**Systematics of Croizatia (Euphorbiaceae)**

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**ABSTRACT.** Croizatia, a genus known from Panama and Venezuela (Euphorbiaceae, Phyllanthoideae), has been considered closely related to the Old World genus Actephila. However, the spinose pollen of Croizatia is very different from the semitectate pollen of Actephila, and the two genera appear clearly distinct. The pollen morphology of Croizatia suggests a possible relationship with the Oldfieldioideae, and it may be the closest extant taxon to a connecting link between the subfamilies. Three species of Croizatia are tentatively recognized, including a new species, Croizatia panamensis; but species delimitations must be regarded as provisional.

The Euphorbiaceous genus Croizatia (Steyermark 1952), named for the eminent student of the systematics of the Euphorbiaceae, Leon Croizat-Chaly (Steyermark 1983), has long been regarded as of uncertain affinity. The first species published, C. neotropica (Steyermark 1952), was described from a fruiting specimen collected in the state of Anzoátegui, Venezuela. Later, Steyermark (1978) added a second species, C. naiguatensis, from another fruiting specimen found on the Cerro Naiguata, Distrito Federal, Venezuela.

Croizat (in Steyermark 1952) stated that the affinities of Croizatia were close to the Old World genus Actephila. In 1978, when C. naiguatensis was described, the flowers of both species were still unknown, and the affinities of the genus therefore remained problematical. In the most recent enumeration of Euphorbiaceous genera (Webster 1975), Croizatia was omitted because of its dubious status; but in the synoptic arrangement of tribes of Phyllanthoideae (Webster ined.) its placement appeared to be with either the Wielandieae or Amanoeae. Levin (1984), in a survey of leaf characters in the Phyllanthoideae, reports a greater similarity of Croizatia to Savia and Blotia than to Actephila.

Recently in June 1983, our knowledge of the reproductive morphology of Croizatia improved dramatically due to the collection of flowering specimens of C. naiguatensis. The petaliferous flowers (fig. 1) resemble those of Actephila, as Croizat had predicted; there is an especial similarity to the flowers of the widespread paleotropical species Actephila excelsa (Dalz.) Muell. Arg. The major floral differences observed are the much more reduced petals of staminate flowers and the twice bifid style tips of Croizatia. Although there are other diagnostic characters pointed out by Steyermark (1952), such as the enlarged columella of Croizatia, the overall gross resemblance to Actephila is striking. Indeed, Gentry (1982) has attributed to Rodriguez an unpublished combination under Actephila for C. neotropica and quotes Rodriguez as stating that Croizatia is indistinguishable from Actephila.

Despite the uncertainty regarding the generic status of Croizatia, the floral, fruit, and leaf characters appear to provide sufficient distinctions to maintain it as separate from Actephila. Furthermore, examination of the pollen grains with scanning electron microscopy shows that the pollen of Croizatia (figs. 2, 3) is very different from that of Actephila (fig. 4). The pollen grains of A. collinsae are 40–49 (x = 46) µm in diameter, subprolate, and tricolporate with large, well-defined colpi; the exine is rather finely semitectate-reticulate. These characters agree rather well with the light microscopic observations on other species of Actephila: A. excelsa (Punt 1962), A. nitidula Gagnep., and A. ovalis Gagnep. (Köhler 1965). Both Punt and Köhler have noted the resemblance of the pollen grains of Actephila to those of Andrachne (s.l.). In contrast, the pollen grains of Croizatia naiguatensis are spherical, 46–56 (x = 51) µm in diameter, with the colpi greatly shortened (ca. 10 µm long), the lalongate germ pore well developed (ca. 10 µm broad); the exine is tectate-perforate and ornamented with conical, sharply-pointed spines ca. 3–4 µm high.
Table 1. Comparison of morphological characters of Croizatia with those of Phyllanthoideae and Oldfieldioideae.

