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Systematic Anatomy of Euphorbiaceae Subfamily Oldfieldioideae I. Overview

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SYSTEMATIC ANATOMY OF EUPHORBIACEAE SUBFAMILY OLDFIELDIOIDEAE. I. OVERVIEW[1]

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ABSTRACT

The biovulate subfamily Oldfieldioideae of Euphorbiaceae, characterized by spiny pollen, is an otherwise apparently diverse assemblage of mostly Southern Hemisphere trees and shrubs that traditionally have been allied with genera of Phyllanthoideae and Porantheroideae sensu Pax and Hoffmann. Although fairly diverse anatomically, the following structures characterize the subfamily with only a few exceptions: pinnate brochidodromous venation with generally randomly organized tertiary and higher order venation; foliar and petiolar glands absent; unicellular or unbranched uniseriate trichomes; latex absent; mucilaginous epidermis or hypodermis; brachyparacytic stomata; vessel elements with simple perforation plates and alternate, often very small, intervascular pits; thick-walled nonseptate imperforate tracheary elements; numerous narrow heterocellular rays; and abundant axial xylem parenchyma in diffuse to somewhat banded patterns and often bearing prismatic crystals. Anatomically, the shrubby Australian ericoid genera form a well-defined group with obvious affinities to the more arborescent Australasian genera, which show clear relationships to each other; the African and neotropical genera bearing compound leaves form another distinct group; the remaining genera are somewhat more isolated and seem to represent, in various cases, elements that are primitive within the subfamily or elements derived from the group bearing compound leaves. Presence of theoid teeth and palmately compound leaves in Oldfieldioideae are features consistent with Dilleniid origin for Euphorbiaceae.

As a taxonomic entity the euphorbiaceous subfamily Oldfieldioideae Köhler & Webster dates conceptually from the palynological studies of Punt (1962) and Köhler (1965) who noted the spiny pollen that characterizes the group; the assemblage recognized by pollen structure was subsequently formalized nomenclaturally as a new subfamily (Webster, 1967). In essence, pollen characters circumscribed a group of genera that previously had been assigned to the biovulate subfamilies Phyllanthoideae and Porantheroideae in the system of Pax & Hoffmann (1931). Webster's first (1975) classification of oldfieldioid genera contained several novel taxonomic associations at variance with earlier classifications, notably those of Pax & Hoffmann (1931) and Hutchinson (1969).

Interest in the anatomy of Oldfieldioideae stemmed from the need for comparative data to aid placement of the problematic genus *Picrodendron* Planchon (Hayden, 1977). Despite a number of publications dealing with the anatomy of oldfieldioid genera (Appendix 2), detailed information for most of the subfamily is lacking. Once *Picro-*dendron was shown to be a member of Oldfieldioideae (Hayden, 1977; see also Hayden et al., 1984, and Hakki, 1985), an anatomical survey of the entire subfamily was initiated (Hayden, 1980) to assess relationships from data independent of reproductive (including pollen) morphology. Based in part on these anatomical studies, classification of Oldfieldioideae has been modified from Webster's (1975) original proposal; two broadly similar classifications, one by G. L. Webster (the preceding issue) and another by G. A. Levin and M. G. Simpson (this issue), are proposed elsewhere.

HISTORY

Classifications of Euphorbiaceae from the first half of the 19th century (e.g., Jussieu, 1824; Endlicher, 1836–1840) offer little insight into relationships among oldfieldioid genera. At this formative time in the definition of Euphorbiaceae (Webster, 1987) the few oldfieldioid genera known were often scattered widely in the family; moreover, some were referred to other families. Genera

of Pseudanthinae (or Caletieae in the traditional/ narrow sense) were the first to be classified together, undoubtedly because of their shared ericoid xeromorphic habit and common provenance in Australia. Baillon (1858) grouped *Micrantheum* Desf. with *Pseudanthus* Sieber ex Sprengel, to which Agardh (1858) added *Stachystemon* Planchon, establishing the composition of Caletieae that was followed in all subsequent studies until the addition, first, of *Neoroepera* Muell. Arg. by Kohler (1965) and, now, the inclusion of all Australasian oldfieldioids as proposed by Levin & Simpson (1994, this issue) and Webster (1994). During the intervening years, however, the use of cotyledon width as the primary criterion for subdivision of the family (Mueller, 1866; Pax, 1890; Pax & Hoffmann, 1931) relegated the genera of Pseudanthinae (as Caletieae) to the Stenolobeae, a small group of Australian xerophytes with narrow cotyledons. Their somewhat isolated position in Stenolobeae minimized association of Pseudanthinae with other oldfieldioid genera.

Other oldfieldioid genera similarly suffered early taxonomic assignments that delayed consideration of relationships with the rest of the subfamily. Baillon (1858) submerged *Podocalyx* Klotzsch within the phyllanthoid genus *Richeria* Vahl, a disposition followed well into this century. *Oldfieldia* Benth. & Hook. f. was temporarily considered sapindaceous (Mueller, 1866; Baillon, 1878). Worse, the relationships of *Picrodendron* were long obscured by a series of misassignments at both the generic and familial levels (Hayden et al., 1984).

Aside from Caletieae sensu stricto, the genera of Oldfieldioideae were scattered widely in Mueller's (1866) treatment of the family for the *Prodromus*; *Mischodon* Thwaites was included with uniovulate genera, following an earlier error of Baillon (1858), *Oldfieldia* was still banished to Sapindaceae, and the remaining five oldfieldioid genera in his treatment were each assigned to different subtribes of Phyllantheae. Greater cohesiveness is apparent in a later publication of Baillon (1878). For example: *Choriceras* Baillon was included within Caletieae; *Austrobuxus* Miq. (as *Buraeavia* Baill.), *Longetia* Baillon ex Muell. Arg., *Petalostigma* F. Muell., and *Hyaenanche* Lambert formed a sequence; and *Dissiliaria* F. Muell. ex Baill. followed *Richeria* (which included the oldfieldioid *Podocalyx*). (See Webster (1987) for commentary on Baillon's peculiar "serial" system to indicate relationships.) Additional elements were gradually accreted to this loosely defined nucleus of oldfieldioid genera. Bentham (1880), in his treatment of Euphorbiaceae in the *Genera Plantarum*,

included, using current nomenclature, *Dissiliaria*, *Longetia*, *Austrobuxus*, *Hyaenanche*, *Mischodon*, *Oldfieldia*, *Piranhea* Baillon, and only one nonoldfieldioid genus, *Bischofia* Blume, within genera 46–54. Although these plants constituted three discrete groups in his conspectus, Bentham (1878) expressed some doubt about their relatedness and he chose to associate *Neoroepera* and *Petalostigma* with other phyllanthoid genera. Pax (1890) treated oldfieldioid genera much as had Bentham; *Tetracoccus* Engelm. ex C. Parry, however, was included, and Pax & Hoffmann (1931) added *Petalostigma*, *Androstachys* Prain, and *Aristogeitonia* Prain to various subtribes consisting largely of oldfieldioid genera. Perhaps the first clear indication of the relatedness of oldfieldioid genera can be found in Pax's (1925) essay on Euphorbiaceae, which includes the phylogenetic tree reproduced in Figure 1. Although much of the detail in this phylogenetic tree may be challenged seriously in the light of present knowledge, it does show oldfieldioid genera (as usual, minus Pseudanthinae) comprising a clade distinct from other biovulate Euphorbiaceae.

In the disposition of genera, Hurusawa's (1954) classification of Euphorbiaceae essentially follows that of Pax & Hoffmann (1931) and thus contains no new insights on classification of oldfieldioid genera. In light of Pax's (1925) phylogeny and because of its disregard for the palynological data available at the time (Punt, 1962; Köhler, 1965), Hutchinson's (1969) classification was a retrograde development; oldfieldioid genera were widely distributed in five of 12 biovulate tribes, with three tribes mixing oldfieldioid and phyllanthoid elements. Hutchinson was the first, however, to associate *Paradrypetes* Kuhlm. with other oldfieldioid genera.

Airy Shaw (1965) entertained serious doubts about inclusion of several oldfieldioid genera in Euphorbiaceae. Accordingly, he proposed Androstachydaceae, of uncertain relationships, to accommodate *Androstachys*; he recognized Picrodendraceae as distinct from but allied to Euphorbiaceae; and he viewed *Aristogeitonia*, *Calaenodendron* Standley, *Mischodon*, *Oldfieldia*, and *Piranhea* as occupying an intermediate position between these families (Airy Shaw, 1966, 1972, 1973). Airy Shaw (1983) continued to accept an isolated taxonomic position for Stenolobeae (including Pseudanthinae), but he did, consistently, group the remaining Australasian genera of Oldfieldioideae in adjacent tribes in several of his informal or tentative classification systems (e.g., Airy Shaw, 1975, 1980b, 1983).
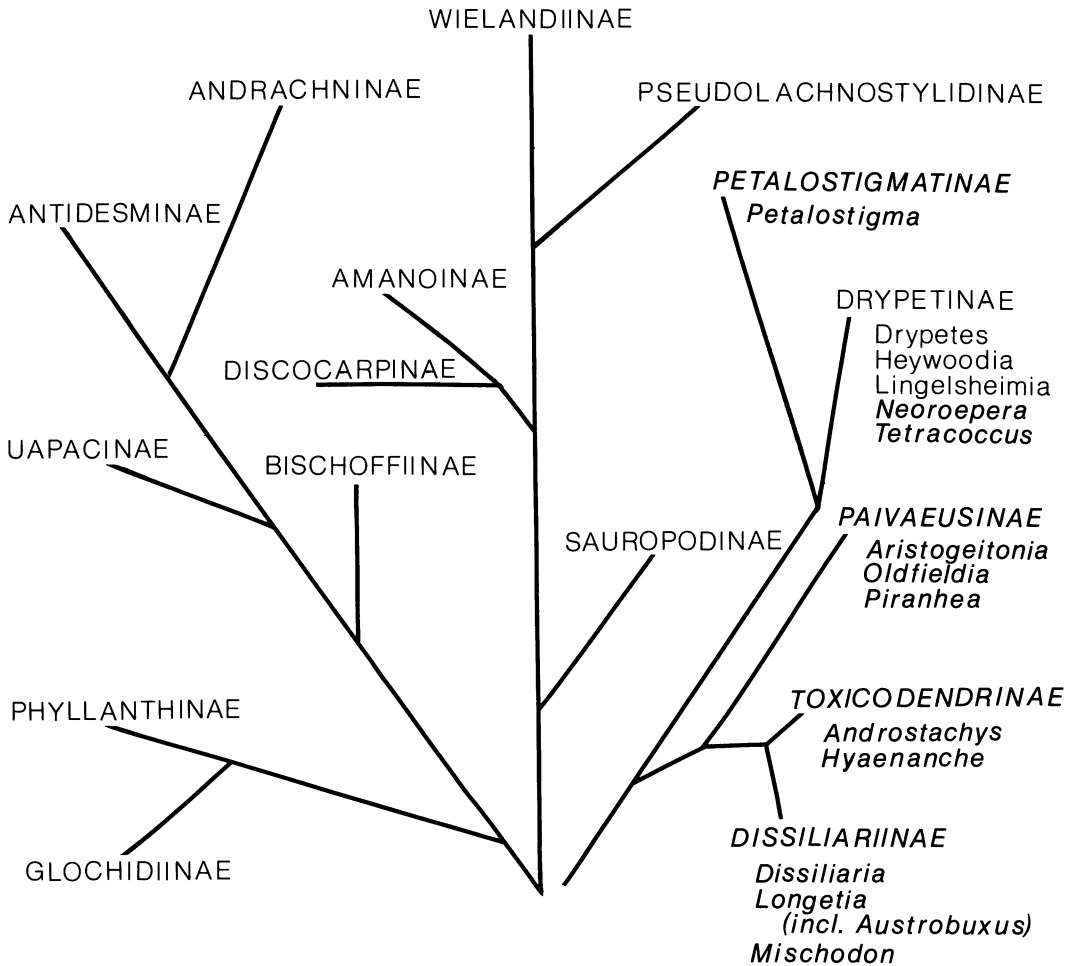
FIGURE 1.   Relationships of subtribes of Phyllantheae, after Pax (1925). Right-hand clade is the earliest published phylogram of Oldfieldioideae. Generic composition of subtribes, where indicated, follows Pax & Hoffmann (1931); oldfieldioid taxa are in bold italics. Other than Pseudantheae, *Podocalyx* (treated as a subgenus of *Richeria* [Antidesminae]) is the only element of Oldfieldioideae known to Pax and not included in the phylogram.

