ticodendron* (Fig. 2B). One of the earliest known collections (*Lankester s.n.*, 1925), found recently by Aaron Goldberg at US, had been identified by an *Alnus* specialist as *A.*

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FIGURE 1. Mature tree of *Ticodendron incognitum* in forest at Monteverde, Costa Rica (Gentry et al. 71474).

*acuminata* subsp. *arguta*. Herbaria have scores of collections of *Alnus* from Central America, but why so few of *Ticodendron*? Why didn't industrious collectors like Brenes, Otón Jimenéz, Matuda, Pittier, Standley, Tonduz, or Williams collect it? Actually some of them may have; a recently rediscovered specimen at F with an early annotation "not Flacourt." made us take Steyermark off the above list at the last minute. Alternatively, why was this species not described by one of the early botanists who did collect it? It is conceivable that the species has been described, e.g., from

sterile material, in a large genus, where no one thought to look.

The most likely reason that *Ticodendron* has gone so little collected and so long incognito is that it is most common in wet primary forest where intensive and persistent sampling of trees has begun only recently. Certainly trees are difficult to collect, and *Ticodendron* may have been overlooked for that reason. Also, the flowering period is apparently rather short and the flowers are inconspicuous. Many places accessible now by road were undoubtedly completely isolated 40 or 50 years ago.



FIGURE 2.—A. Fruiting specimen of *Ticodendron incognitum* (Gentry et al. 71474).—B. Young sapling of *Ticodendron incognitum* (Hammel & Rivera 17834).

Another answer might be conservatism. If good field botanists find fallen fruits beneath a tree with leaves that don't "fit" the fruits—i.e., because the fruits of *Ticodendron* do not look like those of *Alnus*—they may assume the fruits came from some other source and not pursue the matter. How many would waste their time to collect a difficult specimen of *Alnus* in primary forest when it could so easily be found along the road? Likewise, even if they do collect it with fruits or flowers attached, they are unlikely to describe it right away if they don't know in which family to place it. The tree

looks so familiar and is so common, surely it has already been described! This concept is suggested by field notes on the Lankester specimen: "Woodland tree . . . having a distinctly European appearance."

According to label information, the first botanist to collect *Ticodendron* (see below) thought it might be a genus of Polygonaceae close to *Coccoloba*. A more recent sterile collection, the only one from Nicaragua, was also first identified tentatively as a species of *Ruprechtia* (Polygonaceae). This family is implicated by a conspicuous amplexicaule scar

left on the twigs of *Ticodendron* by the large, paired stipules. Thus, the belated discovery of *Ticodendron* by botanists is curious and yet perhaps explainable by the fact that although it looks very much like something well known, e.g., Polygonaceae, oak or alder, it really is something different.

The earliest known collection of *Ticodendron*, recognized at US by R. Foster, was made in Costa Rica by Carlos Wercklé (probably between 1900 and 1910). Eight other collections (all from Costa Rica, except as indicated) prior to the 1980s have been found: C. H. Lankester (1925), Austin Smith (1938), Steyermark (1942, Guatemala), W. H. Hatheway (1965, 1966), Luis Poveda (1974), and John Pipoly (1979, Nicaragua).

For nearly a decade before specimens from Costa Rica and Panama (1986) began to arrive and arouse interest at the Missouri Botanical Garden, botanists at the Herbario Nacional de Costa Rica had regarded the plant as an unknown of considerable interest, possibly related to Hamamelidales. However, few, if any, others were aware of the existence and significance of this taxon. By then, fruits and male flowers were known; the species was assumed to be dioecious, but female flowers were still needed. When the existence of a fairly common and conspicuous Costa Rican tree that defied identification by the usual route became more widely known, a three-year-long stream of correspondence ensued. The goal was to motivate collectors in Costa Rica and Panama and specialists around the world, from paleobotanists to phytochemists, to gather and analyze the appropriate material in order to place this new tree among its proper relatives.

#### DISTRIBUTION AND HABITAT

The single species of Ticodendraceae is known from southern Mexico to central Panama at elevations from 500 to 2,400 m. A number of collections, most notably those from Mexico, have come to light since the genus was described (Gómez-Laurito & Gómez P., 1989). Below, all known collections are cited. We now have seen specimens from Mexico, Guatemala, Nicaragua, Costa Rica, and Panama, and are confident that other specimens or the plant itself will turn up from the remaining countries of Mesoamerica, where the appropriate habitat occurs.