<table>
<thead>
<tr>
<th>Phyllanthoideae</th>
<th>Croizatia</th>
<th>Oldfieldioideae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phyllatoxy</td>
<td>alternate</td>
<td>alternate, opposite, or whorled</td>
</tr>
<tr>
<td>Stipules</td>
<td>usually +</td>
<td>+, reduced, or 0</td>
</tr>
<tr>
<td>Petals</td>
<td>+ or 0</td>
<td>0</td>
</tr>
<tr>
<td>Staminate disk</td>
<td>mostly extrastaminal</td>
<td>extrastaminal, mostly intrastaminal or 0</td>
</tr>
<tr>
<td>Pollen</td>
<td>mostly 3-4-colporate, not echinate</td>
<td>brevicolpor-ate, echinate</td>
</tr>
<tr>
<td>Ovules</td>
<td>anatropous/hemitropous</td>
<td>hemitropous</td>
</tr>
<tr>
<td>Styles</td>
<td>mostly bifid</td>
<td>twice bifid</td>
</tr>
<tr>
<td>Seeds</td>
<td>ecarunculate</td>
<td>ecarunculate</td>
</tr>
<tr>
<td>Endosperm</td>
<td>+/0</td>
<td>0</td>
</tr>
</tbody>
</table>

This striking difference between the pollen grains of Croizatia and those of Actephila reinforces the impression, based on gross morphological characters, that the two genera are quite distinct.

On the other hand, the echinate, tribrevicolporate pollen found in Croizatia is clearly similar to pollen of Oldfieldioideae as that group was palynologically defined by Köhler (1965) and taxonomically delimited by Webster (1967). There is a close resemblance between the pollen of C. naiguatensis and that of Tetracoccus dioicus Parry (fig. 5) and Podocalyx loranthoides Klotzsch (fig. 6), which are considered to be two of the more primitive members of the Oldfieldioideae on the basis of floral and vegetative characters (Webster ined.). Podocalyx differs from Croizatia in having tetraporate pollen with a tectate-imperforate exine and in its distinctly smaller diameter (ca. 30 µm), while Tetracoccus differs in having 4- to 6-colpoidorate pollen and a tectate-regulate exine with gemmace on the ridges.

Within the Phyllanthoideae, true spines of the “Oldfieldioide” type have heretofore been unrecorded. The pollen grains of some species of Amanoa are irregularly baculate; the sculptural elements are rod-like with the apex sometimes expanded or tapered (fig. 7). The different structure of the “spines” in both Croizatia and Amanoa suggests that the resemblance may be due to convergence and, therefore, not indicative of a close phylogenetic relationship. Another taxon within the Phyllanthoideae which has pollen that bears some resemblance to pollen of the Oldfieldioideae is Securinega durissima J. F. Gmel., illustrated by Webster (1984b); the pollen is oblate, tricolporate with colpi short but not greatly reduced and with a tectate-regulate exine with supratectal spinulose sculptural elements. Although Securinega has been traditionally placed in the Phyllanthoideae, this appears to have been due to the erroneous inclusion of species properly referable to Flueggea (Webster 1984a). The pollen of the type species S. durissima is quite anomalous within the tribe and resembles to a much greater extent pollen of members of the Wielandieae, such as Discocarpus. The “S. durissima” pollen type might conceivably bear an ancestral relationship to typical “Oldfieldioide” pollen; however, much further study is needed concerning the taxonomic position of S. durissima and other Wielandieae before possible links to the Oldfieldioideae can be substantiated.

When the characters of Croizatia are tabulated in comparison with the Phyllanthoideae and Oldfieldioideae (table 1), it clearly agrees better with the Phyllanthoideae in five characters (petals, staminate disk, ovules, styles, and development of endosperm) and with the Oldfieldioideae in only one (pollen). However, most of the resemblance to the Phyllanthoideae involves the common possession of primitive (plesiomorphic) characters. When only derived (apomorphic) characters are considered, Croizatia has two in common with Phyllanthoideae (hemitropous ovules, exalbuminous seeds) and one with Oldfieldioideae (echinate pollen).