DESCRIPTION, CIRCUMSCRIPTION, AND DISTRIBUTION

Plants of Oldfieldioideae are woody, ranging from low depressed shrubs to tall trees. Latex is absent and vestiture consists of unicellular or uniseriate trichomes. Leaves are alternate, opposite, or whorled and may be simple or palmately compound; petiolar and laminar glands are absent; stipules may be present or absent. Leaves may be strongly reduced in xerophytic species. Plants are typically dioecious. Flowers are apetalous, and most lack discs. Stamens range from three to many. Pollen is binucleate, with four to many brevicolporate to pororate apertures; the exine lacks a foot layer, bears a discontinuous interstitium and thick perforate tectum with prominent supratectal spines (Levin & Simpson, 1994, this volume). Gynoecia consist

of two to five carpels; styles are generally undivided; each locule houses a pair of pendulous anatropous ovules. Seeds are often carunculate and usually possess copious endosperm. Reports of n = 12 for *Pseudanthus* (Hassall, 1976), $2n$ = 48 for *Picrodendron* (Fritsch, 1972), n = 24 for *Mischodon* and *Tetracoccus* (Hans, 1973), and n = 24, $2n$ = 48 for *Mischodon* (Sarkar & Datta, 1980) collectively suggest a base number of x = 12 for the subfamily.

The first comprehensive classification of Oldfieldioideae (Webster, 1975) included 21 genera, but several changes in composition have occurred since then. Two newly discovered genera, *Voatamalo* Capuron ex Bosser (1976) and *Whyanbeelia* Airy Shaw & B. Hyland (Airy Shaw, 1976), have

been referred to the subfamily. Two enigmatic genera, *Croizatia* Steyerm. (Webster et al., 1987) and *Paradrypetes* (Levin, 1992), have been assigned to Oldfieldioideae following discovery of diagnostic flowering material and, especially, after study of pollen from these plants. *Kairothamnus* Airy Shaw (1980a) and *Scagea* McPherson (1985) have been segregated from *Austrobuxus* sensu lato, as has *Canaca* Guillaumin, if only tentatively (Webster, 1994). In recent years Radcliffe-Smith has redefined generic limits for several Oldfieldioideae. He has included *Paragelonium* Léandri within *Aristogeitonia* (Radcliffe-Smith, 1988), he segregated *Stachyandra* R.-Sm. from *Androstachys* to accommodate several Madagascan species bearing compound leaves (Radcliffe-Smith, 1990), and he expanded *Pseudanthus* to include *Stachystemon* (Radcliffe-Smith, 1993). The number of genera now stands at 27. (Solely because of the recency of its reclassification, *Stachystemon* is herein treated as a distinct genus.)

Genera of Oldfieldioideae are mostly mono- or oligotypic. *Austrobuxus*, with perhaps 20 species, is the most speciose, followed by *Pseudanthus* (seven species) and *Petalostigma* (six species). The total number of species referable to the subfamily is estimated at 86, approximately 1 percent of the total number of species in Euphorbiaceae.

Oldfieldioideae is largely a southern hemisphere group. Only three genera occur in areas not derived from the breakup of Gondwanaland; these are *Celaenodendron*, from western Mexico, *Picrodendron*, from the Bahamas and Greater Antilles, and *Tetracoccus* from Mexico and the southwest United States. Eight genera and 16 species occur in the New World, six genera and 16 species occur in Africa and Madagascar, one monotypic genus occurs in southern India and Sri Lanka, and 13 genera and 52 species are Australasian. No genus of Oldfieldioideae has a bicontinental distribution, although *Androstachys* and *Aristogeitonia* occur both in Madagascar and Africa.

MATERIALS

This report is based on first-hand examination of 97 leaf and 87 wood specimens of 61 species of Oldfieldioideae. Specimens examined are listed in Appendix 1. The specimens available represent to some degree all genera of the subfamily except *Croizatia* and *Paradrypetes*; it should be noted that leaves of *Voatamalo* and wood of *Kairothamnus*, *Scagea*, and *Stachystemon* are lacking in this study. Previous anatomical literature concerning genera of Oldfieldioideae provided by the publications listed in Appendix 2 has been incorporated into the following account as appropriate.

LEAF ARCHITECTURE

For the most part, leaves are either simple or palmately compound; however, interesting transitional morphologies do exist. Leaves of *Oldfieldia* are palmately compound, with 3–8 leaflets; those of *Celaenodendron*, *Picrodendron*, and *Piranhea* are trifoliolate; both palmately compound and simple leaves occur in *Aristogeitonia*; and leaves of *Parodiodendron* Hunz. are unifoliolate, as evidenced by the minute stipels at the apex of the petiole (Hunziker, 1969) and by the frequent disarticulation of the lamina at the same point (Fig. 4). Finally, leaves of *Micrantheum*, which occur in alternate groups of three (to five), have been interpreted as the leaflets of a palmately compound leaf which, by loss of their common petiole, are sessile on the stem (Baillon, 1858); alternatively, this unique phyllotaxy has been attributed to foliate stipules (Grüning, 1913; Webster & Miller, 1963). For the most part, leaf margins are entire, the few exceptional species being *Austrobuxus cuneatus* (Airy Shaw) Airy Shaw, *A. swainii* (de Beuzev. & C. T. White) Airy Shaw, *Choriceras tricorne* (Benth.) Airy Shaw (Figs. 7, 8), *Dissiliaria muelleri* (Baill.) ex Benth., *Paradrypetes ilicifolia* Kuhlm. (Levin, 1986), *P. subintegrifolia* G. Levin (Levin, 1992), *Tetracoccus dioicus* Parry (only some leaves), and *T. ilicifolius* Coville & Gilman. *Paradrypetes* possesses irregularly spaced spinose teeth (Levin, 1986, 1992). Teeth of *Tetracoccus ilicifolius* are the largest in the subfamily: median veins of these teeth are derived from the looped secondary veins; there are prominent brochidodromouslike loops within the tooth itself; and median veins extend nearly to the apices, which in the specimens examined appear to possess apical caps, at least in young leaves. Teeth of the remaining species are much smaller, consisting of a vein ending in a small protrusion of leaf tissue. Significantly, however, deciduous apical caps are also visible in *Austrobuxus swainii* and *Choriceras tricorne* (Figs. 7, 8). Tooth morphology in Oldfieldioideae thus conforms with the theoid type (Hickey & Wolfe, 1975). Excluding noninformative spinose teeth, theoid teeth are the only type found in Phyllanthoideae, specifically in the genera *Drypetes* Vahl, *Putranjiva* Wall., and *Bischofia*; reduced theoid teeth are also present in Aporuseae (Levin, 1986).

Venation is always pinnate, most frequently festooned brochidodromous (Figs. 2, 3). In addition to brochidodromy, however, leaves of *Longetia*
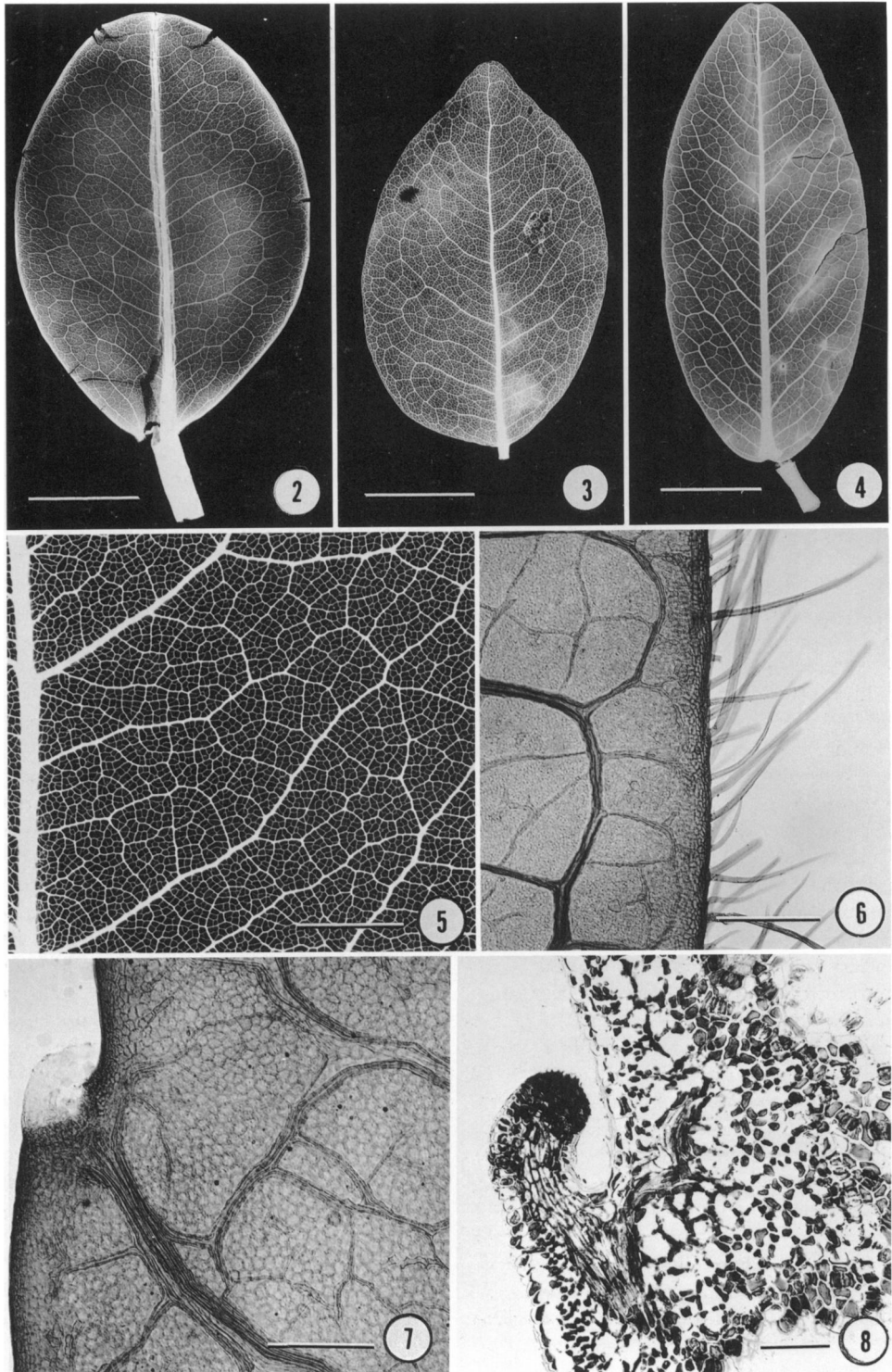
FIGURES 2–8. Leaf architectural features of Oldfieldioideae.—2. *Austrobuxus rubiginosus* (*Baumann-Bodenheim 15010*), cleared leaf, bar = 1 cm.—3. *Celaenodendron mexicanum* (*Ortega 6367*), cleared leaf, bar = 1 cm.—4. *Parodiodendron marginivillosum* (*Hueck 469*), cleared leaf, note disarticulation of petiole from base of lamina, bar = 5 mm.—5. *Picrodendron baccatum* (*Gillis 6963*), note lack of vein orders beyond tertiaries, bar = 2.5

exhibit a tendency toward eucamptodromy whereas those of *Dissiliaria, Petalostigma, Picrodendron,* and *Tetracoccus* tend toward reticulodromy. Leaves of the Australian genera of Pseudanthinae (Caletieae sensu stricto) exhibit a continuum of increasing disorganization, presumably a consequence of xeromorphy: in *Neoreopera* leaves are weakly festooned brochidrodromous; in *Micrantheum* one can find vestiges of brochidodromous venation as well as secondary veins that recurve and ramify or form a weak reticulum; in *Stachystemon* the range is from reticulodromous to kladodromous; and in *Pseudanthus* leaves are all kladodromous (Fig. 9). Primary veins are mostly of moderate size, but, especially in xeromorphic leaves, they may range to stout and massive, e.g., those of *Hyaenanche, Tetracoccus,* and the Australian Pseudanthinae (Fig. 9). Intersecondary veins are usually absent, although one or two simple intersecondaries per intercostal area occur occasionally in *Austrobuxus* and *Mischodon,* and routinely in *Croizatia* (Levin, 1986), *Oldfieldia, Paradrypetes* (Levin, 1986), *Piranhea,* and *Podocalyx.* Intersecondary veins are frequent in several primitive Phyllanthoideae, namely, *Amanoa* Aubl., *Blotia* Leandri, *Heywoodia* Sim, *Petalodiscus* Baill., *Savia* Willd., and *Wielandia* Baill. (Levin, 1986); their presence is thus postulated to be primitive for Oldfieldioideae. Tertiary vein patterns are usually random reticulate; ramified patterns occur in *Hyaenanche,* species of *Austrobuxus,* and those species of Australian Pseudanthinae that possess distinguishable tertiaries; there is a slight tendency toward transverse tertiaries in *Parodiodendron, Paradrypetes* (Levin, 1986), *Petalostigma,* and *Podocalyx;* and the tertiary veins of *Piranhea* have a slight tendency to form orthogonal patterns. Marginal venation is incomplete (Fig. 11) or looped (Fig. 6) in many genera, "hemmed" with a fimbrial vein in the genera with compound leaves (Figs. 10, 12) plus *Dissiliaria* and *Mischodon,* or dominated by a massive intramarginal vein in most Australian Pseudanthinae (Fig. 9). A distinctive furcate-flabellate form of marginal venation occurs in *Hyaenanche.*

