

***PLEODENDRON COSTARICENSE* (CANELLACEAE), A NEW SPECIES FOR COSTA RICA**

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ABSTRACT. *Pleodendron costaricense*, a very rare, lowland rainforest tree known from southern Pacific Costa Rica is described and illustrated. Its only congener, *P. macranthum*, grows about 2000 km to the northeast, in Puerto Rico. The only other member of the family Canellaceae known from Central America is the mostly West Indian, *Canella winterana*, which reaches the Yucatan Peninsula of Mexico.

RESUMEN. Se describe e ilustra *Pleodendron costaricense*, una especie de árboles muy rara en el bosque lluvioso de bajura del Pacífico Sur de Costa Rica. La única otra especie congénérica, *P. macranthum*, se encuentra ca. 2000 km al nordeste, en Puerto Rico. Hasta ahora, la única especie de Canellaceae conocida en Centroamérica era *Canella winterana*, principalmente de las Antillas, que llega a la Península de Yucatán en México.

KEY WORDS / PALABRAS CLAVE: Canellaceae, *Pleodendron*, Central America, Costa Rica, West Indies, disjunct

The new species of *Pleodendron* (Canellaceae) described below was discovered in Costa Rica just as the rediscovery of *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy (Winteraceae) in Madagascar was making news (e.g., Schatz *et al.* 1998, Schatz 2000). Though coincidental, these discoveries nevertheless merit mention together, their respective families being sister taxa (e.g., Karol *et al.* 2000) and among those often considered most closely related to (or least changed from), the earliest angiosperms. Such so-called *living fossils* always stimulate considerable interest; the study of their morphology, biology and ecology can give us insight into what the world was like millions of years ago.

The disjunct occurrence of *Pleodendron* in Costa Rica and Puerto Rico adds another data point to our understanding of the complex biogeography of the region. But what kind of research program is most productive of such discoveries? In our view, general surveys, especially those coupled to a Flora project, can be more productive than efforts to find one specific item. *Takhtajania perrieri* was for many years the object of a concerted exploration of the type locality, but was only recollected as a result of a general botanical inventory of a different area (Schatz *et al.* 1998). Even that material might still lay incorrectly and tentatively determined (Schatz 2000) were it not for the stimulus provided through the *Generic Tree Flora of Madagascar* (Schatz 2001) project. The evidence of *Pleodendron*, coupled with numerous other examples

from the *Manual de Plantas de Costa Rica* project, although anecdotal, clearly demonstrates the value of general surveys and flora projects in stimulating major discoveries (e.g., Zamora *et al.* 2004a). We challenge fund-raisers and grant reviewers, in the current theatre of difficult times, to reconsider the value of generalized research; the rewards are great, many, and unpredictable.

***Pleodendron costaricense* N. Zamora, Hammel & R. Aguilar, sp. nova**

TYPE: Costa Rica; Puntarenas, cantón de Parrita, cuenca del Río Pirrís-Damas; Parrita, pie del Cerro Cabeza de Chancho, camino al Carmen, valle del Río Palo Seco, 300 m, 26 mar 2000 (fl), N. Zamora *et al.* 2986 (holotype: INB, isotypes: BH, CR, JBSD, K, MO, P, U, US). Fig. 1.

Differt a Pleodendro macrantho floribus multo minoribus, petalis circa dimidium brevioribus.

(It differs from *P. macranthum* by its much smaller flowers, the petals shorter by ca. 1/2).

Tree, 15-35 m tall; external bark gray and white, weakly fissured and scaly; internal bark pale pink, aromatic; twigs pale gray, glabrous, lenticelate near apex, often with clusters of bud scale scars, presumably produced during periods of slow growth; terminal buds 9 x 2 mm, ovate-falcate, the young leaves convolutedly folded and their margins minutely