In table 2, the characters of Croizatia are contrasted with two putatively primitive genera, Wielandia and Podocalyx, in the subfamilies Phyllanthoideae and Oldfieldioideae. Here the
TABLE 2. Comparison of morphological characters of *Croizatia* with a primitive genus of Phyllanthoideae (*Wielandia*) and a primitive genus of Oldfieldioideae (*Podocalyx*).

<table>
<thead>
<tr>
<th>Character</th>
<th>Wielandia</th>
<th>Croizatia</th>
<th>Podocalyx</th>
</tr>
</thead>
<tbody>
<tr>
<td>Petals</td>
<td>+</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Staminate anther disk</td>
<td>extrastaminal, annular</td>
<td>extrastaminal, annular</td>
<td>0</td>
</tr>
<tr>
<td>Anthers</td>
<td>introrse</td>
<td>introrse</td>
<td>extrorse</td>
</tr>
<tr>
<td>Pollen</td>
<td>3-4-colporate, not echinate</td>
<td>3-brevicolporate, echinate</td>
<td>4-pororate, echinate</td>
</tr>
<tr>
<td>Ovary</td>
<td>glabrous</td>
<td>glabrous</td>
<td>pubescent</td>
</tr>
<tr>
<td>Ovules</td>
<td>anatropous</td>
<td>hemitropous</td>
<td>anatropous</td>
</tr>
<tr>
<td>Styles</td>
<td>bifid</td>
<td>twice bifid</td>
<td>stigmatiform</td>
</tr>
<tr>
<td>Seeds</td>
<td>not black and shiny</td>
<td>not black and shiny</td>
<td>black and shiny</td>
</tr>
<tr>
<td>Endosperm</td>
<td>0</td>
<td>0</td>
<td>+</td>
</tr>
</tbody>
</table>

Resemblance with *Wielandia* is especially striking, since there are six characters in common that are not shared with *Podocalyx*. *Actephila*, the genus resembling *Croizatia* in aspect, shares these same characters. In contrast, *Podocalyx* shares only a single character (pollen exine ornamentation) not possessed by *Wielandia* and *Actephila*. However, *Croizatia* has only one derived character in common with *Wielandia* (lack of endosperm) and one with *Podocalyx* (echinate pollen).

The available morphological data on the Phyllanthoideae are still so incomplete that at present it would be premature to attempt a detailed cladistic or phenetic analysis. For the present, we are dependent on the character contrasts presented in tables 1 and 2, and unfortunately they tell discordant stories. *Croizatia* shares two derived characters (hemitropous ovules and exalbuminous seeds) with the Phyllanthoideae (although only one with any single genus), while it shares only the echinate pollen character with the Oldfieldioideae. One could argue that on cladistic, as well as phenetic, grounds placement of *Croizatia* in the Phyllanthoideae is indicated. On the other hand, the single pollen character shared with Oldfieldioideae involves a complex of features (spine morphology, shortening of colpus, germ pore configuration), and it seems rather less likely to have evolved independently in different lineages. We thus end on the horns of a dilemma of "quantity" versus "quality" in evaluation of derived characters.

These problems in determining the phylogenetic position of *Croizatia* also raise difficulties in demarcating the boundary between the subfamilies Phyllanthoideae and Oldfieldioideae. If *Croizatia* indeed represents an ancestral link to the Oldfieldioideae, its inclusion on cladistic grounds would result in the introduction of several discordant characters (petaliferous flowers, extrastaminal disk, hemitropous ovules, bifid styles, and exalbuminous seeds) into the subfamilial diagnosis of the Oldfieldioideae. However, its placement in the Phyllanthoideae would not change the status of the Phyllanthoideae as a paraphyletic group, since that subfamily would be paraphyletic in any circumscription (due to its having given rise to the subfamily Acalyphoideae as well) that has been proposed up until now. In the face of inadequate data and the problems of analysis discussed above, it seems expedient to assign *Croizatia* provisionally to the Phyllanthoideae, where it can be placed between *Blotia* and *Actephila*.