High-order venation varies considerably within Oldfieldioideae. Perhaps most notable is the occurrence of ultimate reticula in which vein order is not distinguishable, a feature of *Celaenodendron,*

Picrodendron (Fig. 5), and *Piranhea* (all New World genera with trifoliolate leaves) plus *Androstachys;* this character state is extremely rare in the dicots as a whole (L. J. Hickey, pers. comm.) and is thus a potentially robust synapomorphy linking these genera. Areoles are well developed in the genera with compound leaves (Figs. 5, 12) plus *Dissiliaria, Mischodon, Parodiodendron* (Fig. 6), and *Podocalyx;* otherwise, areoles are imperfectly developed. Areoles are usually arranged randomly, but are oriented in *Celaenodendron* and somewhat oriented in *Picrodendron, Piranhea,* and *Dissiliaria.* Veinlets are usually present and mostly simple or branched; the degree of branching varies widely, tending to be most highly branched in leaves with low regularity of tertiary and higher order veins. Veinlets are absent in *Androstachys* (Fig. 12), but they may appear to be present upon superficial examination because of the columnar sclereids located in each areole (see below).

LEAF ANATOMY

Trichomes have been observed in about two-thirds of the genera of Oldfieldioideae. Many species are glabrescent with age, although mature leaves of *Androstachys, Parodiodendron,* and species of *Petalostigma,* for example, are clearly pubescent. Trichomes are either simple unicellular or uniseriate, generally consisting of less than six cells. Within Pseudanthinae, epidermal emergences range from small papillae to four-celled uniseriate trichomes. The densely packed trichomes of *Androstachys johnsonii* Prain, which consist of a short basal cell and long curly terminal cell, have been suggested by Alvin (1987) to function in absorption of atmospheric moisture (mists and drizzles) in the otherwise extremely arid environment of southern Africa. *Oldfieldia* possesses trichomes similar to those of *Androstachys,* arguing for some degree of relationship between these two genera despite their manifest differences in reproductive morphology. Depending on the species, trichomes of *Austrobuxus* are either simple or bifurcate (malpighiaceous). *Parodiodendron* is unique within the subfamily in possessing strongly ciliate leaf margins (Fig. 6). Rao & Raju (1985) reported uniseriate, stellate, and glandular hairs in *Dissiliaria,* characteristics reminiscent of uniovu-

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mm.—6. *Parodiodendron marginivillosum* (*Hueck 469*), margin of cleared leaf, bar = 250 μm.—7. *Choriceras tricorne* (*Forman s.n.*), tooth at margin of cleared leaf, bar = 250 μm.—8. *Choriceras tricorne* (*Forman s.n.*), paradermal section through tooth at leaf margin, note glandular apex, bar = 100 μm.
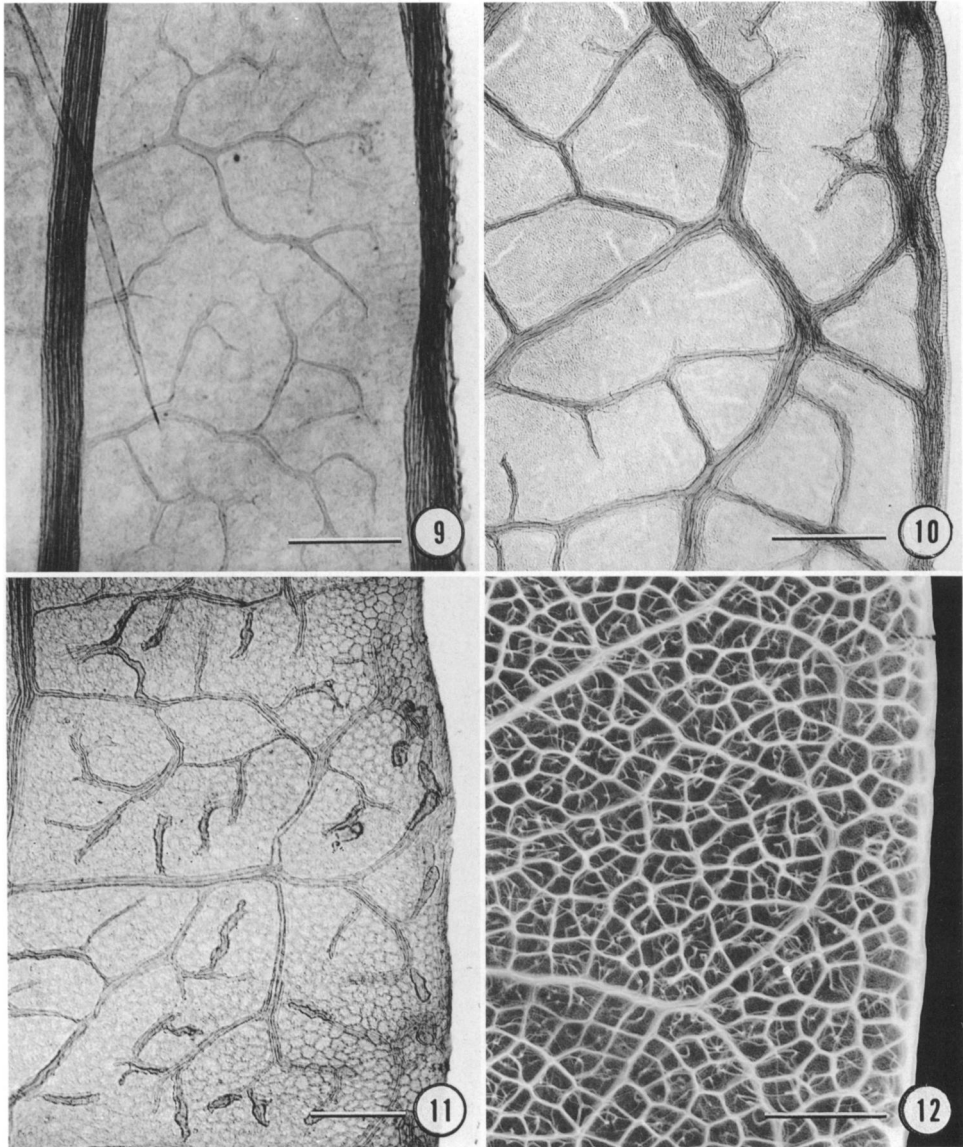
FIGURES 9–12.   Leaf architecture of Oldfieldioideae.—9. *Pseudanthus orientalis* (*Clemens 44092*), kladodromous venation, massive primary and intramarginal veins, bar = 250 μm.—10. *Celaenodendron mexicanum* (*Ortega 6367*), fimbrial vein (far right), bar = 250 μm.—11. *Petalostigma banksii* (*Perry 1981*), branched veinlets with swollen ultimate tracheids, bar = 100 μm.—12. *Androstachys johnsonii* (*Wellcome Chemical Research Laboratory s.n.*), well-developed areoles with columnar sclereids, veinlets absent, bar = 1 mm.

late euphorbs that would be unique to Oldfieldioide-
ae; however, neither trichomes nor their bases were
detected in the leaves available to me.

The epidermis is fundamentally uniseriate. How-
ever, a single layer of hypodermis has been re-
ported for *Paradrypetes* (Milanez, 1935) and some
or all epidermal cells of the Australasian genera
have a horizontal partition resulting in a poorly to
well-defined hypodermis (Figs. 17–19). The inner

cell or chamber thus formed contains mucilage,
which is common in other genera as well. Expansion
of the mucilaginous layer in Australian Pseudan-
thinae greatly distends the adaxial epidermis (Figs.
18, 19); while the grossly expanded mucilaginous
layer may well be an artifact of preparation, it is
derived solely from the lower portions of subdivided
epidermal cells and is not thickly multicellular as
depicted by Gaucher (1902), whose erroneous in-
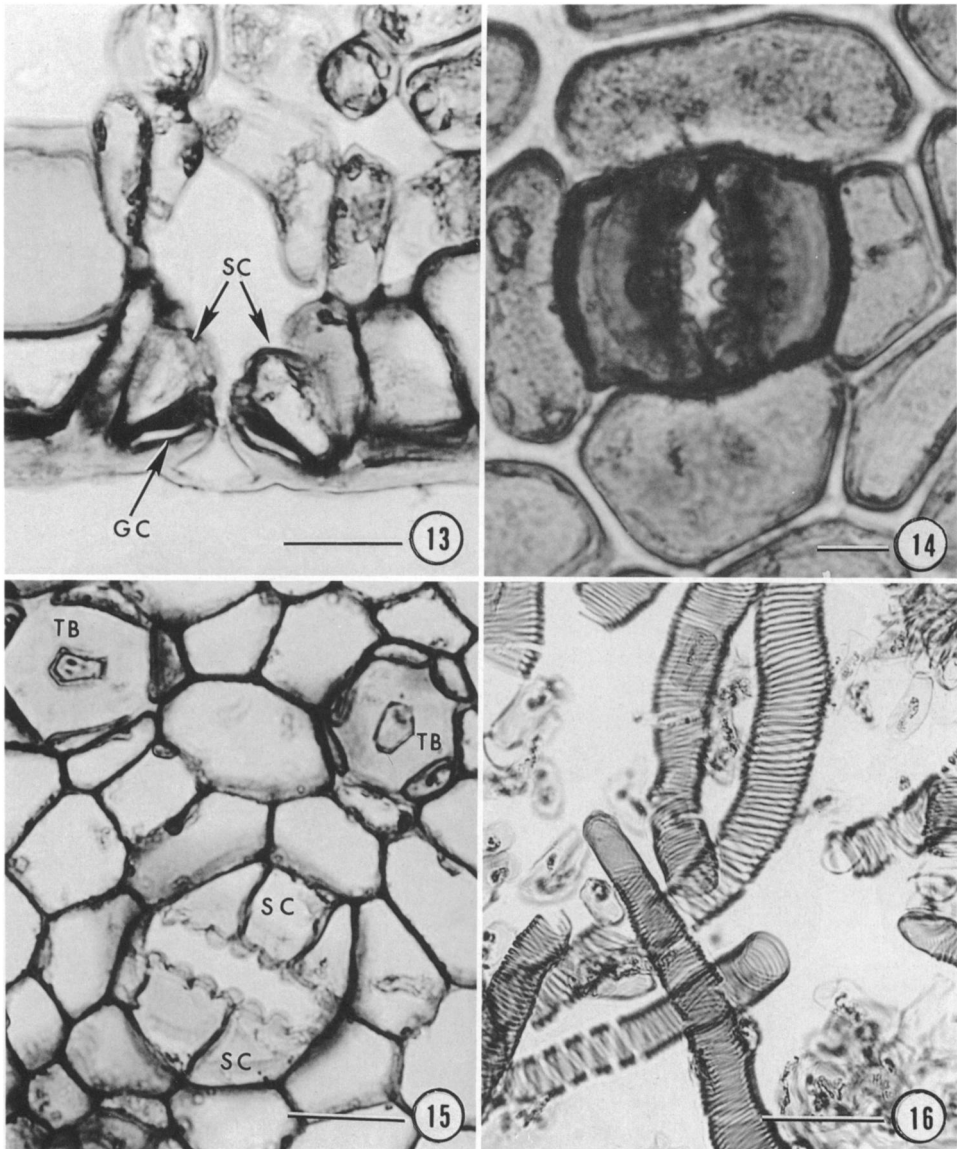
FIGURES 13-16.   Leaf anatomy of Oldfieldioideae.—13. *Longetia buxoides* (*Baumann-Bodenheim 5605*), sto-mate from cross section, bar = 20 μm.—14. *Scagea oligostemon* (*McKee 2352*), surface view of stomate from paradermal section, note crenulate inner anticlinal walls of subsidiary cells visible through stomatal aperture, bar = 10 μm.—15. *Austrobuxus huerlimannii* (*McKee 4850*), subdivided crenulate subsidiary cells and trichome bases from paradermal section, bar = 20 μm.—16. *Podocalyx loranthoides* (*Krukoff 811*), tracheoid idioblasts from macerated mesophyll, bar = 20 μm. GC = guard cell, SC = subsidiary cell, TB = trichome base.