ciliate; stipules lacking. Leaves distichous; petiole 5-12 mm long, canaliculate above, articulate at the base; lamina 7-15.5 x 3.5-5.5 cm, oblong, basally obtuse to acute, sometimes weakly decurrent, apically acute to slightly acuminate, with an acumen to 7 mm long, glabrous on both surfaces, glossy above when dry, the midrib impressed above, raised below and turning reddish when dry, the major lateral veins 12-13 pairs, the tertiary venation conspicuously reticulate on both sides, the margin entire and weakly revolute near the base when dry; numerous, clear, gland dots visible (most readily on upper surface) only with hand lens; flavor peppery hot. Flowers solitary, or in fasciculate clusters of 2-4 flowers, axillary or slightly supra-axillary, sometimes spread along leafless portions of twigs and there born axillary to \pm congested bud scale scars. Pedicels 2-5 mm long, often with numerous, spirally arranged, imbricate bracteoles, the lower ones *ca.* 0.5 mm, the distal ones 1-3 mm, circular or semicircular. Floral buds globose, *ca.* 6 x 6 mm. Calyx cupular or campanulate, glabrous, 3-lobed, with a short tube 1-1.5 mm, the lobes 1-1.5 mm long, rounded and slightly imbricate, minutely ciliate. Petals 12, free, apically obtuse to rounded, glabrous, in three distinct series, the outer 3 petals 5-7 x 3.5-4.5 mm, ovate, succulent (1.3-1.5 mm thick), the next 3 petals 5-7 x 1.6-2.5 mm, lanceolate, succulent (1.0-1.3 mm thick), the innermost 6 petals \pm equal, 3.7-5.3 x 1.5-2 mm, elliptic, \pm membranaceous (*c.* 0.5 mm thick), basally valvate, apically irregularly imbricate, internally faintly striate by the impression of the androecium. Androecium of connate stamens, a staminal column surrounding the ovary, the lower portion 3-5 mm long, the upper portion comprised of *ca.* 24, bisporangiate, longitudinally and extrorsely dehiscent thecae, 1.5-2 mm long, the thecae sessile and dorsally adnate to the staminal column (as the ovary develops, the staminal column appears to split longitudinally and detach circumscissilely at the base). Ovary 4.5-4.8 x 2.3 mm, bottle-shaped, glabrous, unilocular, the placentation parietal with *ca.* 6 rows of paired ovules, the ovules numerous, reniform; stigma capitate, *ca.* 6-lobed. Fruit a berry, 2.5 x 3 cm, obovate, green, smooth, and slightly glaucous; seeds many, 4-5 x 4 mm, ovate to oblong or somewhat reniform, black, shiny, the funicular scar impressed and rounded; endosperm not ruminant.

PARATYPES: COSTA RICA. **Puntarenas:** Cantón de Osa, Península de Osa, Rancho Quemado, camino a Chiquerón, 200 m, 15 ago 1998 (fr), *R. Aguilar 5509* (INB); 30 jul 1999 (fr), *R. Aguilar 5705* (CR, F, INB, MO, NY, P, UPR, US); 11 febr 2000 (fl), *R. Aguilar*

5934 (INB, CR, K, MO, U, US); Cantón de Parrita, cuenca del Río Pirrís-Damas; Parrita, pie del Cerro Cabeza de Chanco, camino al Carmen, valle del Río Palo Seco, 300 m, 26 febr 2000 (fl), *R. Aguilar 6007* (CR, G, HULE, INB); 7 febr 2000 (fl), *B. Hammel 22049* (BH, BM, CR, JVR, INB, K, MEXU, MO, NO, NY, P, PMA, QCA, QCNE, SPF, TEX, UPR, US), 21 febr 2000 (fl), *B. Hammel 22063* (CAS, COL, CR, EAP, F, INB, MICH, MO, US, USJ), 3 jul 2003 (fl, fr.), *J. Salazar et al. 2622* (BH, JBSD). **San José:** Cantón de Tarrazú, Zona Protectora Cerro Nara, cuenca del Río Naranjo y Paquita, faldas del Cerro Nara, bosques arriba de Quebrada Salitrillo, junto al camino, 250 m, 18 mar 1999 (sterile), *A. Rodríguez & V. Ramírez 4682* (INB, CR, MO).

