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Systematics and Palynology of *Picrodendron* Further Evidence for Relationship with the Oldfieldioideae (Euphorbiaceae)

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SYSTEMATICS AND PALYNOLOGY OF PICRODENDRON:
FURTHER EVIDENCE FOR RELATIONSHIP WITH
THE OLDFIELDIOIDEAE (EUPHORBIACEAE)

W. J. HAYDEN, W. T. GILLIS†, D. E. STONE,
C. R. BROOME, AND G. L. WEBSTER

ALTHOUGH KNOWN to botanical science for 285 years, the genus *Picrodendron* Planchon has been poorly understood for most of this time. The most pervasive problem has been that of discerning familial relationships, and there have been additional difficulties in typifying the generic name (Hayden & Reveal, 1980) and in distinguishing its three nominate species. This paper provides a systematic treatment for *Picrodendron* and demonstrates its relationships with Euphorbiaceae subfam. Oldfieldioideae Köhler & Webster as evidenced by data on gross morphology, palynology, anatomy, and cytology.

Picrodendron captured the attention of Dr. William T. Gillis while he was pursuing floristic studies of the Bahama Islands. During the decade preceding his death, Gillis accumulated a considerable amount of information on this problematic genus; he was attempting to complete this long-standing project in the weeks before he died in June, 1979. It has been a privilege tempered with sadness for one of us (W. J. H.) to prepare this paper from Gillis's notes and the contributions that he had solicited from the other authors. Herbarium and field studies reported here were performed by Gillis and form the basis for much of what appears in the generic description and the sections on biogeography and economic uses; taxonomic judgment at the species level is also Gillis's. Broome and Stone contributed descriptions of pollen and most of the discussion concerning the Juglandaceae; information on relationships with the Euphorbiaceae was provided by Webster.

This paper is a tribute and memorial to Gillis, an indefatigable student of the Bahama flora.

MATERIALS AND METHODS

Taxonomic treatment of *Picrodendron* is based on examination of numerous specimens in the wild, in cultivation, and in the herbarium. Herbarium specimens examined are listed in the APPENDIX.

Pollen descriptions are based upon examination of the following specimens. *Austrobuxus carunculatus* (Baillon) Airy Shaw: New Caledonia, Quinne-Tal, Stauffer & Blanchon 5751 (DUKE); New Caledonia, Kouébuni, Hürlimann 571 (US). *Austrobuxus eugeniifolius* (Guillaumin) Airy Shaw: New Caledonia, Guil-

laumin & Baumann-Bodenheim 12908 (US). *Mischodon zeylanicus* Thwaites: Sri Lanka, *De Silva 28* (US). *Oldfieldia africana* Bentham & Hooker f.: Ivory Coast, *Voorhoeve 1963* (MO). *Picrodendron baccatum* (L.) Krug & Urban: Cuba, Santiago, *Clemente 6587* (GH, US); Jamaica, *Harris 12516* (US). *Piranhea longepedunculata* Jablonski: Venezuela, *Blanco 299* (US). *Tetracoccus dioicus* Parry: United States, California, *Munz 12614* (MO). *Tetracoccus hallii* Brandegee: United States, California, *Dressler 1211* (MO); Arizona, *Kearney & Harrison 7530* (US).

For brightfield microscopy, dried pollen was acetolyzed, treated with potassium hydroxide, and mounted in glycerine jelly. Since the pollen grains were nearly spherical, diameter measurements were made without regard to the polar axis; a minimum of 30 grains were measured at $\times 1000$ with a $\times 40$ high dry objective and $\times 25$ oculars. Photomicrographs of acetolyzed grains were taken with a $\times 90$ oil immersion apochromatic objective (n.a. 1.32) and a $\times 10$ negative ocular at $\times 1500$ on Kodak Ortho or Pan sheet film, or at $\times 370$ on Kodak 35 mm High Contrast Copy film. For SEM observations, acetolyzed pollen grains were air dried from 70% ethanol and then coated with gold-palladium (60:40) in a vacuum evaporator. For TEM, dried pollen was fixed for 10–12 hours in 2% glutaraldehyde buffered with 0.1 M Sørensen's phosphate buffer at pH 7.0, washed, and finally postfixed for 2 hours in 2% phosphate-buffered osmium tetroxide. Immediately after stepwise dehydration in ethanol, the pollen was embedded in Spurr resin, standard formulation. Thin sections were poststained either in aqueous potassium permanganate solution or in a uranyl acetate–lead citrate combination.

Observations of seedling morphology in *Picrodendron* were obtained from greenhouse-grown seedlings at the University of Richmond, Richmond, Virginia. The seeds came from plants cultivated at the Fairchild Tropical Garden and originally collected from Driggs Hill, South Andros, Bahama Islands. Voucher specimens for these plants are *Gillis 10924*, *10975*, and *11031* (AAH, FTG, IJ).

TAXONOMIC HISTORY

A century and a half elapsed between the first published record of *Picrodendron* by Sloane (1696) as “*Nux juglans trifolia*. . .” and its ultimate recognition as a distinct genus (Planchon, 1846). It is not surprising, perhaps, that colonial Europeans, overwhelmed by the novelty and diversity of the neotropical flora, associated this plant with the familiar walnut, since there are certain gross resemblances. Consider, for example, the much-quoted but uncritical passage from Browne (1756) describing the “Jamaica walnut”: “The outward part of the fruit is soft and pulpy, when ripe; but the hard ligneous shell, and the partitions and lobes of the seed, as well as parts of the flower, agree perfectly with the general characteristics of the genus.” Linnaeus apparently saw neither living nor herbarium specimens of *Picrodendron*, which he nevertheless named *Juglans baccata* (Linnaeus, 1759), referring to Browne (1756), who had in turn referred to Sloane's (1725) illustration (see FIGURE 1). Amazingly, this link with the Juglandaceae has persisted for over two and a half centuries despite



FIGURE 1. Lectotype of *Picrodendron baccatum* (reproduced from H. Sloane, *A Voyage to the Islands Madera, Barbados, Nieves, S. Christophers and Jamaica* 2: t. 157, fig. 1. 1725).

having been based on very superficial analyses and a decidedly nondefinitive illustration.

Besides being considered a walnut, *Picrodendron* has also been treated as *Tapia* (i.e., *Crateva* L.) (Capparaceae), by Catesby (1734); *Schmidelia* (i.e., *Allophylus* L.) (Sapindaceae), by Richard (1845); and *Rhus* (Anacardiaceae) by Macfadyen (1837). Actually, Macfadyen had misapplied De Candolle's (1825) name *Rhus arborea* (basionym: *Toxicodendron arboreum* Miller). The names of Miller and De Candolle apply to *Allophylus*, but Macfadyen's specimen unmistakably represents what is now known as *Picrodendron*. Macfadyen's error unfortunately threw the application of Planchon's (1846) name *Picrodendron* into uncertainty, for Planchon based the genus on both an authentic Macfadyen specimen (κ!) and the basionym *Rhus arborea* DC. Planchon's species name, *P. arboreum*, is therefore a synonym of *Allophylus* L. Prior to the Sydney Congress of 1981, however, the Code of Botanical Nomenclature was unclear whether, in such a situation, the name *Picrodendron* should be typified by the species represented in the literature citation (i.e., *Rhus arborea/Allophylus*) or by the species represented by the specimen cited (i.e., *Macfadyen s.n.*). Consequently, Hayden and Reveal (1980) proposed to conserve *Picrodendron* from the 1859 publication of Grisebach; full particulars can be found in that paper. However, revisions incorporated into the Code at Sydney (see *Taxon* 30: 103–105, 200–207, 904–911) now permit a different course. New Article 10.4 states, "By conservation, the type of the name of a genus can be a specimen used by the author in the preparation of the protologue, other than the type of a name of an included species." Further, new Article 14.8 reads, "A name may be conserved with a different type from that designated by the author or determined by application of the Code." Thus, we herein retain Planchon's name, to be typified, by conservation, by Macfadyen's specimen of *Picrodendron baccatum*.

Picrodendron has been treated variously as a single species or as two or three insular endemics. Grisebach (1859) realized that the Jamaican *Juglans baccata* L. and *Picrodendron arboreum* Planchon were conspecific with the Cuban *Schmidelia macrocarpa* A. Rich. Grisebach called these plants *Picrodendron juglans*, a superfluous name that was also applied to plants from the Bahamas (Gardiner & Brace, 1889). Urban (1893) restored Linnaeus's epithet, forming *Picrodendron baccatum* (L.) Krug & Urban for Jamaican and Cuban elements, but distinguished Bahamian material as var. *bahamense* Krug & Urban. Britton (1906) preferred to treat Cuban and Bahamian elements as one species, *P. macrocarpum* (A. Rich.) Britton.