*Specimens examined.* MEXICO. OAXACA: Municipio de San Miguel Chimalapa, Cerro Salomón, 1,850 m, 21 Aug. 1986 (fr), *Wendt et al.* 5380 (MO); Municipio de Santiago Comaltepec, La Esperanza, 1,600 m, 30 Sep. 1987 (fl & fr), *Luna* 49 (MO); Municipio Tontontepec,

2 km SW de Tontontepec, 1,900 m, 17 June 1986 (fr), *Torres & Téllez* 8620. GUATEMALA. HUEHUETENANGO: Cerro Cananá, 2,500–2,800 m, 18 July 1942 (st), *Steyermark* 49111 (F). NICARAGUA. ZELAYA: Cerro La Pimienta numbers 1 and 2, 900–1,600 m, 17 Apr. 1979 (st), *Pipoly* 5233 (MO). COSTA RICA. ALAJUELA: Cachí, 1,200 m, 27 Sep. 1925 (st), *Lankester s.n.* (US); Reserva Biológica Monteverde, valle del Río Peñas Blancas, 800 m, 30 Mar. 1989 (fl), *Bello* 773, 774 (MO); 1 Mar. 1990 (immature fr), *Bello* 1971 (MO); 850 m, 28 Mar. 1987 (fl), *Haber & Bello* 6840, 6841, 6842 (MO); 29 Mar. 1987 (fl), 6851, 6852 (MO); 900 m, 30 Mar. 1987 (fl & fr), 6868 (MO); 9 Mar. 1987 (bud), 6909 (MO); 800 m, 24 Mar. 1987 (fl), *Haber & Cruz* 7071, 7072 (MO); 850 m, 5 Apr. 1987 (fl & fr), 7286, 7604 (MO); 750 m, 12 June 1986 (st), *Hammel et al.* 15385 (MO), (fr) 15396 (MO); Reserva Forestal Arenal, Bosque Eterno de los Niños, 1,100 m, 6 Mar. 1990 (fr), *Bello* 2154 (MO); Río Aguas Gatas, 1,000 m, 29 Jan. 1990 (fl), *Bello* 1877 (MO); Río Caño Negro, 1,200 m, 17 Feb. 1990 (fl), *Bello* 1885 (MO); 800 m, 19 Feb. 1990 (fl), *Bello* 1911 (MO); Reserva Forestal de San Ramón, 900 m, 26 Feb. 1988 (sapling), *Burger et al.* 12452 (CR); 900–1,200 m, 13 Mar. 1987 (st), *Gómez-L.* 11403 (CR); 30 Mar. 1987 (fl), *Herrera et al.* 515, 516, 517 (MO); Upala, Bijagua, 1,000 m, 9 July 1988 (fr), *Herrera et al.* 2032 (MO); Zarcero, La Brisa, 1,800 m, 19 July 1938 (fr), *Austin Smith* H970 (F); Zarcero, Volcán Viejo, 1,800 m, 11 Feb. 1986 (fr), *Gómez-L. & Carvajal* 11100 (CR). CARTAGO: Reserva Forestal Tapantí, 1,500–2,000 m, 8 July 1986 (st), *I. Chacón* 1985 (CR). GUANACASTE: Tilarán, Río Chiquito, 1,100 m, 7 June 1987 (fr), *Haber & Bello* 7442 (MO). HEREDIA: Cerro Chompipe, 1,800 m, 17 June 1990 (st), *Hammel et al.* 17815 (CR); Sacramento, Montaña La Isla, 2,300–2,500 m, 13 Jan. 1987 (fr), *Gómez-L.* 11306, 11307 (CR); 3 Apr. 1987 (fl), *Gómez-L. et al.* 11472, 11473 (CR); 17 July 1990 (fr), *Hammel & Rivera* 17834 (CR); Volcán Barva, above San José de la Montaña, 1,950 m, 19 Sep. 1965 (fr), *Hatheway* 1681 (US); 1 May 1966 (st), *Hatheway* 1712 (US). LIMÓN: Cantón de Talamanca, Bratsi, 700 m, 15 July 1989 (st), *Herrera* 3339 (CR); Cantón de Guápiles, Río Blanco, 700 m, 24 Feb. 1990 (st), *Herrera & Schik* 3791 (CR); Río Blanquito, 1,100 m, 26 Feb. 1990 (fr), *Herrera* 3846 (CR); Parque Internacional La Amistad, 650 m, 17 July 1989 (st), *A. Chacón* 190 (CR); Reserva Biológica Hitoy-Cerere, 1,024 m, 3 Sep. 1989 (fr), *Hammel et al.* 17685 (CR). PUNTARENAS: Cantón de Golfito, Quebrada Vaquedano, 500 m, 23 July 1990 (st), *Herrera* 4020; Monteverde, Quebrada Máquina, 1,400 m, 12 Nov. 1988 (fr), *Bello* 447 (MO); 17 Mar. 1990 (immature fr), *Haber* 9809 (MO); 14 July 1990 (fr), *Gentry et al.* 71474 (MO); Parque Nacional Corcorado, Cerro Brujo, 617 m, 19 July 1990 (st), *Herrera et al.* 3969; Reserva Biológica Monteverde, road to TV tower, 1,600 m, 21 July 1985 (fr), *Haber & Bello* 2058 (MO). SAN JOSÉ: Bajo La Hondura, 1,300 m, 21 May 1974 (st), *Poveda* 864 (CR); San Cristóbal, 1,650 m, 1900–1910? (fr), *Wercklé s.n.* (US). PANAMA. BOCAS DEL TORO: Fortuna Dam area, 1,250 m, 11 Feb. 1986 (sterile with old fallen fruits), *McPherson & Hammel* 8401 (MO). CHIRIQUÍ: Fortuna Dam area, 1,100–1,300 m, 7 Sep. 1987 (st), *McPherson* 11659 (MO); 26 Apr. 1988 (fl), *McPherson* 12493 (MO); N slope of Volcán Barú, 1,750–1,900 m, 13 Jan. 1989 (st), *McPherson* 13525 (MO). COCLÉ: N of El Copé, 750 m, 22 June 1988 (st), *McPherson* 12615 (MO).