HISTORY OF DISCOVERY. Given the combined expertise of botanists in Costa Rican along with the essentially instant and global collaboration possible through the Internet, any fertile, native plant that we can't immediately place to family is motive for much excitement. When this plant first came to our attention, sometime after August 1998, having only a rather meager collection with fruits, we remained puzzled by it for several months, and anxiously awaited the appearance of better material, especially flowers, for more than a year. Our ephemeral conjectures included such families as Annonaceae, Capparaceae, Ebenaceae. This large, lowland rainforest tree, with *Annona*- or *Diospyros*-like leaves, but with baccate fruits with numerous, small, black seeds, had us all stumped. As time wore on, our determination to get to the bottom of the mystery grew. In an evening of carefully examining, dissecting, squeezing, and sniffing the specimens, generally of highly animated consultation among numerous botanists then present at the *Instituto Nacional de Biodiversidad* (INBio), a strong smell memory - that of the fruits and seeds of *Virola* (Myristicaceae) - came to us on crushing the seeds of our mystery plant. Although all Costa Rican Myristicaceae have fruits with a single, large seed, we opened Cronquist (1981) to see if some odd, South American genus might fit our plant. More than anything else it was our quirky smell memory, and Cronquist's treatment of Canellaceae as closely related (and described on the immediately subsequent page) to Myristicaceae, that got us on track. The description of Canellaceae fit our plant to a tee, and the thrill was tangible. Leaf material sent for DNA analysis to a colleague working on the phylogeny of the early angiosperms placed our plant squarely within Canellaceae (Elizabeth Zimmers, pers. com.).

And finally, flowering material, gathered more than a year after the original collection, also confirmed our identification.

Why, one might now ask, did it take us so long, to figure out the family of this plant? First, it wasn't really very long, by "Takhtajanian" standards; the first collection of *Takhtajania perrieri* remained without definite placement as to family, as well as undescribed, for 54 years (Schatz 2000). More to the point, however, is the tautological observation that we can't know what we don't know. Canellaceae had never been found in Costa Rica, are known from Mesoamerica - and there, essentially only from the Yucatan of Mexico - only by one species, *Canella winterana* (L.) Gaertn., none of us trying to figure out the mystery hardly remembered having heard of the family, let alone had ever had direct experience with it, and we hadn't yet invited our "Internet" colleagues into the search. Thus, in retrospect, we came to a solution of our mystery as quickly as we did, in part because of experience, and in part, as is often the case with such matters, because of luck.

PHENOLOGY. Flowering material of *Pleodendron costaricense* has been collected in February and March. Not all flowers open at the same time; anthesis occurs as a successive process. We also noted that in a particular season, some branches apparently did not flower at all. The fully mature flowers (Figs. 2 & 3, C), remain globose, the petals \pm erect and spreading to only a small, circular opening. Fruits are nearly mature by late July and last into August.

MORPHOLOGY, RELATIONSHIPS & BIOGEOGRAPHY. This species is recognized as belonging to the Canellaceae by virtue of its alternate, entire, exstipulate, coriaceous, aromatic leaves, and flowers with three sepals, stamens connate into a staminal column with extrorse anthers, and an ovary with parietal placentation that in fruit is a berry.

Two (*Canella* and *Warburgia*) of the six genera of Canellaceae have consistently five-merous corollas and androecia (e.g., Tieghem 1899, Wilson 1966). In addition *Warburgia* is five-carpellate. *Cinnamodendron* and *Cinnamosma* are variable in merosity of corolla, androecium and ovary (e.g., Schatz 2001, Wilson 1966). *Canella* has two carpels, and *Cinnamodendron* has 2-4 carpels (J. Salazar, pers. com.). *Capsicodendron* (Occioni 1943) and *Pleodendron* have three-merous corollas and ovaries. The petals of *Canella* are basally

connate and *Cinnamosma* has a salverform corolla. All other genera have free petals. *Pleodendron ekmanii* Urb. was described from sterile material from Haiti, but preliminary evidence indicates that it is more likely conspecific with one of the species of *Cinnamodendron* known from the Greater Antilles (J. Salazar, pers. com.). *Pleodendron macranthum* (Baill.) Tiegh. has been interpreted as having 11 or 12 petals in four "false" (Baillon 1882) series of three petals each, or more decidedly as 12 petals disposed in four alternate verticels (Tieghem 1899, Little *et al.* 1988). In his comparative study of the floral morphology of the genera of Canellaceae, Wilson (1966: 340) found *P. macranthum*'s 12 petals to be in just two series of six, each with an apparent "alternation of large and small petals." Thus, *Pleodendron* has essentially three-merous flowers throughout (3 sepals, 12 petals, 24 bisporangiate thecae, 6 carpels; see Table 1).