Small (1917) distinguished plants from Hispaniola as a third species, *Picrodendron medium* Small, and his concepts of the three species can be summarized as follows: *P. baccatum* from Jamaica, characterized by dark leaflets with acute apices, long fruiting pedicels, and spherical fruits with thin endocarp; *P. macrocarpum* from Cuba and the Bahamas, characterized by blunt, pale leaflets, short fruiting pedicels, and somewhat ovoid fruits with thick endocarp; and *P. medium* from Hispaniola, characterized by leaflets similar to those of *P. baccatum*, and endocarp similar to that of *P. macrocarpum*. Small's distinctions seem trivial; moreover, these three epithets have been used frequently in senses

other than those outlined by Small (Gómez de la Maza & Roig y Mesa, 1916; Urban, 1920; Barker & Dardeau, 1930; Moscoso, 1943; Howard, 1955; Adams, 1972).

As noted above, early concepts of the relationships of *Picrodendron* varied widely, and disparate taxonomic associations have persisted throughout most of its subsequent history. Varying opinions regarding its relationships include placement in or association with the Simaroubaceae (Planchon, 1846; Bentham & Hooker, 1862; Urban, 1920; Barker & Dardeau, 1930; Moscoso, 1943), Juglandaceae (Grisebach, 1859), Burseraceae (Grisebach, 1866), Terebinthaceae (Hallier, 1908), Picrodendraceae (Small, 1917, and numerous recent authors), Euphorbiaceae (Fawcett & Rendle, 1917; Thorne, 1976; Webster, 1975; Takhtajan, 1980; Cronquist, 1981), and Bombacaceae (Hallier, 1921). The family Picrodendraceae has been assigned to the Juglandales (Cronquist, 1968; Hutchinson, 1973), Rutales (Scholz, 1964; Takhtajan, 1966), and Euphorbiales (Novák, 1961; Takhtajan, 1969; Airy Shaw, 1973; Cronquist, 1978).

ECONOMIC IMPORTANCE

There are several recorded uses of *Picrodendron*, all of minor economic consequence. In Hispaniola the plants are commonly grown as a windbreak. In Jamaica the fruits are occasionally eaten, although Fawcett and Rendle (1920) stated that this should be done with caution. León and Alain (1951) reported that the leaves are eaten by animals. Curiously, one of its common names in the Dominican Republic, "mata becerro," means "calf killer." Jiménez (pers. comm.) reported that in the Dominican Republic leaves of *Picrodendron* are reduced to powder and used to kill bedbugs and lice. Sawyer (1955) reported that on Great Inagua a tea made from the leaves is used in the treatment of poisoning from eating fish; additional medicinal uses were reported in Roig y Mesa (1945). The viscid exocarps of *Picrodendron* fruits have been employed for their saponin in washing clothes. Record and Hess (1943) mentioned that the wood, which finishes smoothly and is resistant to decay, has been used in naval construction and turnery.

SYSTEMATIC TREATMENT

Picrodendron Planchon, London J. Bot. **5**: 579. 1846, nom. cons. prop. TYPE: "Jamaicae, Mac Fadyen, in herb. Hook.," typ. cons. [*Juglans baccata* L. = *P. baccatum* (L.) Krug & Urban].

Tree to 12 m, dioecious (rarely monoecious); bark rough, bitter to taste, gray, furrowed to shaggy in age; shoots finely pubescent. Leaves alternate, palmately trifoliolate, 1–2 dm long, deciduous prior to flowering; stipules inconspicuous, early deciduous; petioles 4–10 cm long, minutely pubescent; leaflets with the petiolules 0.5–2.5 cm long, joined at base, the blades 1.5–11 cm long, elliptic, oblong, ovate, or obovate, obtuse to emarginate apically, unequal basally on lateral leaflets, otherwise symmetrical, pinnately veined, finely reticulate, with the upper surface glabrous to glabrate and occasionally with tiny hairs proximally on midvein, the lower surface slightly paler green than the upper, glabrate

to puberulent but densely pubescent on major veins. Flowering first during third year. Staminate flowers in stalked, puberulent catkins borne in axils of leaves of previous season's growth, appearing before or with leaves in compressed heads, elongating to loosely clustered spikes; flowers greenish yellow, subtended by (1 to) 3 (to 7) bracts, these imbricate, to 1.5 mm long, with central one larger and overlapping laterals, acute, deltoid; perianth absent; stamens 3 to 54, on convex hemispherical receptacle, the filaments free, shorter than anthers (less than 0.5 mm), short-subulate, glabrous, the anthers 2-celled, basifixed, to 1.5 mm long, oval, notched at apex and cordate at base, sparingly puberulent especially at tip, dehiscing longitudinally when mature, slightly extrorse; pollen spinose-verrucate, 5- to 8-porate; pistil absent. Pistillate flowers axillary, borne singly on shoots of current season; pedicels 2–4 cm long, abruptly widened below the finely pubescent, concave receptacle; flowers green, subtended by 4 or 5 valvate bracts, these ascending-recurvate, sepeloid, \pm unequal, 2.5–8 mm long, lanceolate, gland bearing, remotely toothed or ciliate; staminodes absent; ovary superior, sessile, ovoid, 2-carpellate, naked; the style terminal, slightly longer than ovary, columnar, the stigmas 2, divergent, longer than style, stout-subulate, with revolute margins; ovules 2 per locule, pendulous from central axis, anatropous, the raphe ventral, the integuments 2, the obturator cushionlike, reddish brown, attached to placenta above ovules, covering micropyles, withering in fruit. Fruits smooth, 2-locular, indehiscent, globose to ovoid drupes, 1.5–2.5 cm long, yellow-orange to yellowish green at maturity, nodding, dry black; exocarp thin, fleshy, with numerous vesicles bearing bitter juice; endocarp 1.5–2 mm thick, woody to bony, brittle, marked by 4 equidistant longitudinal lines. Seed(s) 1 (all but 1 ovule usually aborting) (rarely 2, with 1 in each locule), nearly terete to irregularly ovoid; endosperm lacking; testa membranaceous, enclosed between folds of cotyledons; hypocotyl and micropyle superior; epicotyl large, turned back on funicle at right angles to cotyledons; cotyledons plicate, corrugated; nucellus convoluted.

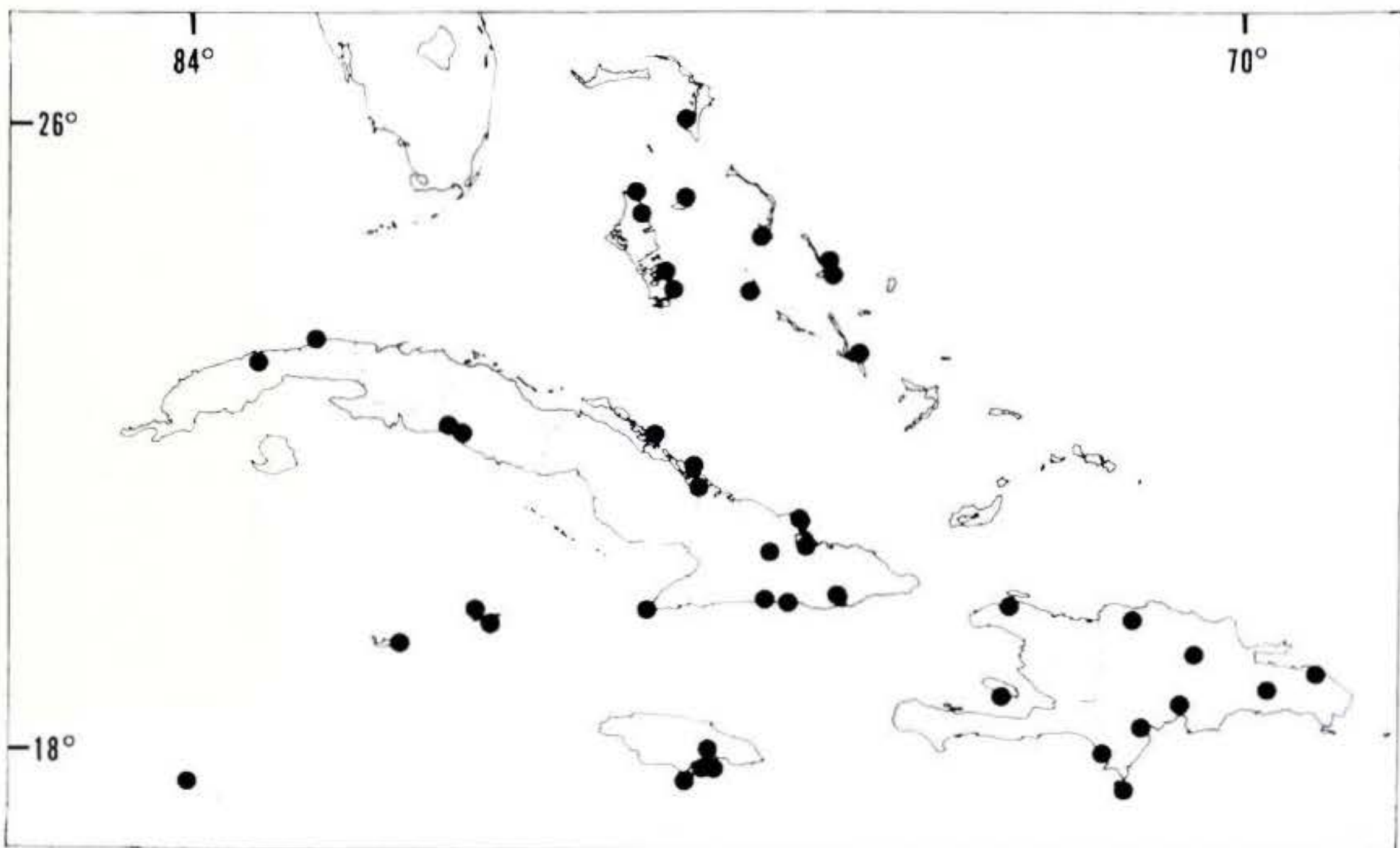
A monotypic neotropical genus found on the Bahama Islands, Cayman Islands, Cuba, Hispaniola, Jamaica, and the Swan Islands (see MAP 1).