*Ticodendron* grows in mid-elevation cloud forests on both sides of the continental divide throughout Mesoamerica. It is most often found in very diverse, evergreen forests wetter and somewhat lower (2,400 m at most) than those dominated by oak, and is typically found on deep, humic soils. At its lowest it descends to 500 m in the Osa peninsula of Costa Rica. Otherwise, in the southern part of its range, where the isthmus is divided sharply by the central mountain chain into wet (Atlantic) and dry (Pacific) sides, the species is more common and descends lower (650 m) on the Atlantic slopes. However, near San José, Costa Rica, numerous populations are known from the very wet southern (Pacific) slopes of the Cordillera Central. In this part of its range *Ticodendron* flowers from January through April, and the fruits mature several months later. Germination has not been observed, but from the numerous young saplings observed we surmise that germination is hypogeal.

#### RELATIONSHIPS

Even with detailed analyses, which follow, Ticodendraceae finds its position in the Hamamelidae sensu Cronquist (but see Hickey & Taylor, 1991) and Fagales almost by default. Outside Hamamelidae, Euphorbiaceae were considered (because of some similarity to *Picodendron*) but rejected because *Ticodendron* lacks their characteristic obturators (Tobe, 1991). The very reduced unisexual flowers lead by overall similarity to the "higher" Hamamelidae, where many of the old Amentiferae lie. Pollen data also lead there but by way of an array of features unique among dicots (Feuer, 1991; Zavada & Dilcher, 1986).

In the end, Ticodendraceae has been described as a distinct family because it has been shown neither to share any rigorously supported synapomorphy or set of synapomorphies with any taxon already described nor does it fit comfortably in overall similarity within any described family. By a process of elimination, its ordinal placement seemed most likely among Juglandales, Myricales, or Fagales. Urticales were rejected early because *Ticodendron* lacks the foliar trichomes characteristic of that order (Tobe, pers. comm.). *Ticodendron* also does not coincide with Urticales in pistillate flower (Tobe, 1991) and sieve-element characters (Behnke, 1991). *Ticodendron* is eliminated from Juglandales and Myricales because of floral and trichome considerations. Taken together, the details of wood and bark anatomy (Carlquist, 1991), leaf anatomy (Hickey & Taylor, 1991), sieve-element characters (Behnke, 1991), and floral anatomy (Tobe, 1991) suggest that *Ticoden-*

*dron* cannot be placed exactly within any of the compared families, but that it does not conflict seriously with placement in Fagales. Hickey & Taylor (1991) place *Ticodendron* closest to a fossil, the fagalean genus *Fagopsis*.