Thus considered, the only sure floral differences between the two known species of *Pleodendron*, *P. macranthum*, and *P. costaricense*, are the much smaller peduncles and petals in the latter (less than 1/2 as long as those of *P. macranthum*). The fruits of the two are also quite different (see Fig. 3, D & E). Other possible floral differences are subject to interpretation, e.g., in mature flowers of *P. costaricense* we see three series (3+3+6) of petals (Fig. 1, H), the outer two thicker than the inner one, whereas *P. macranthum* has been interpreted to have four (3+3+3+3) or two (6+6) series. Nevertheless, the transverse sections through the median part of a flower of *P. macranthum* (Wilson 1966: 338, Fig. 16) and *P. costaricense* (Fig. 1, H) are very similar.

Besides *P. costaricense*, the only other member of the Canellaceae that occurs in Central America is the relatively widespread, mostly West Indian *Canella winterana*, which reaches the Yucatan Peninsula of Mexico. Otherwise, this family of only about 15 species is known from southern Florida (*Canella*), the West Indies (*Canella*, *Cinnamodendron*, *Pleodendron*), northeastern South America (*Canella*, *Cinnamodendron*), southeastern Brazil (*Capsicodendron*, *Cinnamodendron*), southeastern Africa (*Warburgia*), and Madagascar (*Cinnamosma*). *Pleodendron costaricense*, apparently typical for most New World members of the family (e.g., Zanoni 2004), is of very local distribution, so far known from only two, rather distant sites, along the southern pacific coast of Costa Rica, at 200-300 m elevation. The species itself is disjunct by about 2000 km from its presumed phylogenetically closest rela-

tive, *Pleodendron macranthum* (Puerto Rico).

The fossil record of the Canellaceae is insufficient to reveal much about its biogeographic history, but two genera have been recognized in Tertiary deposits of Latin America. Hollick and Berry (1924) describe leaves of *Canella* from beds estimated as Pliocene in age from Bahia, Brazil, and Graham and Jarzen (1969) report pollen of *Pleodendron* from the middle Oligocene of Puerto Rico.

Although apparently rare, a possible phytogeographic relation between southern Costa Rica (or southern Central America) and the Caribbean is demonstrated by several species (in other families) that we know to be disjunct between Costa Rica and the West Indies, e.g., *Pera oppositifolia* Griseb. (Euphorbiaceae), *Ziziphus chloroxylon* (L.) Oliv. (Rhamnaceae), and *Freziera grisebachii* Krug & Urb. (Theaceae). If we were also to include taxa such as *Colpothrinax* and *Acoelorrhaphie wrightii* (Griseb. & H. Wendl.) H. Wendl. ex Becc. (Arecaceae) that are endemic to the Mesoamerican/Caribbean region, the list would certainly be much larger. Fournier (1966), Gómez P. (1986), and Zamora *et al.* (2004b) also mention this phytogeographic relationship. Within Mesoamerica, recent general floristic work has uncovered Costa Rican species of *Nyssa* and *Tetranema* disjunct with their geographically nearest congeners in Mexico and Honduras, respectively, as well as species of *Amelanchier*, *Bakeridesia*, *Bouvardia*, *Chiangiodendron*, *Deherainia*, *Gymnosporia*, *Hintonia*, *Maytenus*, *Oecopetalum*, and *Reccia* that are disjunct from as far north as Mexico, and no closer than Belize (Zamora *et al.* 2004a). Rather than a direct relationship with South America, as is especially common with species of the wet lowlands of southern Central America, such species as *Pleodendron costaricense* seem to have arrived via a much more complex, northern route.

Within the Canellales (Canellaceae + Winteraceae), the widespread, Neotropical *Drimys granadensis* L.f. (Winteraceae) is *P. costaricense*'s geographically closest relative. It can be found as close as 1000 m upslope and a few km to the east of the *P. costaricense* localities, but probably got there by a much different route, via the ancient, Southern Hemisphere temperate forests (e.g., Berry *et al.* 2004). The discovery of *Pleodendron costaricense* is another data point supporting the growing conclusion (e.g., Burnham & Graham 1999, Wendt 1993) that the forests of Central

America have a more complex origin than previously thought.