Picrodendron baccatum (L.) Krug & Urban, Bot. Jahrb. Syst. **15**: 308. 1893. *Juglans baccata* L. Syst. Nat. ed. 10. 1272. 1759. LECTOTYPE: Sloane, Voy. Isl. Madera, Barbados, Nieves, S. Christophers & Jamaica **2**: t. 157, fig. 1. 1725. The type is in the Sloane Herbarium, H.S. 5: 49 (BM!). *Picrodendron juglans* Griseb. Fl. Brit. W. Indian Is. **2**: 177. 1859, nom. superfl. FIGURE 2.

Schmidelia macrocarpa A. Rich. in Sagra, Hist. Phys. Pol. Nat. Cuba **10**: 116. pl. 30. 1845. TYPE: Cuba, Sagra s.n. (lectotype, P, Herb. Rich.). *Picrodendron macrocarpum* (A. Rich.) Britton, Bull. New York Bot. Gard. **4**: 139. 1906.

Picrodendron baccatum var. *bahamense* Krug & Urban, Bot. Jahrb. Syst. **15**: 308. 1893. TYPE: Bahama Is., Hog Is. [now Paradise Is., off New Providence], March [?], Eggers 4402 (holotype, B, destroyed).

Picrodendron medium Small, Bull. New York Bot. Gard. **18**: 185. 1917. TYPE: Santo Domingo, Prov. Azua, northeast of Azua, 20 March 1913, Rose et al. 4042 (holotype, NY!; isotype, US!).



MAP 1. Distribution of collections of *Picrodendron* examined (not including cultivated material).

Since examination of herbarium material and of living plants both in cultivation and in the field has failed to uncover any reliable means of separating the three previously distinguished species, we consider the genus to be monotypic, consisting of the somewhat variable *P. baccatum* (L.) Krug & Urban. Other authors (Record & Hess, 1943; Adams, 1972) have expressed doubts about the distinctness of these entities, and monotypic status has been advocated by Gillis (1974) and Correll (pers. comm.).

Although adult phyllotaxy is consistently alternate, the first pair of leaves above the cotyledons on seedlings is opposite. These first true leaves are otherwise similar to later-formed foliage. Of the natural populations of *Picrodendron* studied, all appear to be strictly dioecious. However, one tree cultivated on the estate of Mrs. Alvin R. Jennings in Coral Gables, Florida, is consistently monoecious, producing staminate flowers before pistillate ones. Other trees, presumably from the same introduction, are strictly unisexual (staminate). Thus, this tree appears to be an exceptional individual, not representing any deviant population.

Of 220 herbarium specimens examined, only six were of pistillate material in flower. Pistillate flowers are probably seldom gathered because they generally appear for only a week to ten days each year, usually during the first two weeks in May, and they are green much like the leaves and are therefore inconspicuous.

A profusion of common names suggests that *Picrodendron* is well known to local inhabitants throughout its geographic range. In the Bahamas it is known as blackwood or olive; in the Cayman Islands, black ironwood, cherry, or wild plum; in Cuba, aceituna, gua negro, guayo, llana, llanilla, mangle negro, roblecillo, vanilla-prieta, yana prieta, yanilla, or yanilla-prieta; in the Dominican

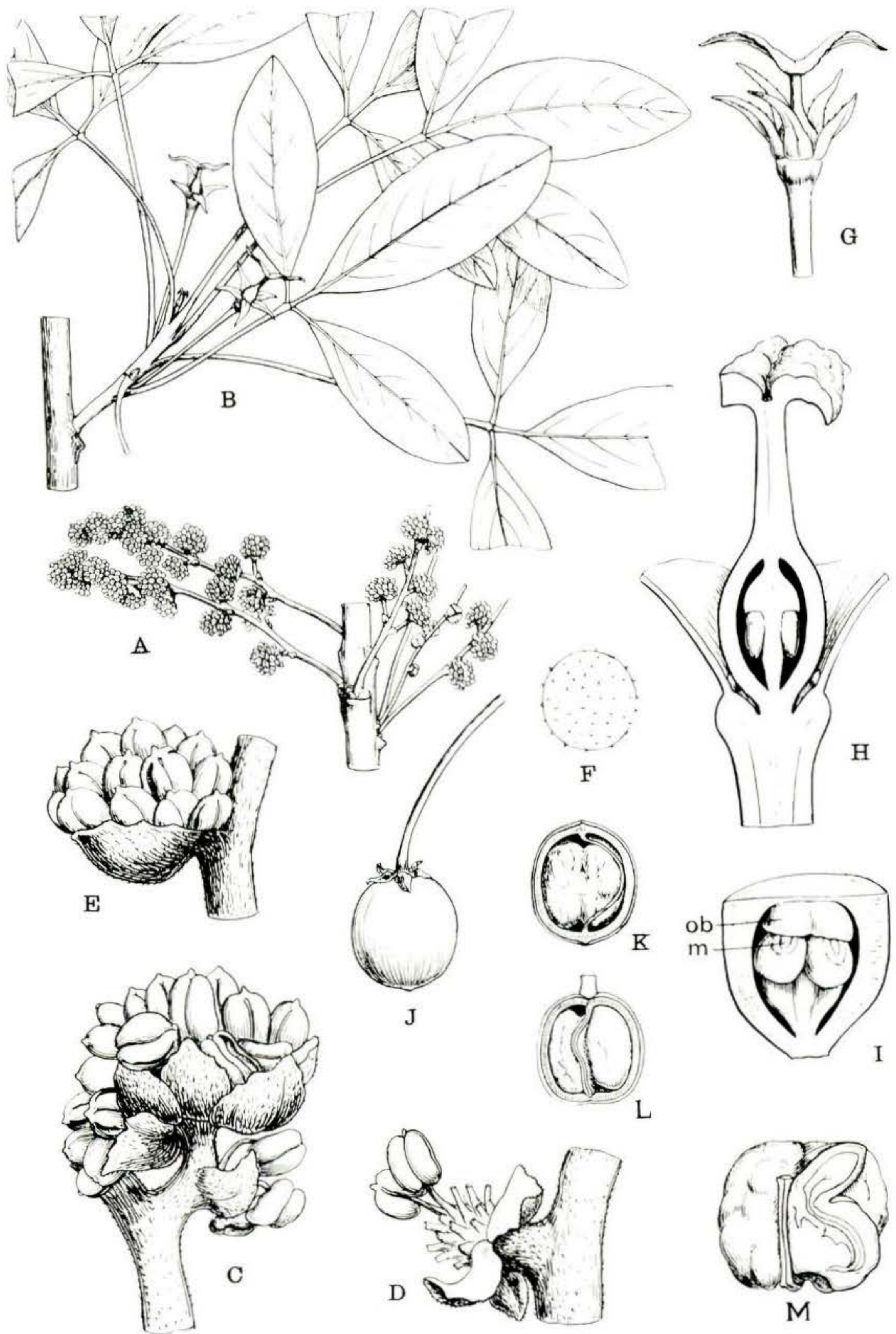


FIGURE 2. *Picrodendron baccatum*: A, twig with staminate inflorescences, $\times .45$; B, twig with pistillate inflorescences, $\times .45$; C-E, staminate flowers, $\times 8$; F, pollen grain, $\times 460$; G, pistillate flower, $\times 2.3$; H, pistillate flower, longitudinal section, showing 2 locules (note glands at base of perianth), $\times 5.75$; I, ovary, longitudinal section, showing

Republic, lembe, manzanilla (manzanillo), or mata becerro; in Haiti, gris-gris noir or simarouba; and in Jamaica, Jamaican walnut or wild plum.

EXCLUDED SPECIES. *Picrodendron arboreum* (Miller) Planchon, London J. Bot. 5: 579. 1846, based on *Toxicodendron arboreum* Miller, Gard. Dict. ed. 8. *Toxicodendron* no. 8. 1768. TYPE: Miller s.n. (BM!). *Rhus arborea* (Miller) DC. Prodr. 2: 73. 1825, non *R. arborea* Macfad. Fl. Jamaica 1: 227. 1837 (= *Allophylus cobbe* (L.) Raeuschel, *sensu* Leenhouts, 1967).