Although these problems of classification are challenging and interesting, study of the morphology of *Croizatia* is most significant in elucidating phylogenetic and biogeographic relationships. The link between *Croizatia* and *Podocalyx* clearly suggests that the Oldfieldioideae is of South American origin, even though the living taxa now occur widely in other parts of the southern hemisphere (Africa, Madagascar, Ceylon, Indonesia, and Australasia). *Croizatia* and *Actephila* are vicariants of West Gondwanaland and East Gondwanaland, respectively (sensu Raven and Axelrod 1974). The progenitor of *Croizatia* presumably migrated from Africa/Madagascar, where the primitive Phyllanthoideae are concentrated, across a narrower Atlantic; but since *Actephila* is known...
only from India to Australasia, other now-extinct taxa may have been involved. Martin (1974, 1982) indicates that relatively advanced Oldfieldioideae of the Austrobozux alliance were present in Australasia in the Paleocene, so that the initial differentiation of Croizatia would appear to have been in the late Cretaceous.

### Systematic Treatment

**CROIZATIA Steyermark**, Fieldiana 28:308, fig. 57. 1952.—Type: Croizatia neotropica Steyermark.

Dioecious trees or shrubs; indumentum simple. Leaves alternate, entire, pinnately veined, without embedded glands, petiolate; stipules deciduous or persistent. Flowers in axillary clusters; bracts inconspicuous. Staminate flowers pedicellate; sepals 5, imbricate, entire; petals 5, much shorter than sepals, pubescent, entire; disk annular, glabrous; stamens 5, free, anthers intorse; pollen grains globose, exine with conical spines; pistillode trifid. Pistillate flowers pedicellate; sepals 5, imbricate, entire, persistent in fruit; petals 5, much shorter than sepals, pubescent, entire; disk annular, glabrous; ovary pubescent, 3-locular; styles free, slender, twice bifid; ovules paired in each locule, hemitropical. Fruit a capsule; columella distally expanded into 3 broad papery wings; seeds paired or solitary in each locule, ecarunculate; endosperm absent; cotyledons greenish, contortuplicate, much broader than and about as long as the radicle.

### Key to the Species

Fruiting pedicels not over 2 cm long; lateral nerves of leaf blades 7–10. 2. C. naiguatensis

Fruiting pedicels over 2 cm long; lateral nerves of leaf blades 12–15 on each side. 1. C. neotropica

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1. **CROIZATIA NEOTROPICA Steyermark**, Fieldiana 28:309, fig. 57. 1952.—Type: Venezuela, Anzoátegui, Quebrada Seca, E of Bergantín, 18 Mar 1945, Steyermark 61523 (holotype: VEN!).


2. **CROIZATIA NAIGUATENSIS** Steyermark, Brittonia 30:40, fig. 1. 1978.—Type: Venezuela, Distrito Federal, Cerro Naiguatá, upper reaches of Quebrada del Mata de Platan, 2000 m, 7 Dec 1973, S. Tillett, G. & B. Morillo & B. Manara 82 (holotype: VEN!; isotype: DAV!).