HABITAT, DISTRIBUTION AND CONSERVATION. We know of only two mature individuals and one sapling of this species, in the wild. All occur on the Pacific lowlands of southern Costa Rica, in tropical wet forest formation (Tosi 1969), on well-drained soils with red clays. Although both mature individuals produce abundant fruits with seed, we have found only one seedling and have not been able to germinate any seeds. Both of these individuals occur at the edge of roads; the Parrita plant along a much-traveled gravel road, recently improved to provide access to a hydroelectric project, and the Osa plant along a more or less abandoned logging trail (Fig. 3, A & B). None of these individuals occurs on land with a governmental conservation category that prohibits logging.

To say that *Pleodendron costaricense* is rare and endangered is almost an understatement; the formal IUCN Red List rating of this species calculates to be, unambiguously, Critically Endangered (CR D). Although the mature individuals hardly seem reproductively viable, the one known sapling from the Cerro Nara area, and the one we have nurtured from the single seedling encountered, do insert a minor note of hope.

Far too rare to have any known economic use, *Pleodendron costaricense* nevertheless merits all possible effort to bring it back from the verge of extinction. It is a living dinosaur that harbours information about the history of the Earth; its tenuous hold at the edge of roads should make it a poster-child for campaigns to save the biogeographic libraries that such species and the forests around them represent. Some members of the Canellaceae are locally well known in other parts of the world, and especially because of their aromatic essential oils, have been used for condiment, tonic, stimulants, incense, and herbal medicine [e.g., *Canella winterana* - Canella bark, *Cinnamodendron corticosum* Miers - False Winter's bark, *Cinnamosma fragrans* Baill. - Saro oil, *Warburgia sartoris* (Bertol. f.) Chiov. - Pepper bark]. Human nature leads common folk the world over always to ask "what's it used for?" and to assume (formerly to esteem, now more often to suspect) the work of a field botanist as equivalent to "looking for medicines." Sometimes we scientists are caught up in such efforts, witness the recent and passing wave of bioprospecting, but what really drives us is this thrill

of discovery. During the last 15 years, in the course of a general botanical inventory of Costa Rica, aimed, in part, at the production of a modern flora of the country, we have recorded nearly 1000 new species or country records, numerous of them representing significant disjuncts from their previous known ranges or closest relatives (see Zamora *et al.* 2004a for a more complete account, and *e.g.*, Grayum & Hammel 1995, Hammel & Zamora 1990, 1993, for specific examples). Although some are more exciting than others, every single species found new, or recorded new distribution, is full of related bytes of information about the history of life; that is what motivates our science.