BIOGEOGRAPHY AND ECOLOGY

Picrodendron, together with 20 other genera, has a Greater Antillean distribution that omits Puerto Rico (Howard, 1973). *Picrodendron baccatum* is one of several species (e.g., *Catalpa punctata* Griseb., *Pseudocarpidium wrightii* Millsp., *Heliotropium ternatum* Vahl, *Linociera bumelioides* Griseb.) that are found in both the Bahamas and the Greater Antilles.

In the Bahamas, *Picrodendron* grows on the islands situated on the Great and Little Bahama banks. Neither the Great nor the Little Bahama Bank has ever been connected by land to the Greater Antilles. However, during low-water stages of the Pleistocene, the greatly enlarged above-water portion of the Great Bahama Bank extended to within only 25–35 miles of the enlarged Cuban platform, greatly enhancing the chances of dispersal to the Bahamas from Cuba. Even today, the northern fringing Cuban Islands are less than 150 miles from South Andros on the Great Bahama Bank.

The Great and Little Bahama banks are also believed never to have been connected to each other by land. The Northwest Providence Channel, which separates them today, has probably not been less than 20 miles wide during the last million years. Migration from Cuba to the Great Bahama Bank and thence to the Little Bahama Bank is not difficult to postulate. As yet, *Picrodendron* has not moved across the Crooked Island Passage—a very important biogeographical barrier to plant and animal migration—to the islands of the Bahamas or the Turks and Caicos islands to the southeast.

Ecologically, *Picrodendron* is a calciphile that apparently has some degree of salt tolerance. Specimens have often been collected from limestone substrates, either in arid habitats or near the landward margins of mangrove formations. Seifrizz (1943) noted that it grows together with mangroves in Cuba, where it is often situated between zones of *Avicennia germinans* (L.) L. and *Laguncularia racemosa* (L.) Gaertner f. Howard (1955) also recorded it on Beata Island, near mangroves and in association with other coastal species such as *Suriana maritima* L., *Thespesia populnea* (L.) Solander ex Corrêa, and

paired ovules of 1 locule (ob = obturator, m = micropyle), $\times 11.5$; J, fruit, $\times .75$; K, 1-seeded fruit, longitudinal section (note displaced septum), $\times .45$; L, 2-seeded fruit, longitudinal section, $\times .45$; M, seed, sectioned to show radicle and cotyledons, $\times 1.75$. (Reproduced from W. FAWCETT & A. B. RENDLE, *Flora of Jamaica* 4: fig. 90. 1920, with permission of Trustees of British Museum (Natural History).)

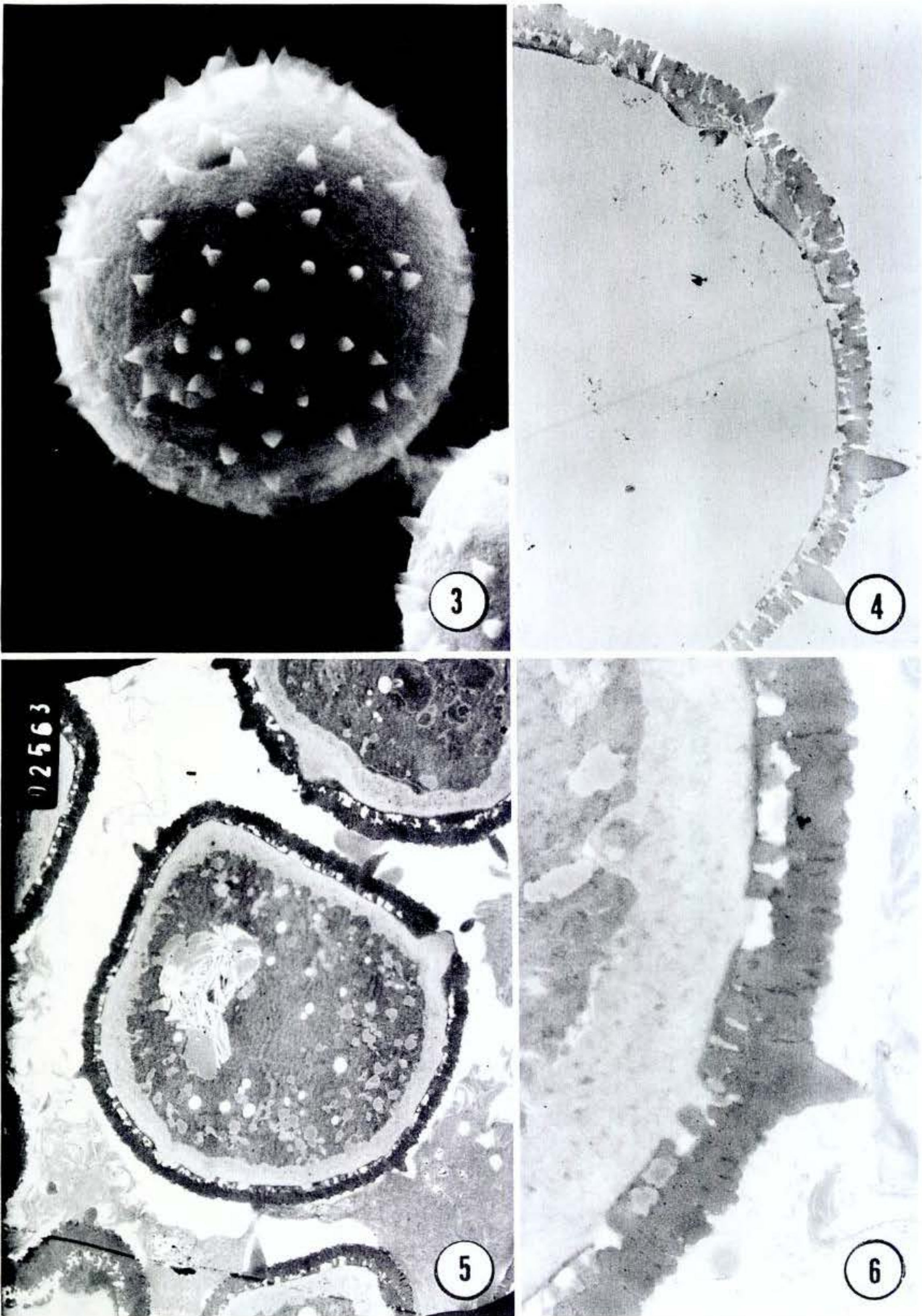
Amyris elemifera L. On the other hand, Asprey and Robbins (1953) included it as a constituent of "dry limestone scrub forests" in Jamaica. Presumably, suitable habitats for *Picrodendron* are widespread in the West Indies; its somewhat restricted geographic distribution is thus all the more interesting.