Although the pollen data show the highest similarity with Myricaceae (Feuer, 1991), other characters argue strongly against placing *Ticodendron* nearer to Myricales than Fagales. Even the pollen data show considerable similarity with the coryloid Betulaceae (Corylaceae sensu Carlquist). This agrees with the data from bark and wood anatomy (Carlquist, 1991) and sieve-element characters (Behnke, 1991), as well as the observation that the nutlets of *Carpinus* are remarkably similar in shape and sculpturing to (though much smaller than) the endocarp of *Ticodendron*. Although the floral anatomy of *Ticodendron* has a superficial resemblance to *Nothofagus* (Tobe, 1991)—which itself comprises a distinct family, sister to Betulaceae rather than to Fagaceae (cf. Jones, 1986; Nixon, 1989)—among Betulaceae, *Ticodendron* perianth characteristics are more like those of the coryloid genera (Tobe, 1991) (see Table 1).

In Cronquist's (1981) Hamamelidae, *Ticodendron* would find a home in Fagales simply by modifying the key to orders to include plants with hemitropous ovules. On the basis of floral anatomy (Tobe, 1991) and wood and bark anatomy (Carlquist, 1991), Ticodendraceae would be more primitive within Fagales than other families. With our present knowledge, the best estimate of relationships of *Ticodendron* is represented by placing it in its own family within the order Fagales, where it is distinctive for its drupaceous fruits, four-lobed ovary, and hemitropous ovules.

#### BIOGEOGRAPHY

Ticodendraceae is endemic to Mesoamerica, and by virtue of its alliance to the higher Hamamelidae is probably a remnant of the Tertiary Laurasian flora. As such, its discovery and distribution are significant at a level with the trigonobalanoid Fagaceae of Colombia, *Alfaroa* and *Oreomunnea* (Juglandaceae), *Molinadendron* and *Matudaea* (Hamamelidaceae), and *Nyssa talamancana* Hammel & Zamora (Cornaceae) (see Hammel & Zamora, 1990; Nixon & Crepet, 1989; van der Hammen & Cleef, 1983). The fossil histories of these or related taxa tell us that they are remnants of a once widespread northern forest. Indeed, according to leaf characteristics (Hickey & Taylor, 1991) *Ticodendron* appears to be most closely related to a fossil from Oligocene deposits in Colorado. The rather obvious extrapolation is that fossils of *Ti-*

TABLE 1. Characteristics of *Ticodendron* and some of the taxa with which it has been compared. Data are mostly from papers in this compendium and Cronquist (1981).

	TICO*	OSTR	BETU	MYRI	ULMA	HAMA	NOTH	JUCL	PICR	CECR	CASU
PERIANTH											
Male	absent	= <sup>b</sup>	x	=	x	x	x	x	=	x	=
Female	present	=	x	x	=	=	=	=	x	=	x
POLLEN	triporate	=	=	=	x	x	x	=	x	?	=
Endexine	absent	=	x	=	x	x	x	x	?	?	x
STYLES	2	=	=	=	=	±	±	=	=	1	=
CARPELS	2	=	=	=	=	=	±	=	=	1	=
LOCULES	4	2	2	1	x	2	2 or 3	1	2	1	2
OVULE	1/locule	2	=	=	=	=	2	=	2	=	2
Placentation	pendulous	=	=	erect	=	=	=	erect	= <sup>c</sup>	?	erect
	axile	=	=	basal	apic	=	=	basal	=	basal	?
	hemitropous	ana	ana	ortho	ana	ana	ana	ortho	?	ortho	=?
	unitegmic	=	=	=	bi	=	=	=	bi	bi	bi
FRUIT	drupe	nut	nut	=	=	caps	nut	=	=	±	nut
	no cupule	=	=	=?	=	=	x	=	=	=	x?
SEEDS	1	=	=	=	=	x	=	=	=	=	=
LEAVES	simple	=	=	=	=	=	=	x	=	=	?
STIPULES	present	=	=	x	=	=	=	=	=	=	x
SHARED											
(= or ±)	17	13	11	11	10	10	9	9	9	7	6

\* Expansion of abbreviations of taxa: *Ticodendron*, *Ostryopsis*, *Betula*, *Myrica*, *Ulmaceae*, *Hamamelidaceae*, *Nothofagus*, *Juglans*, *Picrodendron*, *Cecropiaceae*, *Casuarinaceae*.

<sup>b</sup> Symbols are compared to *Ticodendron*: = same as, x different, ± variable but including, ? unknown or uncertain; where convenient the character state itself is presented.

<sup>c</sup> Ovules pendulous from an obturator.