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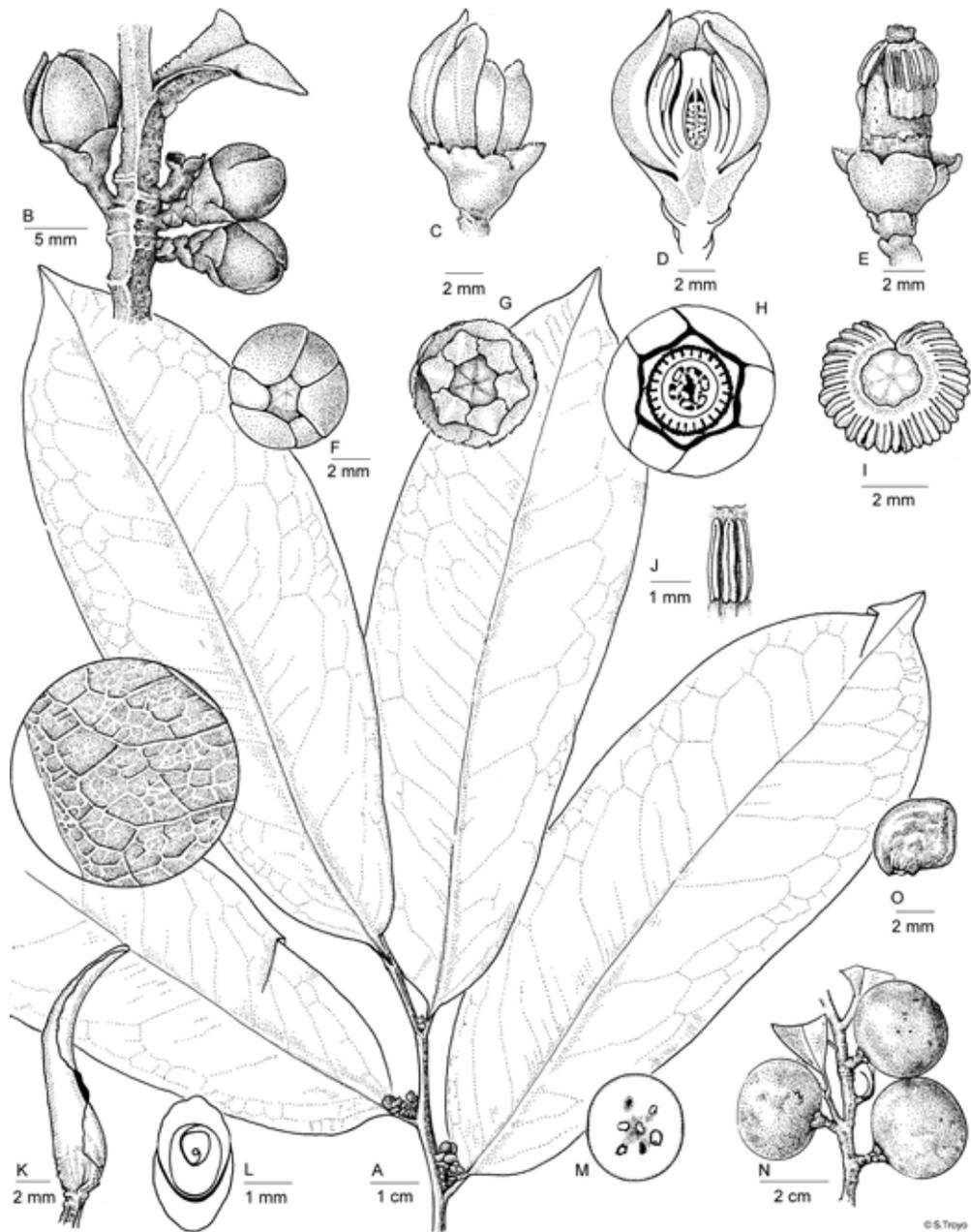


Fig. 1. *Pleodendron costaricense* N. Zamora, Hammel & R. Aguilar. -A. Branch with flower buds. -B. Nearly mature flower and buds on stem below leaf. -C. Lateral view of flower with four petals removed, showing one of the first series and second series, and two of the third. -D. Median longitudinal section of flower. -E. Lateral view of flower with all petals removed showing split and circumscissile androecium. -F. Top view of mature flower. -G. Top view of flower with outer two series of petals removed. -H. Median transverse section of flower. -I. Top view of androecium and stigma. -J. Lateral view of three thecae. -K. Terminal bud. -L. Transverse section of terminal bud. -M. Median transverse section of fruit. -N. Branch with fruits. -O. Seed. (A-L from the type, Zamora *et al.* 2986; M-O from Aguilar 5705.).

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Table 1. Summary of distinguishing floral characters of genera of Canellaceae, and of *Pleodendron costaricense*. Data compiled from Baillon (1882), Little *et al.* (1988), Occioni (1943), J. Salazar (pers. com.), Schatz (2001), Tieghem (1899), Wilson (1966).

	No. Petals	No. of Series of Petals	Fusion of Petals	No. of Thecae	No. of Carpels
<i>Canella</i>	5	1	basally connate	20	2
<i>Capsicodendron</i>	6 or 8	2	free	12--20	3
<i>Cinnamodendron</i>	6 or 10	2	free	14--20	2--4
<i>Cinnamosma</i>	3--6	1	connate (corolla salverform)	14--20	3--5
<i>Pleodendron macranthum</i>	12	4 (2)	free	24	6
<i>Pleodendron costaricense</i>	12	3 (2)	free	24	6
<i>Warburgia</i>	10	2	free	20	5



Fig. 2. *Pleodendron costaricense* N. Zamora, Hammel & R. Aguilar. Branch with mature flowers seen from above. (Photo from type gathering, Zamora *et al.* 2986, by R. Aguilar.)