POLLEN

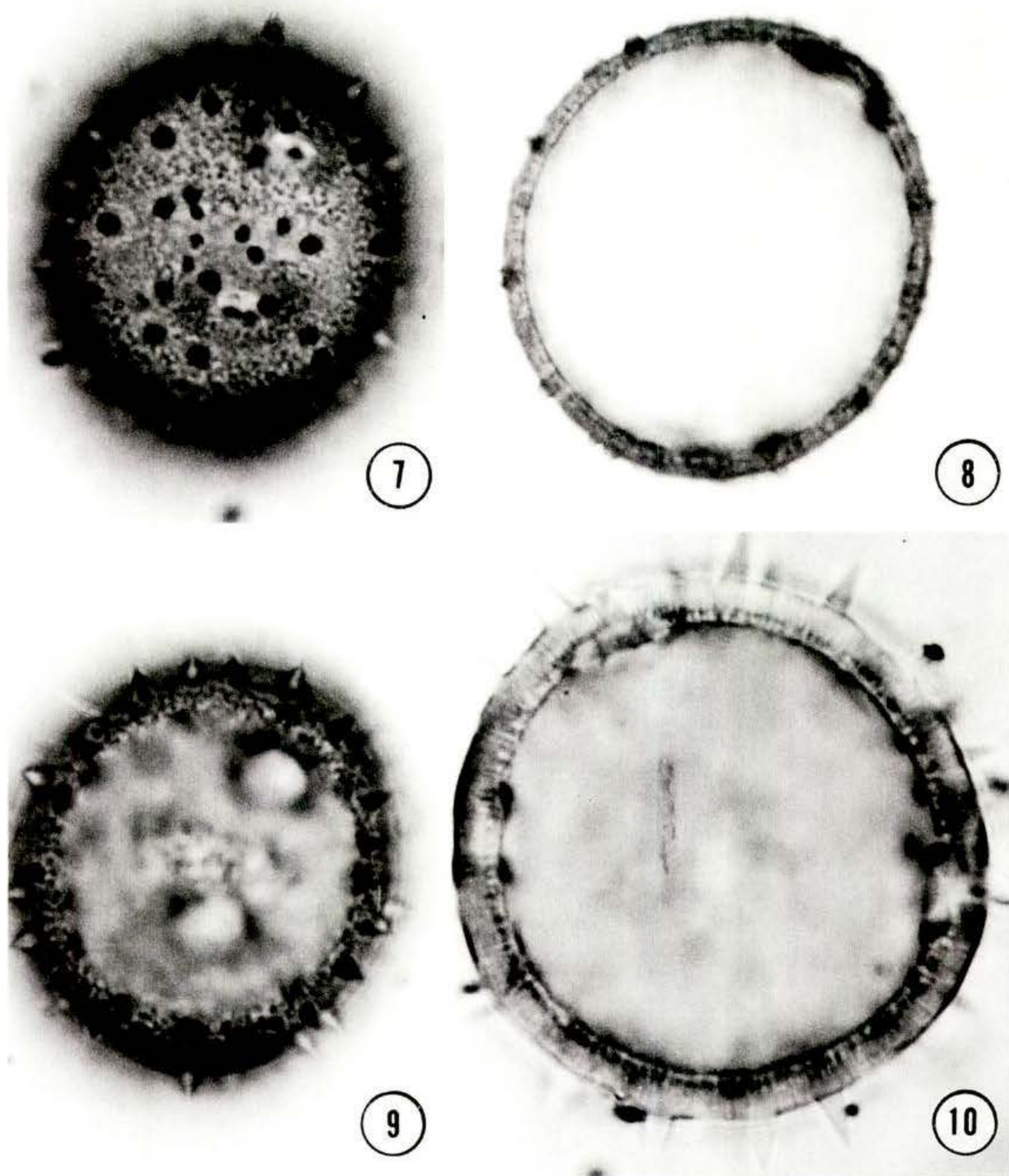
PICRODENDRON (FIGURES 3–9). The pollen of *Picrodendron baccatum* was described by Erdtman (1952) as 5- to 8-colporate, oblate-spheroidal, with an average diameter of 34 μm , spinuliferous, with sexine thicker than nexine, and with ectosexine thicker than endosexine. We have refined this brightfield microscope description based on whole mounts and epoxy sections stained in basic fuchsin: Pollen grains 5- to 8-zonicolporate, radially symmetrical, isopolar, oblate-spheroidal, 26 \times 29 μm . Amb circular. Colpi short, L:W ratio 4:1 or less, ora lalongate to circular. NPC: 545, 645, 745, 845. Exine spinose, tectate-perforate. Ectosexine about twice as thick as endosexine. Nexine extremely thin and discontinuous.

Electron microscope (SEM and TEM) observations add substantially to the understanding of *Picrodendron* pollen: Exine sculpturing echinate, the spinules to 3 μm long, well spaced, with clusters of 3 to 5 around colpi, the interspinule area densely verrucate. Ectosexine 0.6–0.8 μm thick, structured from more or less cylindrical rods, with bacula incompletely fused distally, the tectal surface verrucate, traversed to varying degrees by irregular channels, some of which coincident with gaps in endosexine and nexine to form intact passage to surface. Endosexine 0.2–0.4 μm thick, tapering to extinction near aperture, with narrow to broad columnar struts unevenly spaced, fused in massive columns in few areas, absent in other areas so nexine only loosely attached. Nexine extremely thin, 0.06–0.25 μm , serving as footlayer for endosexinous struts, frequently discontinuous in mesocolpial regions, forming pronounced wedge-shaped thickenings of 2 distinct layers near aperture: nexine-1 (footlayer in contact with endosexine), with point of thickening initiated about 1 μm from colpus rim, becoming lamellate at edge of os, extending across aperture in both acetolyzed and unacetolyzed grains; nexine-2, with thickening moderate, initiated about 1 μm from edge of os, appearing to extend across aperture in acetolyzed and unacetolyzed grains to form thin membrane. Intine as thick as or thicker than exine, 1–2 μm , divisible into 2 layers, outer one less electron dense, inner one granular. Intine relatively thin in mesocolpial regions, normally abutting nexine, but extending through gaps to contact sexine directly, expanding into lens-shaped thickening in aperture region and protruding up through os.

OLDFIELDIOIDEAE (FIGURES 10–20). Erdtman (1952) first surveyed several members of the subfamily, but Köhler's (1965) treatment of the pollen morphology of the biovulate Euphorbiaceae is quite comprehensive and serves in a substantial way to document the brightfield microscope observations. The chief difference between Köhler's description and our study is reflected in the NPC formulae for the group: we interpret the grains as brevicolporate instead of



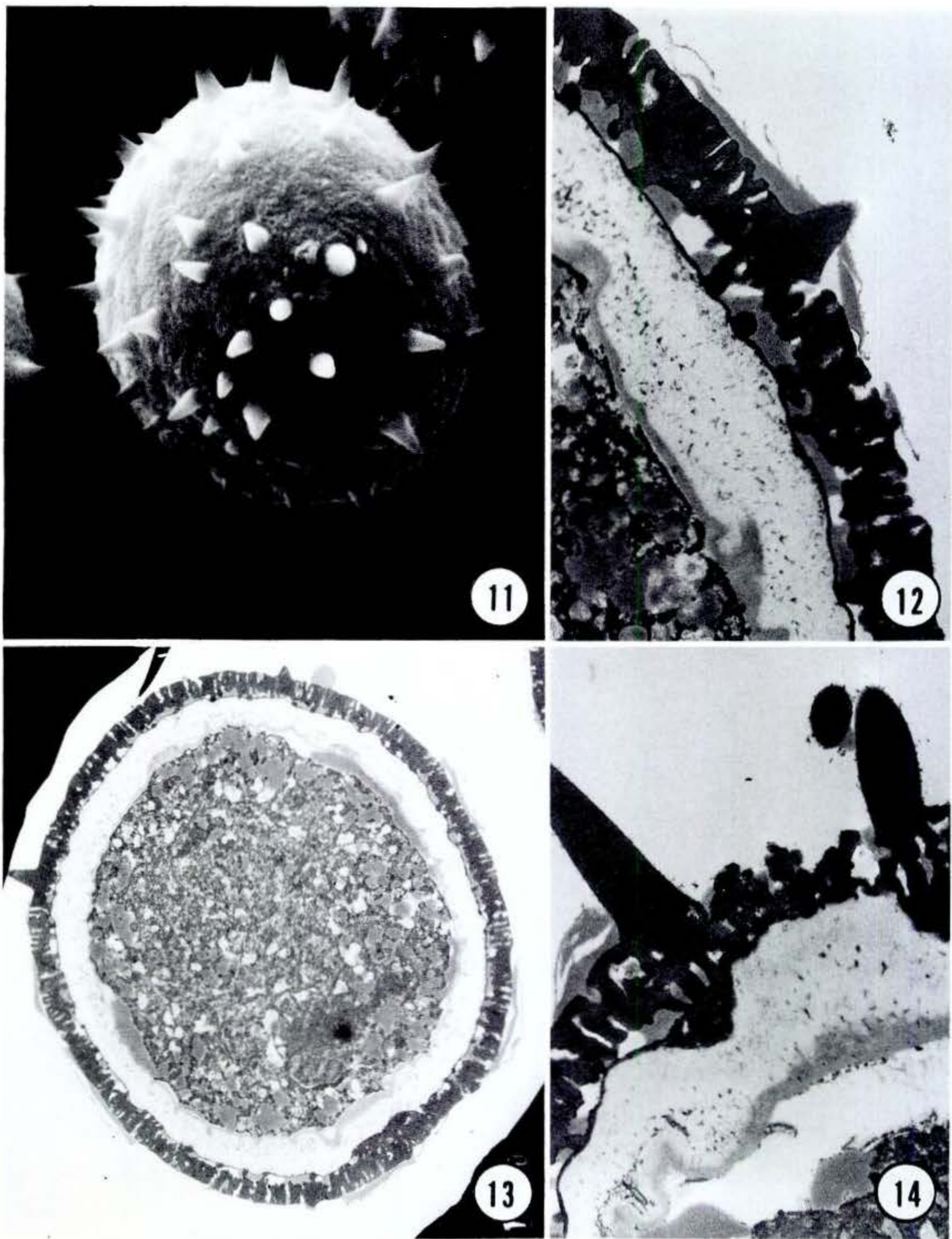
FIGURES 3-6. Pollen of *Picrodendron baccatum*. 3, *Harris 12516*, scanning electron micrograph of acetolyzed grain showing 2 slightly elongate pores, $\times 1800$. 4-6, transmission electron micrographs of *Clemente 6587*: 4, acetolyzed grain, $\times 4000$; 5, glutaraldehyde- OsO_4 -fixed grain, $\times 2200$; 6, glutaraldehyde- OsO_4 -fixed grain, $\times 10,000$.



FIGURES 7-10. Brightfield photomicrographs of pollen, $\times 1480$. 7-9, *Picrodendron baccatum* (Clemente 6587), single acetolyzed grain (whole-mount): 7, top focus, showing 2 short colpi; 8, optical cross section; 9, lower focus showing outline of 2 ora. 10, *Austrobuxus carunculatus* (Hürlimann 571), acetolyzed grain at optical cross section, nexine thickenings prominent at aperture.