terpretation has been reiterated by others (e.g., Metcalfe & Chalk, 1950; Raju & Rao, 1977). So far, no mucilage has been detected in *Aristogei-tonia, Celaenodendron, Mischodon, Piranhea,* and *Podocalyx*. Mucilaginous epidermis is known in several Phyllanthoideae, for example, *Actephila* Bl., *Antidesma* L., *Aporusa* Bl., *Amanoa, Bac-caurea* Lour., *Bridelia* Willd., *Hyeronima* Fr. Al-lem, *Phyllanthus* L., *Richeria,* and *Savia* (Met-calfe & Chalk, 1950). In surface view, anticlinal walls of epidermal cells are generally straight (Figs. 14, 15), the only exceptions being *Aristogeitonia, Celaenodendron, Piranhea,* (all members of Pi-crodendreae), and *Dissiliaria,* in which these walls have a wavy outline; intriguingly, paradermal sec-tions of *Aristogeitonia* and *Celaenodendron* reveal
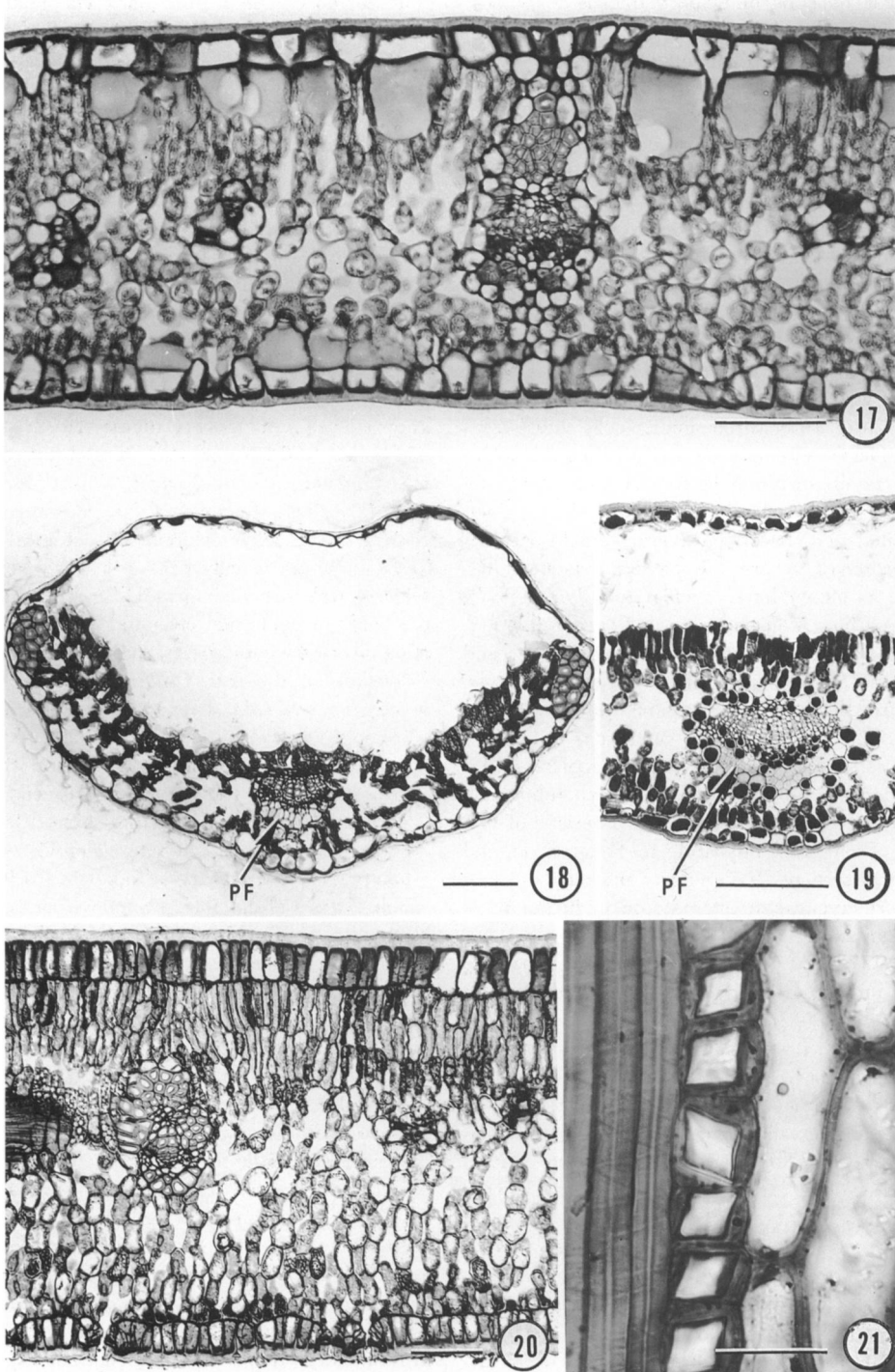
FIGURES 17–21. Leaf anatomy and wood parenchyma of Oldfieldioideae.—17. *Longetia buxoides* (*Baumann-Bodenheim 5605*), leaf cross section, note chambered mucilaginous epidermal cells, bar = 100 μm.—18. *Pseudanthus orientalis* (*Wilson 679*), leaf cross section, note grossly expanded mucilaginous hypodermis and prominent intra-marginal veins, bar = 100 μm.—19. *Micrantheum hexandrum* (*McGillivray 3196*), cross section of primary vein, note grossly expanded mucilaginous hypodermis, bar = 100 μm.—20. *Hyaenanche globosa* (*Godfrey SH 1257*), cross section of leaf, bar = 100 μm.—21. *Piranhea trifoliata* (*Ducke s.n.*, *USw 31485*), normal and chambered crystalliferous axial xylem parenchyma cells, bar = 15 μm. PF = phloem fibers.

the inner portions of epidermal cells to possess straight anticlinal walls.

Leaves are overwhelmingly hypostomatic, although both hypo- and amphistomatic conditions occur in species of *Petalostigma* and *Tetracoccus*. Stomatal type is anomocytic in *Podocalyx*, paracytic in *Paradrypetes* (Levin, 1986), but otherwise brachyparacytic (Fig. 14) or derived from a brachyparacytic pattern. For example, intruding lobes of adjacent cells tend to form an anomocytic pattern in *Tetracoccus* as viewed from the surface; paradermal sections, however, reveal typical brachyparacytic configurations. The most frequent modification of stomatal type is the tendency for one or both of the subsidiary cells to become subdivided into two or three smaller cells; subdivision of subsidiary cells may be a consistent feature in a given taxon, or it may be sporadic, affecting only some stomata or only one subsidiary cell of a given pair. Subdivided brachyparacytic stomata occur in *Androstachys*, where the pattern has been described as incompletely cyclocytic (Alvin, 1987), *Aristogeitonia*, some species of *Austrobuxus* (Fig. 15), *Hyaenanche*, *Mischodon*, *Picrodendron*, and *Pseudanthus*. The paracytic stomata of *Paradrypetes* are also subdivided in a similar fashion (Levin, 1986). The distribution of subdivided subsidiary cells does not follow any obvious taxonomic grouping within the subfamily. Within Phyllanthoideae, brachyparacytic stomata are characteristic of Brideilieae, Drypeteae, Phyllantheae–Fleuggeinae, and certain genera of Wielandieae; moreover, subdivided brachyparacytic stomata occur in *Lachnostylis* Turcz. and *Bridelia* (Levin, 1986). Raju & Rao (1977) reported brachyparacytic stomata to be the most common type among woody genera throughout Euphorbiaceae.

In most genera subsidiary cells extend partially over the inner periclinal walls of adjacent guard cells in a "semi-piggyback" fashion (Fig. 13); the inner anticlinal walls of subsidiary cells thus delimit an inward extension of the stomatal pore. Within Phyllanthoideae, Levin (1986) noted a similar spatial relationship of guard and subsidiary cells only in *Drypetes*. The inner anticlinal walls of "piggyback" subsidiary cells may have crenulate outlines (Figs. 14, 15), a feature first observed by Solereder (1908) in *Micrantheum* and *Pseudanthus* that now proves characteristic of the Australasian genera (*Mischodon* and certain species of *Austrobuxus* excluded) plus the South African genus *Hyaenanche*; this feature defines a distinct clade within the subfamily. Crenulate subsidiary cells are only weakly developed in the single specimen of *Whyanbeelia* available for study. In contrast to most genera, subsidiary and guard cells are coplanar in *Oldfieldia* and *Parodiodendron*.

Mesophyll is bilateral except in some species of *Petalostigma* with isobilateral leaves; leaves of *Hyaenanche* approach an isobilateral condition (Fig. 20). Spongy mesophyll with well-developed intercellular spaces but a tendency toward vertical alignment of cells occurs in *Androstachys*, *Oldfieldia*, *Picrodendron*, and *Piranhea*, all members of Picrodendreae. Mesophyll usually contains scattered druses; prismatic crystals are also present in *Aristogeitonia*, *Austrobuxus*, *Dissiliaria*, *Hyaenanche*, *Longetia*, and *Micrantheum*. Mesophyll of *Paradrypetes* contains raphide bundles (Milanez, 1935; Levin, 1986), a structure otherwise unknown in Euphorbiaceae (Gaucher, 1902; Metcalfe & Chalk, 1950). No crystals were observed in the mesophyll of *Celaenodendron*, *Parodiodendron*, and *Piranhea*. Except for *Androstachys* and *Stachyandra*, foliar sclereids are absent; areoles of these genera usually contain a single columnar sclereid with ramified tips that run parallel with the bases of epidermal cells and eventually intermingle with trichome bases and the bundle sheath extensions of the veins. Alvin (1987) has interpreted the sclereids of *Androstachys* to function in apoplastic transport from its water-absorbant trichomes. It is intriguing to speculate that the vertically oriented spongy mesophyll cells of *Androstachys* may have served as a preadaptation for the evolution of its columnar sclereids. Another unique mesophyll feature is found in *Podocalyx*, which bears unbranched, sinuous tracheoid idioblasts with spirally thickened, nonlignified walls (Fig. 16). These elements, occurring most frequently between the junction of palisade and spongy layers, are sufficiently abundant to obscure the presence of veinlets in clearings; they are not, however, directly connected to any vasculature.