*codendron* and its associated Laurasian taxa must exist and ought to be sought in North America, Europe, and Asia.

Both the high mountains and lowlands of southern Central America have floras dominated by relatively recently (ca. Pliocene) arrived taxa; the rising mountains were invaded by northern species and the lowlands by South American species across the isthmus (Gentry, 1982b; Grayum & Churchill, 1987; Hammel, 1986; Rich & Rich, 1983; Standley, 1937). However, *Ticodendron* and all of the other above-mentioned Laurasian taxa, endemic to the region between southern Mexico and northern Columbia, are found for the most part in wet to moist mid-elevation forests. These areas, more than anywhere else in the tropics, are characterized by the kind of mild, humid and aseasonal climate that was prevalent across the Northern Hemisphere in Paleogene (65–25 mya) times. Further exploration and careful phytogeographical analysis in the areas where *Ticodendron* grows, especially along the isolated, wet Caribbean slopes is likely to reveal additional archaic forms that may, in some cases, give us direct, living insight into the kinds of species widespread in the northern forests tens of millions of years earlier.

#### LITERATURE CITED

- BEHNKE, H.-D. 1991. Sieve-element characters of *Ticodendron*. Ann. Missouri Bot. Gard. 78: 131–134.
- CARLQUIST, S. 1991. Wood and bark anatomy of *Ticodendron*: comments on relationships. Ann. Missouri Bot. Gard. 78: 96–104.
- CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- FEUER, S. 1991. Pollen morphology and the systematic relationships of *Ticodendron incognitum*. Ann. Missouri Bot. Gard. 78: 143–151.
- GENTRY, A. H. 1982a. Phytogeographic patterns as evidence for a Chocó refuge. Pp. 112–136 in G. T. Prance (editor), Biological Diversification in the Tropics. Columbia Univ. Press, New York.
- . 1982b. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Missouri Bot. Gard. 69: 557–593.
- GÓMEZ-LAURITO, J. & L. D. GÓMEZ P. 1989. *Ticodendron*: a new tree from Central America. Ann. Missouri Bot. Gard. 76: 1148–1151.
- & ———. 1991. Ticodendraceae: a new family of flowering plants. Ann. Missouri Bot. Gard. 78: 87–88.
- GRAYUM, M. H. & H. W. CHURCHILL. 1987. An introduction to the pteridophyte flora of Finca La Selva, Costa Rica. Amer. Fern J. 77: 73–89.
- HAMMEL, B. E. 1986. Characteristics of phytogeographical analysis of a subset of the flora of La Selva (Costa Rica). Selbyana 9: 149–155.
- & N. A. ZAMORA. 1990. *Nyssa talamancana* (Cornaceae), an addition to the remnant Laurasian Tertiary flora of southern Central America. Brittonia 42: 165–170.
- HICKEY, L. H. & D. W. TAYLOR. 1991. The leaf architecture of *Ticodendron* and the application of foliar characters in discerning its relationships. Ann. Missouri Bot. Gard. 78: 105–130.
- JONES, J. H. 1986. Evolution of the Fagaceae: the implication of foliar features. Ann. Missouri Bot. Gard. 73: 228–275.
- NIXON, K. C. 1989. Origins of Fagaceae. Pp. 23–43 in P. R. Crane & S. Blackmore (editors), Evolution, Systematics, and Fossil History of the Hamamelidae. Clarendon, Oxford.
- & W. L. CREPET. 1989. *Trigonobalanus* (Fagaceae): taxonomic status and phylogenetic relationships. Amer. J. Bot. 76: 826–841.
- RICH, P. V. & T. H. RICH. 1983. The Central American dispersal route: biotic history and paleogeography. Pp. 12–34 in D. H. Janzen (editor), Costa Rican Natural History. Univ. Chicago Press, Chicago, Illinois.
- STANDLEY, P. 1937. Flora of Costa Rica. Field Mus. Nat. Hist., Bot. Ser. 18: 5–63.
- TOBE, H. 1991. Reproductive morphology, anatomy, and relationships of *Ticodendron*. Ann. Missouri Bot. Gard. 78: 135–142.
- VAN DER HAMMEN, T. & A. CLEEF. 1983. *Trigonobalanus* and the tropical amphipacific element in the North Andean forest. J. Biogeogr. 10: 437–440.
- ZAVADA, M. & D. DILCHER. 1986. Comparative pollen morphology and its relationships to phylogeny of pollen in Hamamelidae. Ann. Missouri Bot. Gard. 73: 348–377.