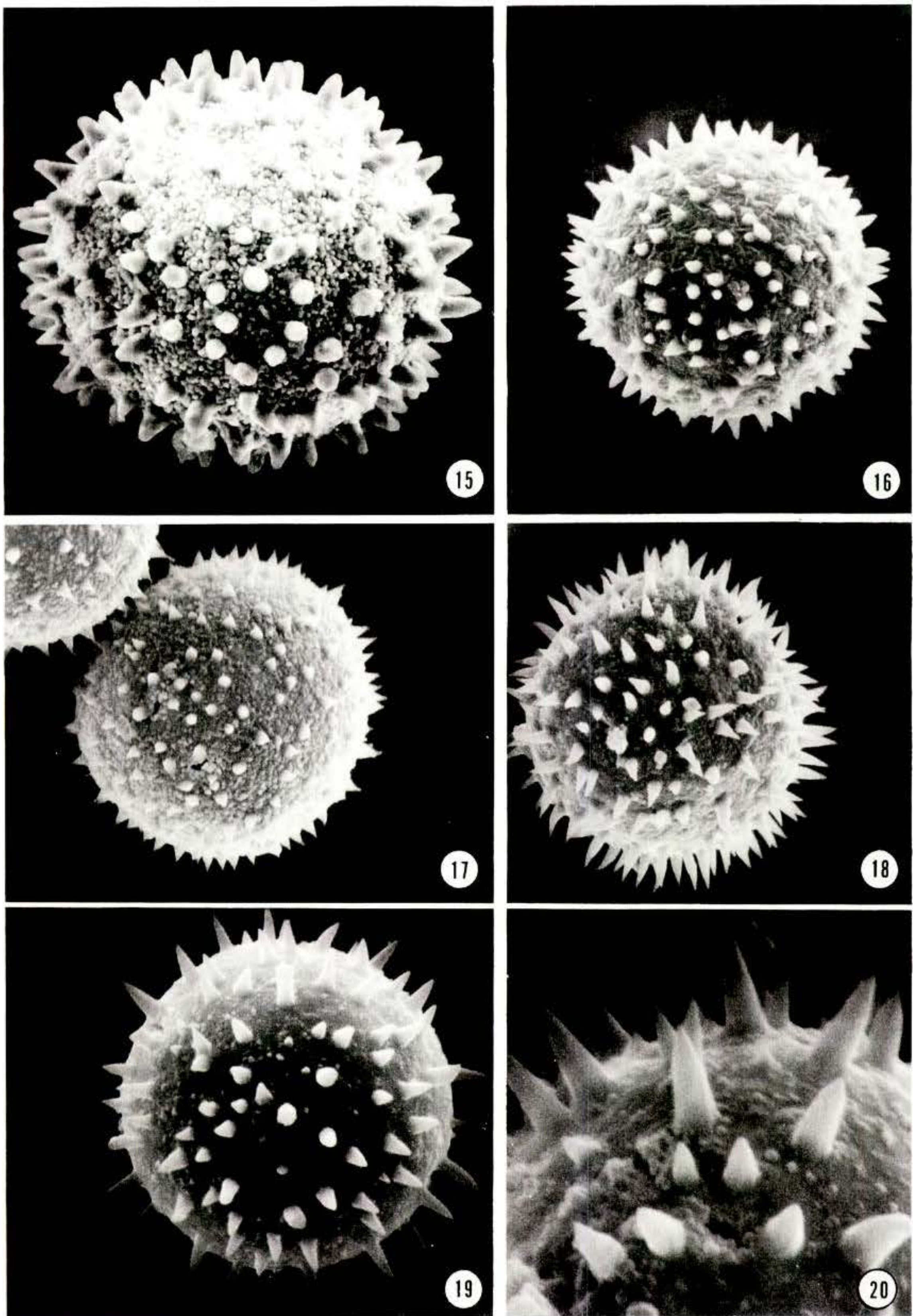
simply colpate. The apertures, whether elongate or not, are all distinctly compound, and we see no reason not to consider the nexine opening in each aperture as an os. Köhler refers to the os in his general description of his "*Tetracoccus*-type" of pollen, but he calls it an "oroid" in his "*Longetia*-type."

Based on our generalized brightfield microscope observations of the taxa listed above, oldfieldioid pollen can be described as follows: 4-7 zoniporate



FIGURES 11–14. Pollen of *Austrobuxus carunculatus*. 11, *Hürlimann 571*, scanning electron micrograph of acetolyzed grain, $\times 1720$. 12–14, *Stauffer & Blanchon 5751*, transmission electron micrographs of grains fixed in glutaraldehyde- OsO_4 : 12, $\times 6000$; 13, $\times 1800$; 14, $\times 6000$.

to colpororate, radially symmetrical, isopolar or paraisopolar, oblate-spheroidal to suboblate, medium size ($25\text{--}40\ \mu\text{m}$). Amb circular. Colpi lolongate, very short and inconspicuous (L:W ratio 3:1 or less), both colpi and pores often indistinct. Ora usually larger than colpi, lalongate, round, or lolongate, delim-



FIGURES 15–20. Scanning electron micrographs of acetolyzed pollen grains of species of Euphorbiaceae subfam. Oldfieldioideae: 15, *Tetracoccus dioicus* (Munz 12614), $\times 1360$; 16, *Oldfieldia africana* (Voorhoeve 1963), $\times 1360$; 17, *Tetracoccus hallii* (Kearney & Harrison 7530), $\times 1360$; 18, *Piranhea longepedunculata* (Blanco 299), $\times 1360$; 19, *Austrobuxus eugeniifolius* (Guillaumin & Baumann-Bodenheim 12908), $\times 1560$; 20, same collection as in FIGURE 19 but different grain, showing detail of aperture, $\times 4080$.

ited and more or less ringed by nexine thickenings formed by several more or less contiguous granules, these thickenings confined to polar ends of colpi in some species, to continuous ring or annulus around entire circumference in others. NPC: 445, 545, 645, 745. Exine tectate-perforate. Sexine much thicker than nexine, with broad-based, solid spines or spinules distributed more or less evenly over verrucate tectum except for clusters around apertures. Endosexine baculate, bacula ramifying distally and fusing to form incomplete tectum. Nexine very thin and occasionally discontinuous, but with prominent thickenings around apertures.

A limited sampling of five genera with SEM and one sample of *Austrobuxus carunculatus* with TEM yields the following ultrastructural description of Oldfieldioideae pollen: Exine sculpturing echinate, the spinules prevalent, becoming spines to 4.1 μm in *Austrobuxus carunculatus*, generally sharp pointed (rounded in some specimens of *Tetracoccus dioicus*), well spaced, the interspinule area sparsely (*Mischodon zeylanicus*) to densely verrucate. Ectosexine 0.9–1.4 μm thick, structured from more or less cylindrical rods, these irregularly fused to form relatively porous, bumpy tectal surface (verrucate) traversed to varying degrees by numerous channels (perforate). Endosexine 0.1–0.4 μm thick, terminating near aperture rim, with narrow to broad columnar struts unevenly spaced so nexine appears loosely attached. Nexine extremely thin, 0.06–0.12 μm , serving as footlayer for endosexinous struts, mostly continuous in interaperture region, forming pronounced wedge-shaped thickening of 2 distinct layers near aperture: nexine-1 (or footlayer in contact with endosexine), with point of thickening initiated ca. 1 μm from edge of os, appearing to extend across aperture in unacetolyzed grains as uniformly thin layer; nexine-2, with thickening initiated ca. 1 μm from edge of inner aperture, apparently terminating abruptly to form os. Intine as thick as or thicker than exine, 1–2 μm , divisible into 2 layers as in *Picrodendron* (inner, electron-dense area much thinner in intercolpial regions than in *Picrodendron*; outer, in contact with nexine, generally thick throughout grain and sprinkled with electron-dense granules and short rods).

DISCUSSION OF RELATIONSHIPS

RELATIONSHIPS AT THE FAMILIAL LEVEL

Picrodendron conforms more closely with the Euphorbiaceae than with any other family to which relationships have been proposed—a conclusion supported by gross morphology, pollen, and chromosome number (discussed below), as well as by vegetative anatomy (Hayden, 1977).

The reduced unisexual flowers of *Picrodendron* fit easily within the enormous range of floral diversity exhibited by the Euphorbiaceae. The strength of this association, however, is in the presence of pendulous anatropous ovules with a ventral raphe and a micropylar obturator (FIGURE 2, I), characters diagnostic for the Euphorbiaceae. Fawcett and Rendle (1917) first pointed out these facts, but their conclusion of euphorbiaceous relationships for *Picrodendron* received delayed recognition because of their erroneous description of the ovary as

inferior. Although this mistake was soon corrected (Fawcett & Rendle, 1920), the damage had already been done: Pax and Hoffmann (1931) excluded *Picrodendron* from the Euphorbiaceae largely because they repeated Fawcett and Rendle's inaccurate perception of ovary position. This unwarranted exclusion from the family by such prominent authorities discouraged any serious reconsideration of relationships with the Euphorbiaceae for several decades.