Vasculature of the primary vein consists of adjacent (colateral) regions of xylem, phloem, and phloem fibers. Little taxonomic significance can be read into the overall configuration of primary vein vasculature, which ranges from broad shallow arcs to more tightly curved u-shaped arcs to closed loops; reduced leaves of desert xerophytes, however, tend to have patterns with minimal curvature (Figs. 18, 19). Phloem fibers of the primary vein in *Petalostigma* and the Australian Pseudanthinae are unlignified (Figs. 18, 19), in sharp contrast to the usual lignified condition of these cells in the rest of the subfamily. Smaller veins are frequently associated with a parenchymatous bundle sheath (Fig. 17). Bundle sheath extensions that are merely parenchymatous occur in *Longetia* (Fig. 17); crys-

tals are present in bundle sheath extensions of *Aristogeitonia, Celaenodendron, Hyaenanche, Mischodon, Oldfieldia, Parodiodendron, Petalostigma, Picrodendron,* and *Piranhea*; and at least some fibrous elements are also present in those of *Androstachys, Mischodon,* and *Piranhea*. Overall, bundle sheath extensions seem best developed in the genera bearing compound leaves, but also occur sporadically elsewhere in the subfamily. Swollen terminal tracheids of veinlets occur in some *Austrobuxus, Choriceras, Hyaenanche, Longetia, Petalostigma* (Fig. 11), and *Tetracoccus*.
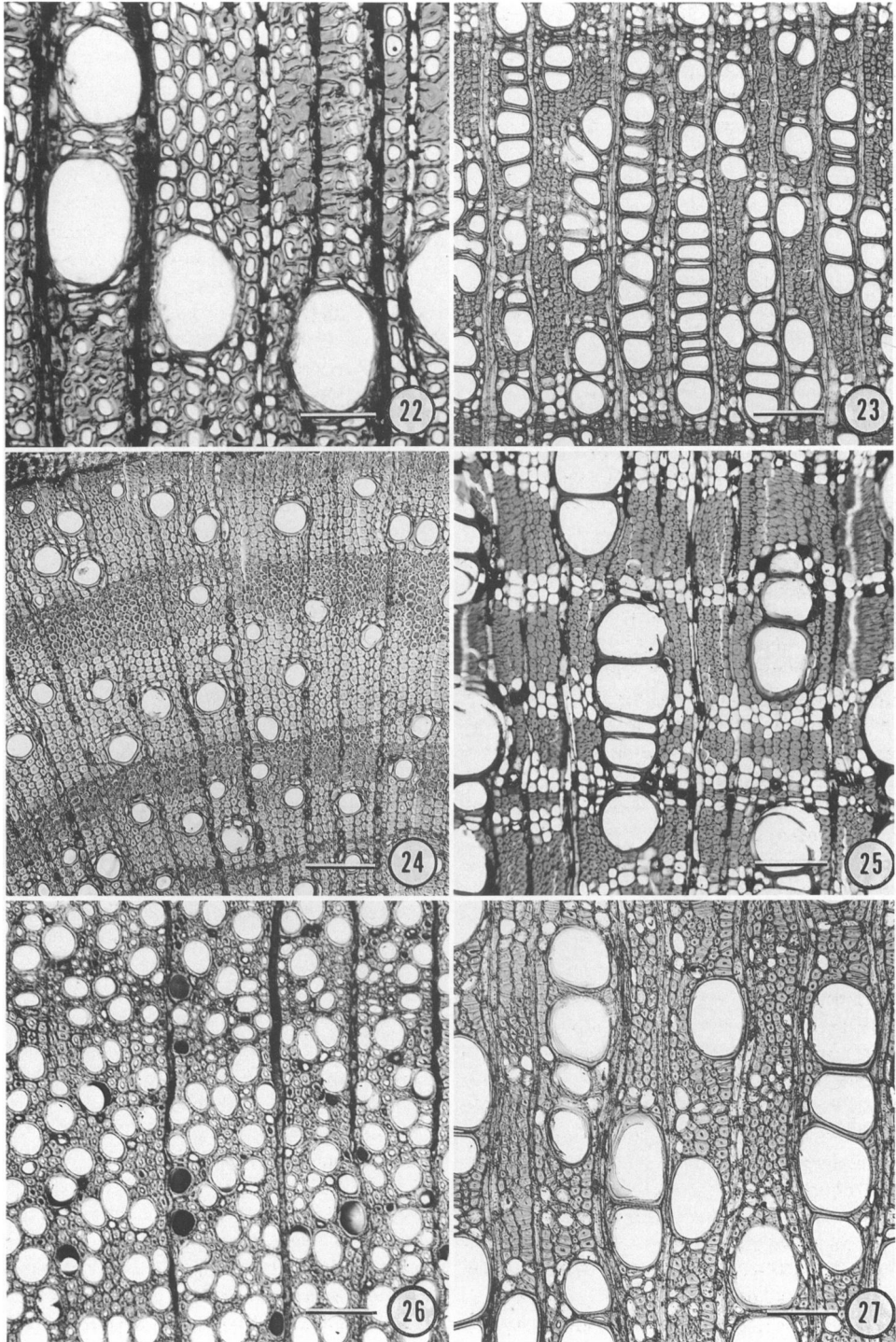
WOOD ANATOMY

Growth rings are often absent or only faintly visible. Growth rings are present, however, in *Androstachys, Celaenodendron* (Fig. 23), *Parodiodendron, Petalostigma, Podocalyx, Tetracoccus,* and Australian Pseudanthinae (Fig. 24); except for *Podocalyx*, from the upper Amazon and Orinoco drainage basins, these are plants of dry habitats with strongly seasonal availability of moisture. Pores are evenly distributed (i.e., diffuse porous in species with growth rings), except in the ring porous wood of *Tetracoccus*, which extends into desert regions of western North America. Pore outlines are mostly circular, generally small, and usually less than 100 μm diam.; pore diameters are often less than 50 μm in the genera mentioned above from dry habitats. Perforation plates are overwhelmingly simple, but scalariform plates are found in *Paradrypetes* (exclusively so according to Mennega (1987), mixed with simple perforations according to Araujo & Mattos Filho (1984)) and mixed simple, scalariform (Fig. 30), and reticulate plates characterize *Podocalyx*. Intervascular pits are transitional in *Paradrypetes* and *Podocalyx*; otherwise they are alternate and mostly small, ca. 5 μm or less. Very small intervascular pits (2–3 μm) are found in *Aristogeitonia, Neoroepera,* and *Pseudanthus*; somewhat larger than usual pits (6–8 μm) occur in *Austrobuxus, Celaenodendron, Parodiodendron, Picrodendron, Piranhea,* and *Podocalyx*. Vessel element lengths for most genera fall within the range of 400–700 μm; vessel elements are somewhat shorter in *Picrodendron* (ca. 300 μm), somewhat longer in *Dissiliaria* (ca. 800 μm), *Austrobuxus* (ca. 950 μm), and *Paradrypetes* (ca. 1200 μm), and longest in *Podocalyx* (ca. 1250 μm). Sculpture on the inner surface of vessels is rare; some vessels of *Choriceras* possess spiral thickenings; thickenings are characteristic of *Whyanbeelia* (spiral only) and *Tetracoccus* (spiral

to reticulate). Tyloses and/or tannins are common in lumina of heartwood vessels; silica deposits occur in lumina of *Whyanbeelia*.

Imperforate tracheary elements bear either simple or bordered pits. Elements with simple pits, i.e., libriform wood fibers, characterize the genera with compound leaves (*Aristogeitonia, Celaenodendron, Oldfieldia, Piranhea,* and *Picrodendron*) plus *Dissiliaria, Hyaenanche,* and *Petalostigma*; some of these may also possess elements with bordered pits. The remaining genera possess only elements with bordered pits; these cells are probably best characterized as fiber-tracheids by virtue of their relatively small pit borders and thick walls. However, because intervascular pits in some oldfieldioids are remarkably small, *Androstachys, Aristogeitonia,* and the Australian genera of Pseudanthinae, for example, pits of imperforate elements may be approximately equal to or slightly larger than intervascular pits in the same wood; by the criteria of Bailey (1936) such elements would be tracheids, by definition, despite their thick walls and pit diameters of 5 μm or less. "Tracheid," with its connotation of primitive conducting element, hardly seems appropriate for such cells. On the other hand, the tracheids of *Podocalyx*, with pit diameters up to 13 μm, attest more convincingly to primitive structure, and both fiber-tracheids and tracheids are present in *Austrobuxus*, distinguishable by both wall thickness (Fig. 22) and pit size. Bands of gelatinous fibers occur in woods of Australian Pseudanthinae (Fig. 24), *Hyaenanche,* and *Tetracoccus*. Imperforate elements often possess such thick cell walls that lumina appear completely closed; Bamber (1974) noted that these thick-walled fibers lack an easily detectable S3 layer in *Austrobuxus, Dissiliaria,* and *Petalostigma*. Fibers are septate only in *Parodiodendron*.

Rays are numerous, generally more than 15 per mm; however, there are more than 20 per mm in Australian Pseudanthinae, and only 12 per mm in *Androstachys* and *Oldfieldia*. High ray frequencies are probably related to the general narrowness of individual rays. Rays are mostly 1-, 2-, or 3-seriate, but up to 4- or 5-seriate rays occur in *Choriceras, Dissiliaria, Aristogeitonia,* and *Tetracoccus* (Fig. 33). Polymerous (vertically fused) rays are usually common (Fig. 32); however, they are infrequent or absent in *Androstachys* (Fig. 31), *Choriceras, Parodiodendron, Tetracoccus,* and the Australian Pseudanthinae. Aggregate rays were observed in *Choriceras* only. Rays are usually heterocellular (Figs. 28, 29), which is generally considered the primitive condition. Homocellular procumbent rays are shared by *Androstachys* and

FIGURES 22–27. Wood anatomy of Oldfieldioideae.—22. *Austrobuxus swainii* (*deBeuzeville s.n., MADw 10449*), note thin- and thick-walled fibers.—23. *Celaenodendron mexicanum* (*Ortega 35, USw 3886*), note long radial multiples of pores and boundaries of growth ring (top and bottom).—24. *Micrantheum hexandrum* (*Whaite & Whaite 3536*), note bands of gelatinous fibers.—25. *Piranhea trifoliata* (*Ducke s.n., USw 31485*), note banded distribution of axial xylem parenchyma.—26. *Androstachys johnsonii* (*Pretoria UIND 2127, Uw 21991*).—27. *Oldfieldia africana* (*Cooper 88, USw 4517*). All bars = 100 μm.

TABLE 1. Wood structure of biovulate euphorbs, after Metcalfe & Chalk (1950).

Feature	Aporusa-type	"Other genera"	Glochidion-type
Perforations	scalariform, simple, or both	simple	simple
Fibers	nonseptate, thick-walled	nonseptate, thick-walled	septate, thin to moderately thick-walled
Parenchyma	abundant, diffuse or narrow bands	abundant, diffuse to wide bands	absent or scanty

some species of *Oldfieldia*, which serves to demonstrate that these woods are not as dramatically distinct as Metcalfe & Chalk (1950) suggested. Homocellular square to erect rays are one of several synapomorphies that mark the Australian genera of Pseudanthinae as a distinct monophyletic group. Vessel to ray pits are of two forms that appear to hold great systematic significance. The most distinctive pattern consists of highly irregular pits that range from circular to elongate with the elongate pits at various orientations: vertical, horizontal, or diagonal (Fig. 28). This irregular pattern is interpreted as primitive by virtue of its resemblance to primitive transitional intervascular pitting, and by its occurrence in *Paradrypetes* and *Podocalyx* (see below); irregular vessel-ray pits have been retained by all arborescent Australasian genera. All other genera possess uniform vessel-ray pits that are circular and alternate. If circular, alternate vessel-ray pits are indeed the derived character state, this feature evolved twice, since the Australian Pseudanthinae (i.e., Caletieae sensu stricto) are clearly derived from the lineage bearing the arborescent genera of Australasia (see below), rather than the lineage of African and American genera. Ray cells generally bear only tannins, but several exceptions occur: prismatic crystals are sporadic in *Podocalyx*, abundant in *Paradrypetes* (Araujo & Mattos Filho, 1984); silica deposits are common in *Petalostigma*; and sclerified cells bearing a prismatic crystal are abundant in *Aristogeitonia*, *Mischodon*, and *Tetracoccus fasciculatus*; these crystalliferous cells are only rarely present in *Voatamalo*. Perforated ray cells are sporadic in *Paradrypetes* (Milanez, 1935), *Podocalyx*, and *Hyaenanche*, but have not been observed in other Oldfieldioideae. Perforated ray cells are fairly widespread in Euphorbiaceae according to Giraud (1983), who recorded this feature in the following phyllanthoid genera: *Aporusa*, *Baccaurea*, *Bridelia*, *Cleistanthus* Hook. f. ex Planch., *Drypetes*, *Hyeronima*, and *Richeria*. Perforated ray cells are also present in *Putranjiva* (Nazma et al., 1981) and *Amanoa* (unpublished obs.).