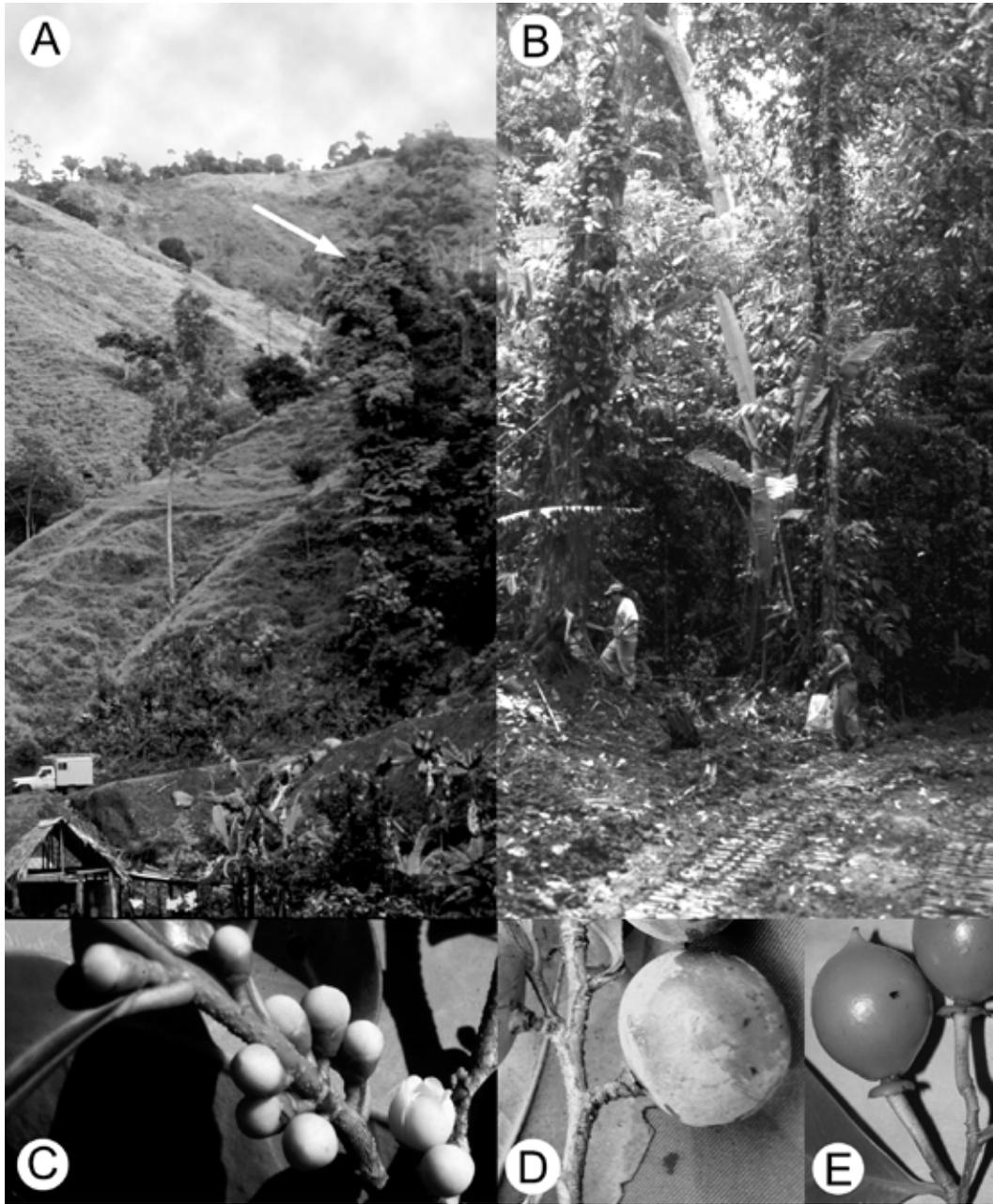


Fig. 3. A-D, *Pleodendron costaricense* N. Zamora, Hammel & R. Aguilar. -A. Parrita locality and individual (arrow). -B. Osa locality and individual (trunk in front of R. Aguilar, person on left; other person is L. Bohs). -C. Branch with flower buds and open flower. -D. Fruiting branch. -E. *Pleodendron macranthum* (Baill.) Tiegh. Fruiting branch (Salazar *et al.* 2409; BH, JBSD).