The absence of floral discs and of endosperm in mature seeds is unusual for the Euphorbiaceae, but these conditions are not unknown in the family. Also, *Picrodendron* is unusual (but not alone) within the Euphorbiaceae in having a drupaceous fruit instead of the more common schizocarpous capsule. These divergences are few; far more characteristics would have to be reconciled if *Picrodendron* were to be placed in any of the other families to which it has been assigned in the past (see Hayden, 1977, for detailed comparisons with some other families).

Erdtman's (1952) comment on the similarity of *Picrodendron* pollen with that of *Pseudanthus* Sieber ex Sprengel is largely responsible for revitalizing the notion of a relationship with the Euphorbiaceae. Indeed, the obvious similarities in pollen wall sculpturing and architecture between *Picrodendron* and certain Euphorbiaceae argue for a close relationship. On the other hand, *Picrodendron* shares few pollen features with the Juglandaceae (Stone & Broome, 1975) or the Rhoipteleaceae (Stone & Broome, 1971), with which it has been associated (Cronquist, 1968; Hutchinson, 1973), and it is not similar to the Simaroubaceae (Erdtman, 1952). Of particular note are the granular elements in the Juglandaceae ("structure grenue" of Van Campo & Lugardon, 1973) that are fused in varying degrees to form the columellae of the endosexine region. The bacula of *Picrodendron* and *Austrobuxus* Miq. are typical cylindrical rods; they may vary in size but would never be characterized as granular. The perforate ectosexine of *Picrodendron* and *Austrobuxus* is in marked contrast to the homogeneous tectum of the Juglandaceae, which is without pits or pockets except for the ultrafine channels that traverse the wall (Stone *et al.*, 1964). These aspects, as well as the more obvious differences in pollen sculpturing and aperture construction, leave little doubt that *Picrodendron* has more in common with the Euphorbiaceae than it does with the Juglandaceae. Overall, pollen of *Picrodendron* falls easily within Köhler's (1965) "Tetracoccus-type" of Euphorbiaceae subfam. Oldfieldioideae.

Relationship with the Oldfieldioideae is also confirmed cytologically. Fritsch (1972) reported a chromosome number of $2n = 48$ for *Picrodendron*. Members of the Euphorbiaceae-Oldfieldioideae are not well known cytologically, but published counts of $n = 24$ for *Mischodon* Thwaites and $2n = 24$ for *Tetracoccus* Engelm. ex Parry (Hans, 1973) suggest that the count for *Picrodendron* is consistent with a base number of 12 for the subfamily. On the other hand, members of the Juglandaceae—with the exception of several tetraploid hickories in *Carya* Nutt. sect. *CARYA*—are uniformly $n = 16$ (Stone & Broome, 1975). The Simaroubaceae have an assortment of chromosome numbers: reports of $n = 12$ are known for *Brucea* J. F. Miller and *Picrasma* Blume, $n = 13$ for *Castela* Turpin, $2n = 26$ for *Holacantha* A. Gray, $n = 16$ for *Simarouba* Aublet, $2n = 26$ for *Klainedoxa* Pierre, $2n = 28$ for *Irvingia* Hooker f., $2n =$

36 for *Quassia* L., and $n = 31$, $2n = 62$, 86 for *Ailanthus* Desf. (Darlington & Wylie, 1955; Moore, 1973, 1977). Of these simaroubaceous genera, only *Klainedoxa* and *Irvingia* were ever closely associated with *Picrodendron* (Hayden, 1977), but the known chromosome counts do not support such a relationship.

The paucity of fossils in most angiosperm groups tends to confer special significance upon any known fossils. Thus, the discovery of fossilized seeds and fruits of *Rosenkrantzia picrodendroides* B. Koch from the Cretaceous-Tertiary boundary of West Greenland is of interest because of their resemblance to *Picrodendron* (Koch, 1972). The fossil fruits are interpreted as either nuts or drupes and contain one or two seeds encased in a tough, woody pericarp (mesocarp?). The seeds are pendulous from an apical placenta and contain folded cotyledons but no endosperm. Presence of long-petiolate, trifoliolate leaves in associated fossil beds suggests an even greater list of similarities with *Picrodendron*. Although the fossil is unicarpellate and *Picrodendron* is bicarpellate, Koch was not deterred from perceiving a close relationship between these plants; furthermore, this disparity prompted an elaborate hypothetical derivation of both plants, consistent with Small's (1917) placement of the Picrodendraceae between the Juglandaceae and the Fagaceae.

Koch's thesis is difficult to evaluate, partly because of its complexity but mainly because of its awkward use of several morphological terms. For example, the pedicel is consistently referred to as a petiole; possible dehiscence mechanisms are discussed at some length, yet the fruit of *Rosenkrantzia* is described as a nut or drupe; the unicarpellate fruit is interpreted as having four dehiscence valves; and a protuberance on the fossil seed is described as a style base. Koch's hypothetical derivation involves the fusion of paired, reflexed, unicarpellate flowers such that basal placentation (as in the Juglandaceae) gave rise to the apical placentation of *Picrodendron*. At the gross morphological level we know of no evidence that convincingly supports the special criteria of Koch's hypothesis. Finally, as a consequence of his concepts of placentation in *Picrodendron*, Koch ultimately concluded that the resemblances of fruits of *Rosenkrantzia* and *Picrodendron* are merely superficial; we feel compelled to observe that such a conclusion seriously erodes the original basis for Koch's own hypothesis.

Consequently, the existence of *Rosenkrantzia* does not strengthen the association of *Picrodendron* with the Juglandaceae, and we are disinclined to perceive any relationship between *Rosenkrantzia* and *Picrodendron*, although a reevaluation of this conclusion may be necessary if the four obscure valves of *Rosenkrantzia* prove to be evidence for a multicarpellate condition. Our proposed relationship with the Euphorbiaceae requires no elaborate derivation and is thus simpler than Koch's hypothesis.

RELATIONSHIPS WITHIN EUPHORBIACEAE

The presence of two ovules per carpel and spiny pollen grains indicates that the proper placement of *Picrodendron* is within subfamily Oldfieldioideae (Webster, 1967). In a conspectus of suprageneric taxa of the Euphorbiaceae, Webster (1975) assigned *Picrodendron* to a monogeneric tribe within this subfamily.

In searching for the nearest relative of *Picrodendron* within the Oldfieldioideae, we are impressed with certain similarities to the tribe Hyaenancheae (Baillon ex Mueller-Arg.) Hutchinson, especially to members of subtribe Paivaeusinae Pax & Hoffm. According to Webster's (1975) classification, the Paivaeusinae includes *Aristogeitonia* Prain and *Oldfieldia* Benth, from Africa; *Celaenodendron* Standley, from Mexico; and *Piranhea* Baillon, from northern South America. Airy Shaw (1966, 1973) has associated these genera with *Picrodendron*. Not only do they have compound leaves similar to those of *Picrodendron*, but they are also closest anatomically (Hayden, 1977, 1980) and palynologically. Webster and Lynch (unpubl.), in a more comprehensive survey of Oldfieldioideae pollen than is presented here, reached the same conclusion concerning palynological similarity of *Picrodendron* and the Paivaeusinae. On the basis of a combination of several morphological characters, especially the alternate, stipulate, strictly trifoliolate leaves, dioecy, and elongate styles, *Picrodendron* appears closer to the South American genus *Piranhea* than it does to the African *Aristogeitonia* or *Oldfieldia*. Some features of leaf anatomy of *Picrodendron* likewise compare most closely with *Piranhea*, but certain wood features are better matched by *Oldfieldia* (Hayden, 1977, 1980). In view of the obviously reticulate nature of relationships in the Oldfieldioideae, this does not appear to be a very serious discrepancy.

Despite the above-mentioned similarities with the Paivaeusinae, *Picrodendron* differs from all of the genera of Hyaenancheae in having a distinctive cluster of reproductive characters: staminate flowers with reduced calyx, borne in aments; floral disc absent in both sexes; styles elongate and basally connate; and drupaceous fruits with large, ecarunculate seeds containing plicate cotyledons. On morphological grounds, therefore, *Picrodendron* appears sufficiently divergent within subfam. Oldfieldioideae to be recognized on its own. This reasoning led Webster (1975) to establish the tribe Picrodendreae (Small) Webster. However, when the Oldfieldioideae as a whole are better known, the strength of evidence from anatomy and palynology may prove sufficient to classify *Picrodendron* as an advanced subtribe adjacent to the Paivaeusinae within tribe Hyaenancheae.

It may be speculated that the distinctive reproductive characters of *Picrodendron* reflect an adaptive shift from insect to wind pollination. However, the lack of reduction of spines in the pollen is rather curious, since it is contrary to the trend evident in other taxa of anemophilous Euphorbiaceae (e.g., Hyaenancheae subtribe Dissiliariinae Pax & Hoffm., or many genera of tribe Acalypheae Dumort.). Possibly there is some sort of balance between wind and insect pollination in *Picrodendron*, a hypothesis that needs testing by field observation.