Axial xylem parenchyma is mostly diffuse and diffuse-in-aggregates (Fig. 27), with bands also present in *Aristogeitonia*, *Dissiliaria*, *Parodiodendron* (strictly initial bands), *Picrodendron*, *Piranhea* (Fig. 25), and *Voatamalo*; on the other hand, parenchyma is infrequent and restricted to a few abaxial scanty paratracheal cells in *Androstachys*, *Stachyandra*, and the Australian genera of Pseudanthinae (Fig. 24). Parenchyma strands usually contain both ordinary cells and short sclerified cells bearing a single prismatic crystal (Fig. 21); crystalliferous parenchyma is absent, however, in *Paradrypetes*, *Podocalyx*, *Petalostigma*, *Whyanbeelia*, the Australian genera of Pseudanthinae, and most specimens of *Tetracoccus*. Since sclerified crystalliferous axial xylem parenchyma cells are common in several phyllanthoid woods (e.g., *Amanoa* and *Drypetes*), presence of such cells may be considered primitive for Oldfieldioideae; their loss may well be synapomorphous for *Petalostigma*, *Whyanbeelia*, and the Australian genera of Pseudanthinae; loss in others (e.g., *Paradrypetes*, *Podocalyx*, and most specimens of *Tetracoccus*) may represent convergent developments.

ORIGIN OF OLDFIELDIOIDEAE

EVIDENCE FROM WOOD ANATOMY

The analysis of wood structure of biovulate euphorbs contained in Metcalfe & Chalk (1950) provides a convenient starting point for discussion of relationships between Phyllanthoideae and Oldfieldioideae. In this work, three groups of genera were distinguished, as indicated in Table 1. At the most superficial of levels, woods of Oldfieldioideae, largely included in Metcalfe & Chalk's "other genera," may be characterized as a combination of the vessel features of *Glochidion*-type woods and the fiber and parenchyma features of *Aporusa*-type woods, the latter two categories consisting primarily of phyllanthoid genera. In some instances these three coarsely defined categories provide a useful perspective for placing genera; for example, the re-

moval of *Neowawraea* Rock, which has *Glochidion*-type wood, from *Drypetes*, which has *Aporusa*-type wood, and its subsequent submergence into *Flueggea* Willd., which also has *Glochidion*-type wood (Hayden & Brandt, 1984; Hayden, 1987).

However, as wood structure of biovulate euphorbs has become better known, genera with wood that is transitional between the three categories cloud what once appeared to be a clear picture. For example, Mennega (1984) found tribal placement of *Jablonskia* Webster difficult, essentially because the wood of *Jablonskia* has an unusual combination of characters: specifically, vessel features of *Aporusa*-type woods and fiber and parenchyma features of *Glochidion*-type woods. In short, *Jablonskia* represents the reverse of the combination that characterizes most oldfieldioids. Mennega (1987) has noted additional transitional genera in her extensive survey of wood structure in Phyllanthoideae; moreover, woods of some phyllanthoids, e.g., *Lachnostylis* Turcz. and *Savia*, match the typical oldfieldioid pattern described above. Further, within Oldfieldioideae, *Podocalyx* and *Paradrypetes* possess essentially typical expressions of *Aporusa*-type structure. Clearly, the simple rubric of three wood types for biovulate euphorbs requires modification.

An evolutionary perspective of anatomical characters helps to clarify some of the complexity seen in woods of biovulate euphorbs. In accord with widely accepted hypotheses of wood evolution, Mennega (1987) has identified woods with long vessel elements, long scalariform perforation plates, medium to large intervascular pits, long thick-walled nonseptate fibers with bordered pits on both radial and tangential walls, and diffuse or narrowly banded axial xylem parenchyma to be primitive within Phyllanthoideae. Extant genera such as *Aporusa*, *Blotia*, and *Protomegabaria* Hutch. retain these features. Carlquist (1975) has argued convincingly that primitive vessel features are adaptive only in uniformly moist forest environments that impose minimal demands for water conduction. It may be assumed that adaptive radiation of primitive biovulate euphorbs into drier, or seasonally drier, habitats would be accompanied by evolution of more advanced vessel features. Similarly, one may reasonably suppose exploitation of nonforest and/or seasonal habitats to be associated with modification of mechanical and storage requirements of the wood; such changes would be manifest in both fiber and parenchyma features. Much of the diversity of biovulate euphorb wood structure may thus be interpreted in terms of divergence from primitive

Aporusa-type structure, an ecologically restrictive syndrome of xylem features.

Within Phyllanthoideae, *Aporusa*- and *Glochidion*-type structure represent evolutionary extremes, but numerous transitional forms can be identified from Mennega's (1987) data. For example, tracking both perforation plates and development of septate fibers yields the following series of forms that may be viewed as intermediates between *Aporusa*- and *Glochidion*-type structure: *Actephila*, *Chascotheca* Urb., and *Pentabrachium* Muell. Arg. with exclusively scalariform perforations and some septate fibers; *Celianella* Jabl., *Didymocystis* Kuhlm., and *Jablonskia* with mixed simple and scalariform perforations and some septate fibers; *Astrocasia* Rob. & Greenm. and *Discocarpus* Klotzsch with simple perforations, but only some septate fibers. Similarly, within *Aporusa*-type woods, there is a clear transition of perforation plates from exclusively scalariform in *Aporusa*, *Heywoodia*, *Hyeronima*, *Maesobotrya* Benth., and *Putranjiva*, to mixed simple and scalariform in numerous genera and, finally, to exclusively simple in *Lachnostylis* and *Savia*. Of course, such sequences of extant genera should not be interpreted as the actual course of xylem evolution within Phyllanthoideae.

In terms of the gross vessel, fiber, and parenchyma features of Table 1, the evolutionary transformation of wood in Oldfieldioideae seems parallel to that noted for *Aporusa*-type woods. In comparison, Phyllanthoideae experienced a greater range of wood diversification with the additional development of *Glochidion*-type woods.

Within Oldfieldioideae, *Podocalyx* and *Paradrypetes* stand out as probably the most primitive woods by virtue of their very long vessel elements, multiple perforation plates, and large transitional intervascular pits; presence of perforated ray cells in these genera may also be interpreted as primitive features. Overall, their woods are comparable to primitive phyllanthoid woods with *Aporusa*-type structure. The primitive woods of *Paradrypetes* and *Podocalyx* excepted, Oldfieldioideae generally have exclusively simple perforation plates and have lost perforated ray cells, but otherwise retain the features of *Aporusa*-type structure (cf. comments on *Lachnostylis* and *Savia*, above). Much of the diversity of oldfieldioid woods is restricted largely to what are, perhaps, minor themes such as element size (Figs. 22–27), vessel grouping (Figs. 22–27), ray dimensions (Figs. 31–33), vessel-ray pitting, and parenchyma distribution (Figs. 22–27). These minor themes, however, are responsible for con-
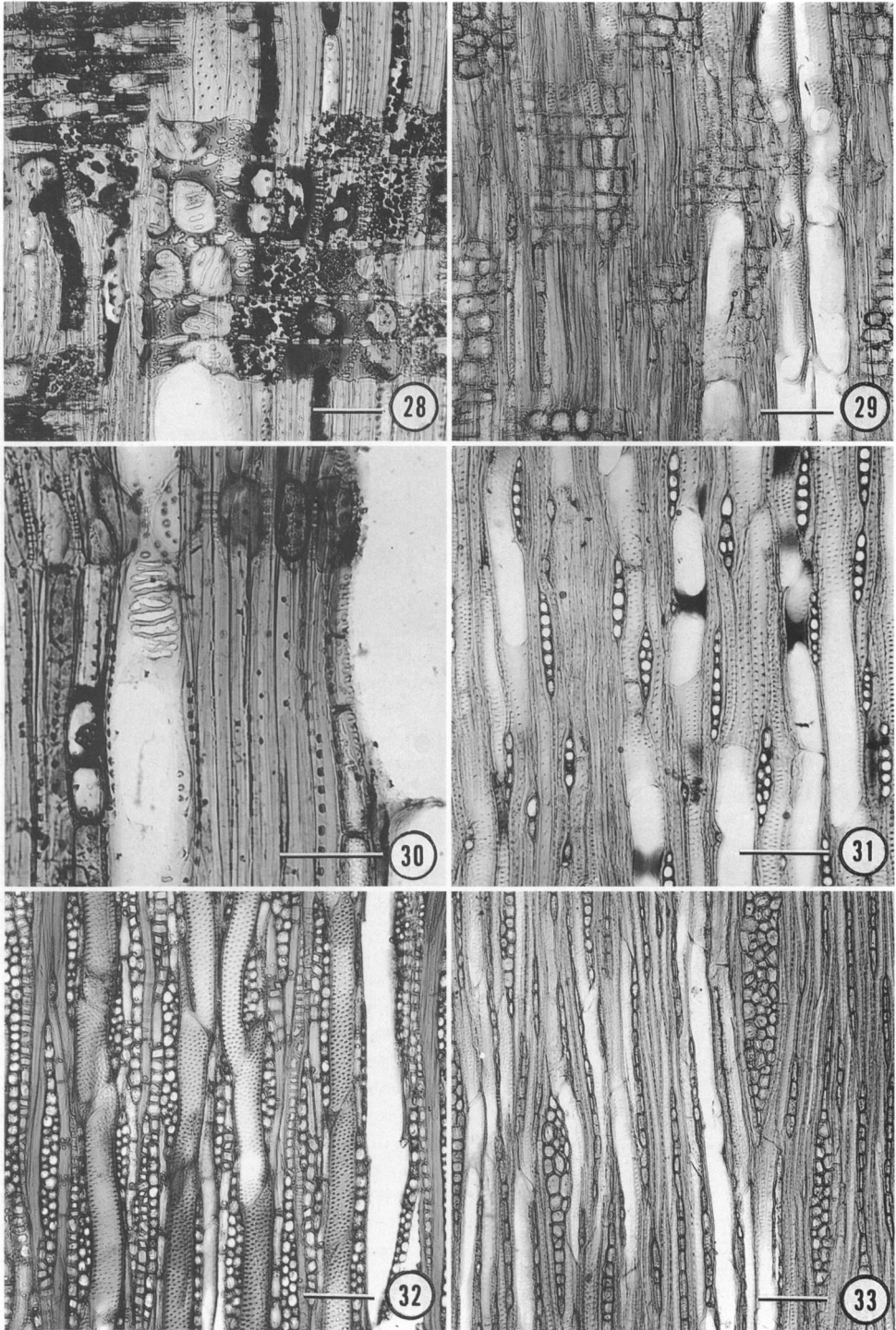
FIGURES 28–33. Wood anatomy of Oldfieldioideae.—28. *Austrobuxus swainii* (*Symington s.n., Uw 21411*), radial section, heterocellular ray and irregular slitlike vessel-ray pits.—29. *Petalostigma* sp. (*SFCw R594-2*), radial section, heterocellular rays and simple perforation plates.—30. *Podocalyx loranthoides* (*Wurdack·& Adderley 42795, MADw 22429*), radial section, scalariform perforation plate.—31. *Androstachys johnsonii* (*Pretoria UIND 2127, Uw 21991*), tangential section, short and narrow rays.—32. *Celaenodendron mexicanum* (*Ortega 35, USw 3886*), tangential section.—33. *Tetracoccus fasciculatus* var. *fasciculatus* (*Johnston 7783*), tangential section, wide rays. All bars = 100 μm.

siderable diversity of oldfieldioid woods; based on wood features alone, it is entirely understandable that Metcalfe & Chalk (1950) sought to associate oldfieldioid genera with woods from other subfamilies.

The presence of somewhat primitive woods (*Paradrypetes* and *Podocalyx*) in Oldfieldioideae suggests that the divergence of Oldfieldioideae from Phyllanthoideae occurred quite early in the evolution of Euphorbiaceae, from ancestral stocks with relatively primitive *Aporusa*-type woods. The symplesiomorphous nature of wood features at the evolutionary transition between the subfamilies precludes the possibility of specifying one or another phyllanthoid group as closest to the origin of Oldfieldioideae based on this tissue alone.

Septate fibers, common in phyllanthoids with *Glochidion*-type structure, occur in only one oldfieldioid, *Parodiodendron*. One prominent difference, however, between this wood and the *Glochidion*-type phyllanthoids is its fairly abundant parenchyma present in initial bands, diffuse apotracheal and scanty paratracheal configurations. Typical expressions of *Glochidion*-type structure include very little parenchyma at all. The occurrence of septate fibers in *Parodiodendron* may thus represent convergence.