Tree 5–7 m high; leaf blades elliptic to obovate, acute or obtuse (less often rounded) at tip, long-attenuate at base, 9–21 cm long, 4–9 cm broad, glabrous or inconspicuously strigose beneath, lateral nerves 7–10 on each side, somewhat prominent with the more delicate tertiary veinlet network; petals 4–9 mm long, stout, glabrous or strigose; stipules scarious, striate, brownish, 7 mm long, deciduous. Staminate flowers in dense axillary clusters; pedicel 3–4 mm long, hirtellous; sepals 5, elliptic, entire, 4–4.5 mm long, 2.5–3 mm broad; petals 5, obovate, subentire, densely long-ciliate, 1–1.3 mm long, and broad; disk massive, smooth and glabrous, 2.5–3 mm across; stamens 5, filaments 2.2–2.5 mm long, hirsutulous below; anthers elliptic, 1.2–1.4 mm long; pistillode 3-lobed, hirsutulous, 1.8–2.2 mm high. Pistillate flowers solitary; pedicel 8–12 mm long in fruit; sepals 4 or 5, lanceolate, obtuse or acute to rounded, strigillose, becoming reflexed and persistent in fruit, 8–10 mm long, 2–3 mm broad; petals (4)5, broadly obovate or suborbicular, ca. 1 mm long and broad, densely ciliate; disk cupuliform, glabrous, entire, ca. 0.4 mm high and 3.5 mm broad; ovary sericeous; styles spreading, 2.8–3 mm long, twice bifid, the unbranched portion 1.5–2 mm long, the primary branches 1.2–1.5 mm long, ultimate tips 0.3–0.5 mm long. Capsule oblate, 3-lobed, 1.3–1.4 cm high, 1.7–2 cm broad, strigillose, reticulate; columella 7–8 mm long, dilated at apex into 3 obovate-oblong wings rounded at apex, 7 mm long, 5 mm broad. Seeds unknown.

Additional collection. **VENEZUELA. Vargas**: trail from Pico de Naiguatá to town of Naiguatá, Fila del...
3. Croizatia panamensis Webster, sp. nov. (fig. 8).—Type: Panamá, Panamá, primary forest along road from El Llano to Cartí-Tupile, 300–500 m, 30 Mar 1973, L. L. Liesner 1279 (holotype: MO!; isotype: DAV!).

Ab C. neotropica differt pedicellis brevioribus seminibus parvioribus, ab C. naiguatense differt foliis majoribus stipulis persistentibus, pedicil- lis longioribus.

Shrub or small tree 1–6 m high, usually with a single main stem; leaf blades chartaceous, gla- brous or sparsely strigose-hispidulous beneath, obovate, abruptly short-acuminate, basally atten- nuate, 22–45 cm long, 5–12 cm broad, with ca. 15 arcuate-ascending lateral nerves connected by intramarginal loops, veins (and to a lesser extent) veinlets prominulous beneath; petioles 0.5–1 cm long and 3–4 mm thick; sti- pules more or less persistent, oblong-lanceo- late, acuminate, ribbed sericeous, 10–20 mm long, 6–7 mm broad. Flowers not observed. Fruiting pedicels hirtellous, 2.5–3.5 mm long, 1.2–2 mm thick; sepals more or less persistent in fruit, reflexed, elliptic-lanceolate, acute or subacute, 8–9 mm long, 3–3.2 mm broad, exter- nally hispidulous; columella ca. 8–9 mm high, 10–11 mm broad; seeds trigonous, smooth, brownish, 7.2–10 mm long, 5.3–6.5 mm broad, hilum medial, ca. 2 mm broad; cotyledons ca. 10 mm long, radicle ca. 5 mm long.

Additional collections. COLOMBIA. Chocó: Villa- conto, cerca de los ríos Quito y Palermo, 120 m, 1
This species is proposed with some hesitation because of the lack of flowering material. However, it appears to differ from Croizatia neotropica and C. naiguatensis in habit (the scarcely branched stems contrasting with both other species) and in the more-or-less persistent stipules. It diverges from C. neotropica in its shorter strigillose fruiting pedicels and smaller seeds, and from C. naiguatensis in its larger leaves and longer fruiting pedicels. Until flowering material of both C. panamensis and C. neotropica is collected, further comparisons would be premature.

A very distinctive collection from Napo Province, Ecuador, Öllgaard et al. 38956 (AAU), resembles Croizatia panamensis, as pointed out by Dr. Michael Huft (pers. comm.). However, although it has the elongated persistent stipules and oblanceolate leaves of the Panama species, the Ecuadorian plant has much longer fruiting pedicels and more acuminate sepals. It may well prove to be a different species, but it does not seem advisable to describe it as new on the basis of the single collection.

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LITERATURE CITED