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APPENDIX. *Picrodendron* specimens examined.

Bahama Islands. GREAT ABACO: Old Ken's Pt., *Brace 2029* (F). ANDROS: Coconut Pt., Conch Sound, *Northrop & Northrop 453* (A, F, GH); Deep Creek, *Brace 5198* (F, NY); coppice near Fresh Creek, *Small & Carter 8833* (F, G, P, US); Morgan's Bluff, low thickets inland from rocky sea cliff, *Proctor 30788* (IJ); Driggs Hill, *Popenoe s.n.*, May 1965 (FTG). CAT: whiteland scrub, the Bight, *Britton & Millspaugh 5884* (F, NY); Industrious Hill, side of cliff near caves, *Byrne 323* (A); Port Howe plantation house, *Byrne 364* (A); ledges in open coppice N of Stevenson, *Correll 46153* (F, FTG). ELEUTHERA: rocky plains, vic. of Miller's, *Britton & Millspaugh 5593* (F, NY). EXUMA CHAIN, GREAT GUANA CAY: *Britton & Millspaugh 2895* (F, GH). LONG: Clarence Town, *Britton & Millspaugh 6258* (F, US). NEW PROVIDENCE: *Brace 477* (NY); Paradise Is., center of island, remnant of coppice, *Gillis 11991* (A, IJ).

Cayman Islands. GRAND CAYMAN: logwood woodland on limestone pavement, 0.5 mi N of Joe Conger, *Brunt 1783* (BM, IJ); along track between Old Isaacs and Wintersland, *Proctor 15248* (BM, GH, IJ); 1.5 mi WNW-NW of Brechers, S of Joe Conger, *Proctor 27976* (IJ); E end of island on cliff, *Kings 131* (BM). LITTLE CAYMAN: Snipe Point, dry, rocky woodland, *Proctor 28038* (BM, IJ); S side of Blossom Pt., *Kings 77* (BM, NY). CAYMAN BRAC: W end, edge of dense woodland, *Proctor 29125* (IJ).

Swan Islands. GREAT SWAN: lat. 17°25'N, long. 83°56'W, *Proctor 32534* (BM, II).

Cuba. CAMAGÜEY: Silla de Cayo, Cayo Romano, *Shafer 2505* (BM, F, GH, NY, P, US); Santa Lucia, *Shafer 965* (NY); Cayo Sabinal, *Shafer 1107* (BM, F, NY, US). HABANA: Marianao Beach, coastal thickets, *León s.n.*, Feb. 1921 (GH); Pr. Jaimenito, *Ekman 1207* (G, S, US). ORIENTE: Sardinero, coastal thickets, *Clemente 6587* (GH, US); Manigua Costera, Plaza de Puerto Padre, *Lopez 26* (US); Guantanamo Bay, U.S. Naval Station, *Britton 2259* (NY); Santiago de Cuba, Sardinero, wayside coastal thickets, *Clemente 6604* (GH); Santiago de Cuba, Juragria Beach, coastal cliff, *Clemente 7436* (GH, US); Santiago de Cuba, Siboney, in calcareous soil, *Ekman 8710* (F, US); Santiago de Cuba, near El Nacro along seacoast, *Ekman 9195* (F, G, US); Banes, Puerto Rico, coastal forest, *Ekman 6625* (F, G, US); San Germán, along railroad in forest, *Ekman 6344* (G); Cabo Cruz, coastal thickets, *León 16351* (GH, II, US); Punta Piedra, Nipe Bay, *Britton et al. 12460* (F, GH, NY, US). PINAR DEL RÍO: Bahía Honda, Finca Toscano, coastal thickets, *Alain 1803* (GH, II, US). LAS VILLAS: Cienfuegos, Caunao R., Iguana Point, *Jack 5126* (A, P, US); Caunao R. to Cienfuegos Bay, *Jack 7516* (F, US); Cienfuegos Bay, Punta Sabanilla, coastal thicket, *Britton et al. 4584* (NY); Punta Diablo, Cienfuegos Bay, *Britton & Wilson 5672* (F); Cienfuegos, Faro Villa Nueva, hills and cliffs, Castillo de Jagua, *Combs 646* (GH); Camino de la Costa, E of Castillo de Jagua, *Howard et al. 249* (A, NY); Soledad, Gavilán, *Jack 5824* (A, P, US); Gavilán, *Rehder 1102* (A, P); along Arimao R., *Bangham s.n.*, 22 July 1929 (II). WITHOUT DEFINITE LOCALITY: *Sagra s.n.* (P, Herb. Richard).

Dominican Republic. PROV. AZUA: Monte Río, *Lavastrè 1750* (NY); NE of Azua, *Rose et al. 4042* (NY, US). PROV. BARAHONA: near Barahona, *Fuertes 1535* (BM, F, GH, NY, P, US); Barahona, *Jiménez s.n.* (NY); Beata Is., edge of lagoon on E side, *Howard 12430* (A, BM, US); Beata Is., without further locality, *Ostenfeld 297* (C). PROV. LA VEGA: La Vega City, windbreak, La Escuela de Agricultura, *Padre Cicero et al. 7020* (A, II), *Jiménez 7125* (A, F, II); Bayacanes, near La Vega City, serpentine hills, 300–350 m, *Liogier 11927* (F, II, NY). PROV. MONTE CRISTI: El Tamarindo, Hatillo Palma, *Marcano 5202* (NY, Herb. Jiménez). PROV. PEDERNALES: SE of Cabo Rojo near beach in dogtooth limestone, *Liogier 13910* (NY); Cabo Rojo in thickets, sea level, *Liogier 16872* (NY); Cabo Rojo, *Marcano 4528* (Herb. Jiménez). PROV. EL SEIBO: E of Jovero, between Punta Jáco and Punta Rey, *Abbott 2872* (US).

Haiti. ÎLE DE LA GONÂVE: Mahautière, edge of mangrove, *Ekman 8685* (C, GH); La Mahautière, *Eyerdam 84* (A, F, GH, US); Dubedon, 200 m, *Buch 1009* (II). DÉP. DE L'OUEST: Cabaret, Baie des Moustiques, *Leonard & Leonard 12004* (A, US).

Jamaica. CLARENDON PARISH: Jackson Bay, dry, rocky woodland near sea, *Proctor 29171* (II, NY); Jackson Bay, 0.7 mi by road inland, border of salina, *Proctor 32643* (F, II); Portland Ridge, limestone near seacoast, *Van der Porten s.n.*, 11 July 1950 (II); Portland Ridge, coastal hammock, *West & Arnold 148* (GH). ST. ANDREW PARISH: above Ferry, *Grabham s.n.*, 11 Jan. 1896 (NY); Ferry Peninsula, 100 ft elev., *Campbell 6182* (BM, F); limestone hillside near Ferry, *Harris 12516* (BM, GH, NY, PH, US). ST. CATHERINE PARISH: W base of Port Henderson Hill, scrub woodland, *Proctor 22129* (GH, II); Port Henderson Hill, *Webster & Wilson 4929* (A, II, US); summit of Port Henderson Hill, ca. 700 ft, thickets, *Proctor 32808* (II); Port Henderson Hill, path to Rodney's Lookout, *Adams 12801* (BM); Bracton & Rodney's Lookout, *Gibbs s.n.* (Herb. C. D. Adams); near Ft. Clarence, E side of Great Salt Pond, *Lewis s.n.*, 1 March 1951 (II); Old House Point, on rocky limestone, *Du Quesnay 555* (II); Portland Ridge near coast, *Howard 12001* (A, II, US); Ferry River, Spanish Town Road, *Harris 9046* (F, NY, US); Coleman's Bay, *Tulloch 359* (II); Great Goat Is., rocky woodland, *Proctor 17437* (A, F, II, US); Great Goat Is., *Harris 9313* (A, BM, C, NY), *Harris 12519* (BM, GH, NY, PH, US); Little Goat Is., Old Harbor Bay, near mangrove swamp, *Britton & Hollick 1851* (NY). WITHOUT LOCALITY: *Macfadyen s.n.* (P).

Cultivated. TOBAGO: cultivated at Botanic Station, *Broadway s.n.*, 8 Nov. 1932 (BM). TRINIDAD: Royal Botanic Garden, Port-of-Spain, *Fairchild 2046* (AAH), *Nevling 316* (AAH), *Broadway 7321* (A, AAH, F, NY). U. S. A., FLORIDA, MIAMI: U.S.D.A. Plant Introduction Station, P.I. 98559, M5850, introduced from Trinidad Botanic Garden, *Gillis 7846* (AAH, FTG, IJ), *Fennell 948* (AAH); estate of Mrs. Alvin R. Jennings, *Rehder s.n.*, 30 April 1920 (AAH), *Gillis 9330* (AAH, FTG), *Popenoe 20* (FTG); Fairchild Tropical Garden, introduced from Driggs Hill, South Andros, Bahama Islands, *Gillis 10924, 10975, 11031* (AAH, FTG, IJ).

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