EVIDENCE FROM STOMATAL STRUCTURE

Configuration of the stomatal apparatus is one of the most consistent features of leaves of Oldfieldioideae. Most genera possess brachyparacytic patterns in which the subsidiary cells substantially overlie the adjacent guard cells. In this regard, Levin (1986), upon whose data much of the following is based, has shown stomatal patterns of the phyllanthoid tribes to be fairly diverse; in fact, this character provides important evidence in identifying which phyllanthoids are closest to the origin of Oldfieldioideae. As argued above, it will be necessary only to consider tribes with *Aporusa*-type wood structure. Aporuseae may be eliminated from further consideration by its consistently anisocytic stomata, a pattern never found in Oldfieldioideae. Paracytic or brachyparacytic stomata are found in the remaining tribes under consideration, i.e., Amanoeae, Antidesmeae, Drypeteae, and Wielandieae, with brachyparacytic in only Drypeteae and some Wielandieae. Subsidiary cells in *Drypetes*, like those of most Oldfieldioideae, partially overlie the adjacent guard cells. The brachyparacytic subsidiary cells of *Lachnostylis* (tribe Wielandieae) are frequently subdivided (Levin, 1986), another common character in Oldfieldioideae. Unfortunately, the distribution of stomatal characters in

Phyllanthoideae and Oldfieldioideae precludes any simple statement about the point of divergence of the two subfamilies. Both characater states of three important characters (paracytic-brachyparacytic, entire-subdivided subsidiary cells, and coplanar-"piggyback" subsidiary cells) are found in both groups. This situation may be viewed as an example of Cronquist's (1988) assertion that parallel tendencies are reasonably good indicators of relationships; a rigorous cladistic analysis of Phyllanthoideae and Oldfieldioideae should distinguish the synapomorphic stomatal characters from the parallelisms.

ADDITIONAL EVIDENCE

A number of anatomical characters such as the occurrence of theoid teeth, intersecondary veins, and mucilaginous epidermis in Oldfieldioideae and primitive Phyllanthoideae are consistent with the former's derivation from the latter. Floral structure of Wielandieae is sufficiently generalized to be consistent with ancestral status. However, plesiomorphous characters such as these do not present by themselves an overly compelling case for consanguinity.

On the other hand, the often reduced carpel number and drupaceous fruits of *Drypetes* show greater (or, at least, different) specialization than that found in many Oldfieldioideae. Further, chromosome numbers of $n = 20$ for *Putranjiva* (Gill et al., 1981) and $2n = 40$ for *Drypetes* (Webster, 1967) are difficult to resolve with the counts suggesting $x = 12$ for Oldfieldioideae (see above). Extant Drypeteae are thus unsuitable as progenitors for Oldfieldioideae, but it remains conceivable that these taxa may have shared a common ancestor.

Levin & Simpson (1988) noted that the spinules and discontinuous exine foot layer in pollen of *Securinega* Comm. ex Juss. sensu stricto suggested a close relationship with Oldfieldioideae. Despite exclusively simple perforation plates, the wood of *Securinega* conforms well to the *Aporusa*-type (and thus may be out of place in tribe Phyllantheae, as pointed out by Mennega (1987)). *Securinega* also possesses paracytic stomata (Gaucher, 1902). Further anatomical data would be most useful. In our present state of ignorance, *Securinega* stands as another possible near relative to Oldfieldioideae.

SUMMARY

Taken together, stomatal and wood characters suggest that Oldfieldioideae diverged from the early differentiation of the primitive biovulate tribe Wielandieae perhaps along some of the same lines that

ultimately led to the modern genera *Drypetes* and/ or *Securinega*. In a larger context, presence of theoid teeth and palmately compound leaves in Oldfieldioideae lends support to Dilleniid rather than Rosid derivation of Euphorbiaceae (cf. discussion in Levin (1986)).

RELATIONSHIPS WITHIN OLDFIELDIOIDEAE

Classification of subfamily Oldfieldioideae has been in a state of flux over the past three decades. The following discussion focuses on anatomical data as indicators of relationships within Oldfieldioideae, specifically, the role of anatomy in modification of early classifications of Oldfieldioideae (Köhler, 1965; Webster, 1975) and the extent that anatomy supports the most recent classifications of these plants (Levin & Simpson, 1994; Webster, 1994).

Tribe Croizatieae Webster. Croizatia, the only genus of the tribe, is anatomically unknown.

Tribe Podocalyceae Webster. The genera associated with *Podocalyx* have undergone radical revision in the brief history of Oldfieldioideae. Köhler (1965) grouped *Podocalyx* with several genera of tribe Picrodendreae that have compound leaves plus *Tetracoccus*, whereas Webster (1975) associated it with some of the simple-leaved genera of Picrodendreae plus, again, *Tetracoccus*. As discussed below, the genera of Picrodendreae, whether bearing simple or compound leaves, form a reasonably well-defined clade and are thus better classified elsewhere. Of the two classifications presented in this volume, both link *Podocalyx* with *Paradrypetes*, albeit each in separate subtribes, but only Webster continues to include *Tetracoccus* in this tribe. There are no compelling anatomical synapomorphies that might serve to unite these three genera. The primitive wood features of *Paradrypetes* and *Podocalyx* (see above) suggest that at least these two genera are basal offshoots from the ancestral stem of Oldfieldioideae; as such, they may not be expected to share many synapomorphies with each other. Each genus of Podocalyceae bears at least one strikingly unique autapomorphy: the raphides of *Paradrypetes*, the tracheoid idioblasts of *Podocalyx*, and the ring porous wood of *Tetracoccus*.

The xeromorphic adaptations of *Tetracoccus* might just as easily obscure an early or late divergence from ancestral oldfieldioid stocks. *Tetracoccus* does share alternate vessel-ray pitting with Picrodendreae, and this character could be used to argue for its inclusion in that tribe, as classified by Levin & Simpson (1994, this volume).

Tribe Picrodendreae (Small) Webster. The genera with palmately compound leaves form the conceptual nucleus of tribe Picrodendreae. Bentham (1878) was the first to group together the biovulate euphorbs with compound leaves, associating *Oldfieldia* and *Piranhea* with the non-oldfieldioid genus *Bischofia*. Later, *Aristogeitonia* (Prain, 1912; Pax & Hoffmann, 1922, 1931) and *Celaenodendron* (Hutchinson, 1969) were added to this group, which (minus *Bischofia*) constituted subtribe Paivaeusinae of Webster (1975). (Presence of nonspiny pollen (Köhler, 1965) and *Glochidion*-type wood structure (Mennega, 1987) shows *Bischofia* to be better placed in Phyllanthoideae.) Webster (1975) maintained *Picrodendron* in a monogeneric tribe, but anatomical evidence (Hayden, 1977, 1980, see also below) suggests a close relationship among the oldfieldioid genera with compound leaves. Presently, Picrodendreae includes all oldfieldioids with compound leaves (e.g., *Stachyandra*), plus several others with unifoliolate (*Parodiodendron* and species of *Aristogeitonia*) or evidently simple leaves (*Androstachys, Mischodon,* and *Voatamalo*) (Levin & Simpson, 1994; Webster, 1994). Picrodendreae is characterized anatomically by alternate vessel-ray pits, bundle sheath extensions bearing crystals, well-developed areoles, and fimbrial veins at leaf margins.

Anatomical data support a subdivision of Picrodendreae that has been adopted by Levin & Simpson (1994) and Webster (1994). The first group is African–Madagascan–Sri Lankan and consists of *Androstachys, Aristogeitonia, Mischodon, Stachyandra,* and *Voatamalo*; these genera may be defined by stipules adnate to the petiole (Airy Shaw, 1970, 1972; Bosser, 1976; Radcliffe-Smith, 1988, 1990) and a strong tendency toward unifoliolate or simple leaves. Further, *Aristogeitonia, Mischodon,* and *Voatamalo* possess sclerified ray cells bearing prismatic crystals.

Mischodon was included among the genera of Dissiliariinae by Pax & Hoffman (1931) (see also Fig. 1) and Köhler (1965). I am in complete agreement with Raju (1984), who pointed out several differences in stomata and trichomes between *Mischodon* and genera of Dissiliariinae. *Mischodon* thus bears no compelling anatomical resemblance to any genus of tribe Caletieae sensu lato. Placement in Picrodendreae is definitely superior to any previous classification of the genus, a conclusion confirming, to some extent, suggestions made by Airy Shaw (1972) based on the similarity of stipules of *Aristogeitonia* and *Mischodon*.

The second subgroup of Picrodendreae is neotropical and consists of *Celaenodendron, Picro-*

dendron, and *Piranhea*; these genera are uni-
formly trifoliolate, have alternate phyllotaxy, and
lack the epidermal mucilage which is so widespread
in the family. *Parodiodendron*, also neotropical,
presents an interesting situation. It shares with the
trifoliolate genera alternate phyllotaxy and unusu-
ally large (for Oldfieldioideae) intervascular pits;
but its leaves are unifoliolate and lack the fimbrial
vein characteristic of all other members of the tribe.
Further, *Parodiodendron* is unique within the sub-
family by virtue of its septate wood fibers. Nev-
ertheless, *Parodiodendron* seems best accommo-
dated among the other neotropical Picrodendreae,
especially if its discordant features are viewed as
autapomorphies.

Oldfieldia is not included in either of the above
groups. Anatomically, its trichomes and presence
(in some species) of homocellular procumbent rays
resemble these features in the otherwise rather
different genera *Androstachys* and *Stachyandra*.
Oldfieldia may represent a relictual element de-
rived early from the ancestors to Picrodendreae
prior to its differentiation into otherwise distinct
New and Old World lineages.

Levin & Simpson (1994) include *Tetracoccus*
in Picrodendreae, but aside from the alternate ves-
sel-ray pits of these desert shrubs there is no com-
pelling anatomical support for this placement.

Tribe Caletieae Muell. Arg. With virtually no
contrary opinion on record, *Micrantheum*, *Pseud-
anthus*, and *Stachystemon* have been recognized
as close relatives for well over a century (Agardh,
1858; Mueller, 1866; Bentham, 1880; Grüning,
1913; Pax & Hoffmann, 1931; Hutchinson, 1969).
These shrubby xerophytes of Australia constitute
the traditional circumscription of Tribe Caletieae.
Their gross similarity and narrow "Stenolobeae"-
type cotyledons precluded serious comparison with
other euphorbs prior to the utilization of pollen
characters in the systematics of Euphorbiaceae.
Neoroepera was added to what was then a wholly
Australian tribe by Webster (1975) who was im-
pressed, no doubt, by the numerous scattered ap-
ertures (Punt, 1962; Köhler, 1965) shared by all
four genera. Additional palynological and anatom-
ical studies have refined concepts of relationships
to the extent that, now, all Australasian genera
except *Mischodon* are perceived to constitute a
single clade, the greatly expanded Tribe Caletieae
sensu lato (Levin & Simpson, 1994; Webster,
1994).

The presence of crenulate "piggyback" subsid-
iary cells is a particularly striking synapomorphy
linking all Australasian genera of Oldfieldioideae,
plus the monotypic *Hyaenanche*, endemic to the

western Cape of South Africa. *Hyaenanche* has
no other obvious close relatives within Oldfieldioi-
deae. Anatomically, its marginal venation is re-
markable, but, apparently, autapomorphic. It is
perhaps best viewed as a remnant of the Austral-
asian stem of the subfamily, from which it has been
separated since the breakup of Gondwanaland.
Placement of *Hyaenanche* in a separate mono-
generic subtribe seems appropriate.

Hyaenanche excluded, all other members of
Tribe Caletieae share another epidermal feature,
longitudinally chambered cells that bear copious
mucilage deposits in their lower halves. Taken to-
gether, crenulate subsidiary cells and mucilaginous
epidermis provide a robust definition of the Aus-
tralasian clade. The Australasian genera also tend
to have relatively low rank foliar venation and
poorly defined areoles, but it seems these vein
features are best interpreted as plesiomorphic. The
distinctive epidermal features of Caletieae sensu
lato are found in *Scagea*, which argues strongly
for its placement here and not in Acalyphoideae
or Crotonoideae as suggested by McPherson (1985);
the uniovulate carpels of *Scagea* may thus be
homoplasious with Acalyphoideae, Crotonoideae,
and Euphorbioideae.

Both Webster (1994) and Levin & Simpson
(1994) divide the Australasian oldfieldioids into three
subtribes, Dissiliariinae, Petalostigmatinae, and
Pseudanthinae.

Aside from the epidermal characters that define
the entire Australasian clade of Oldfieldioideae, the
genera of subtribe Dissiliariinae share few phylo-
genetically significant anatomical structures. Woods
of Dissiliariinae have irregular vessel-ray pits (Fig.
28), but this is probably a plesiomorphic feature
in the subfamily. Leaf margins tend to be entire
in Oldfieldioideae, but, as noted above, exceptional
toothed leaves occur in species of *Austrobuxus*,
Choriceras, and *Dissiliaria*, and this feature, too,
is probably plesiomorphic. *Austrobuxus*, with a
preponderance of solitary pores, long vessel ele-
ments (often >1 mm), occasional scalariform per-
forations, and abundant tracheids, seems to be the
least specialized genus of the subtribe in terms of
wood anatomy. Anatomically, *Dissiliaria* stands
apart from the remainder of its tribe by virtue of
high rank venation, well-developed and somewhat
oriented areoles, narrow ultimate tracheids in vein-
lets, fimbrial veins, wavy anticlinal walls of leaf
epidermis cells, bundle sheath extensions, and libri-
form wood fibers.

Whyanbeelia lacks crystal-bearing axial xylem
parenchyma; in this respect it resembles wood of
Petalostigma and Pseudanthinae; its retention in

Dissiliariinae may be challenged on this character. Lack of wood material precludes determining whether *Scagea* and *Kairothamnus* are better included in Dissiliariinae (crystalliferous axial xylem parenchyma present) or either Petalostigmatinae or Pseudanthinae (said crystals absent); pollen suggests relationship with Pseudanthinae (Levin & Simpson, 1994). Subtribe Dissiliariinae appears to be a paraphyletic assemblage at the base of the Australasian clade.

Petalostigma is a distinctive genus of Australia and southern New Guinea characterized, as its name suggests, by broad petaloid stigmas. The presence of crenulate subsidiary cells and chambered epidermal cells with mucilage shows the association of *Petalostigma* with Australasian genera of Oldfieldioideae to be superior to its former association with *Androstachys* (Webster, 1975; Hayden, 1982); this realignment is also supported biogeographically.

Both Levin & Simpson (1994) and Webster (1994) place *Petalostigma* in its own monogeneric tribe, evidently because its pollen bears at least some apertures out of the equatorial plane (Punt, 1962; Köhler, 1965), thus differing from the pollen of Pseudanthinae. Nevertheless, *Petalostigma* shares some anatomical features with Pseudanthinae: lack of crystalliferous axial xylem parenchyma and the presence of nonlignified phloem fibers in foliar veins. In *Petalostigma* the phloem fibers are thin-walled, whereas in Pseudanthinae the walls are so thick that lumina are almost completely occluded, so the similarity is only partial in this regard.

From the numerous comments above in the anatomical descriptions, it is clear that the four Australian genera of subtribe Pseudanthinae (i.e., tribe Caletieae in the traditional or narrow sense) are united by a suite of characters involving leaf architecture, leaf anatomy, and wood structure (see also Hayden, 1981). Many of the anatomical characters of these genera suggest a sequence of increasing xeromorphy involving general reduction of leaf size, increasing disorganization of the venation, and increasing prominence of a massive sclerenchymatous marginal vein. *Neoroepera* is particularly interesting in that *N. buxifolia* Muell. Arg. is similar to Dissiliariinae in some characters (incomplete marginal ultimate venation and lignified phloem fibers in foliar veins), whereas *N. banksii* Benth. conforms with other Pseudantheae (massive intramarginal vein and unlignified phloem fibers). Radcliffe-Smith's (1993) inclusion of *Stachystemon* within *Pseudanthus* increases the diversity of venation patterns in the latter, but otherwise these taxa are quite similar anatomically and evidently very closely related. Levin & Simpson (1994) provide further discussion of the relationships of *Kairothamnus*, *Neoroepera*, *Petalostigma*, and *Scagea* with the other genera of Pseudanthinae.

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APPENDIX 1. Specimens of Oldfieldioideae examined. Xylarium acronyms follow Stern (1988).

Androstachys johnsonii Prain. Leaf: *Gomes & Sousa 2202* (K); *Wellcome Chemical Research Laboratory s.n.* (K). Wood: *Capuron 3594.R.4,* USw 27434 (= CTFw 13817) (TAN); DDw 2385; *Pardy s.n.,* USw 21255 (= Uw 14606); *Pretoria UIND 2127,* Uw 21991; PRFw 20686.

Aristogeitonia monophylla Airy Shaw. Leaf: *Bally & Smith B 14376* (K). Woody twig: *Tanner 3386* (K).

Aristogeitonia sp. *Begue 727.R.1,* CTFw 13770 (TAN).

Austrobuxus brevipes Airy Shaw. Leaf: *Stauffer & Blanchon 5751* (K). Wood: *McPherson 4579* (MO).

Austrobuxus carunculatus (Baill.) Airy Shaw. Leaf: *Baumann-Bodenheim 16087* (US).

Austrobuxus clusiaceus (Baill.) Airy Shaw. Leaf: *McKee 2570* (US); *Webster 14972* (DAV). Woody twig: *Webster 14972* (DAV).

Austrobuxus cuneatus (Airy Shaw) Airy Shaw. Leaf: *McKee 12184* (K).

Austrobuxus eugeniifolius (Guillaum.) Airy Shaw. Leaf: *Guillaumin & Baumann-Bodenheim 12908* (US); *Hürlimann 1331* (US).

Austrobuxus horneanus (A. C. Smith) Airy Shaw. Leaf: *A. C. Smith 6669* (US). Wood: *A. C. Smith 6872,* Aw 28453 (= USw 30522), (A, US).

Austrobuxus huerlimannii Airy Shaw. Leaf: *McKee 4850* (K).

Austrobuxus lugubris Airy Shaw. Leaf: *McKee 25773* (K).

Austrobuxus montanus (Ridl.) Airy Shaw. Leaf: *Wray & Robinson 5424* (K).

Austrobuxus nitidus Miq. Leaf: *Chew & Corner RSNB 4107* (US); *Chew & Corner RSNB 4608* (US). Wood: FPAw DFP 30239; PRFw 21393 (SAR); PRFw 21395 (SAR); *Si Boecca 7983,* USw 29100 (MICH); *Sy-*

mington s.n., Uw 21411 (= KEPw 3602) (KEP); USw 30796, Uw 14635, (= SARFw 13234) (SAR).

Austrobuxus ovalis Airy Shaw. Leaf: *McKee 26894* (K).

Austrobuxus pauciflorus Airy Shaw. Leaf: *Baumann-Bodenheim 14113* (K); *McPherson 3935* (MO). Wood: *McPherson 3923* (MO); *McPherson 3935* (MO); *McPherson 4603* (MO).

Austrobuxus rubiginosus (Guillaum.) Airy Shaw. Leaf: *Baumann-Bodenheim 15010* (US); *Hürlimann 1486* (US).

Austrobuxus swainii (de Beuzev. & C. T. White) Airy Shaw. Leaf: *Boorman s.n.* (NSW); *Hewitt s.n.* (NSW); *Johnson & Constable s.n.* (NSW). Wood: *de Beuzeville s.n.*, MADw 10449 (= FPAw DFP 8606).

Austrobuxus vieillardii (Guillaum.) Airy Shaw. Leaf: *Schmid 2514* (K). Wood: *McKee 25222*, FPAw DFP 33881 (K).

Austrobuxus sp. Leaf: *University of California, Davis Greenhouse B73.173*. Wood: *Hyland 6918* (DAV); *Webster & Hyland 18927* (DAV).

Celaenodendron mexicanum Standley. Leaf: *Ortega 4962* (US); *Ortega 6367* (US). Wood: *Ortega 35*, USw 3886 (= Aw 4494, MADw 29901, MAD-SJRw 1200); *Ortega 6367* (US); Uw 21735 (= Aw 30657).

Choriceras tricorne (Benth.) Airy Shaw. Leaf: *Forman s.n.* (LAE, US). Wood: *Pullen 7135*, MADw 29097, FPAw-Pullen 7135 (A, CANB, K, L, LAE).

Dissiliaria baloghioides F. v. Muell. Leaf: *Bailey s.n.* (US); *Francis & White s.n.* (US). Wood: *Bailey's Queensland Woods 366*, Aw 26736; PRFw 28015; USw 32037, Uw 14625 (= FPAw DFP 3127).

Hyaenanche globosa (Gaertn.) Lam. Leaf: *Bayliss BS-BRI 576* (US); *Godfrey SH-1257* (US); *Werderman & Oberdieck 528* (US); *Böhmer & Verdoucq s.n.* (PRE); *Botanical Research Institute Pretoria s.n.* (PRE); *Werderman & Oberdieck 528* (US).

Kairothamnus phyllanthoides (Airy Shaw) Airy Shaw. Leaf: *Johns NGF 47324* (K); *Streimann NGF 45108* (K).

Longetia buxoides (Baill.) Airy Shaw. Leaf: *Baumann-Bodenheim 5605* (US). Wood: *Baumann-Bodenheim 5605* (US).

Micrantheum demissum F. v. Muell. Leaf: *Hunt 2802* (US). Woody twig: *Hunt 2802* (US).

Micrantheum ericoides Desf. Leaf: *Hotchkiss 428* (US); *Johnson & Constable 19095* (US). Woody twig: *Cambage 495* (NSW).

Micrantheum hexandrum Hook. f. Leaf: *Boorman s.n.* (US); *McGillivray 3196* (DAV); *Schodde 1177* (US). Woody twig: *Boorman s.n.* (US); *Whaite & Whaite 3536* (NSW).

Mischodon zeylanicus Thwaites. Leaf: *Ripley 05* (US); *Wheeler 12079* (US). Wood: *Jayasuriya 2434* (PDA); *Wheeler 12079* (US).

Neoroepera banksii Benth. Leaf: *Banks & Solander s.n.* (US). Woody twig: *Horner & Taylor s.n.* (NSW).

Neoroepera buxifolia White. Leaf: *White 12095* (US). Woody twig: *White 12095* (US).

Oldfieldia africana Benth. & Hook. f. Leaf: *Cooper 88* (K, MAD, US); *Cooper 439* (US). Wood: *Commercial sample*, USw 19900; *Cooper 88*, USw 4517, Uw 14636 (= Aw 16930, MADw 30131, MAD-SJRw 13738) (K, MAD, US); *Cooper 111*, USw 4538, (= Aw 16931, MADw 30132, MAD-SJRw 13761) (K, MAD); *Cooper 295*, USw 4882, (= Aw 16932, MAD-SJRw 15207) (MAD).

Oldfieldia dactylophylla (Welw. ex Oliv.) Léonard. Wood:

Cons. For. Tanganyika Territory 254, Uw 10951 (PRFw 13495).

Oldfieldia macrocarpa Léonard. Wood: *Dechamps (Comité Nat. du Kivu) s.n.*, TERVw 1605 (BR).

Oldfieldia somalensis (Chiov.) Milne-Redhead. Leaf: *Perdue & Kibuwa 10005* (NA). Wood: *Schlieben 6371 (wood no. 558)*, Uw 15635 (= MAD-SJRw 34030).

Oldfieldia sp. Wood: *Dechamps 330*, TERVw 7522; *Dechamps 335*, TERVw 7527; *Dechamps 655*, TERVw 8499 (BR).

Parodiodendron marginivillosum (Speg.) Hunziker. Leaf: *Hueck 469* (US). Wood: *Vervoorst & Cuezzo 7.610C* (LIL).

Petalostigma banksii Britten & S. Moore. Leaf: *Perry 1981* (US); *Perry 3531* (US); *Perry 3562* (US). Wood: *Doherty s.n.*, USw 21280.

Petalostigma "glabrescens" (probably referable to *P. pubescens* or *P. triloculare*). Leaf: *Clemens 42580* (US); *Wilson 679* (US). Wood: SFCw R 594-2.

Petalostigma pubescens Domin. Leaf: *White 12421* (US). Wood: SFCw R 594-3; SFCw R 977-256; *White s.n.*, PRFw 17591.

Petalostigma quadriloculare F. v. Muell. Leaf: *Clemens 42561* (US); *Lazarides 6669* (US). Wood: PRFw 2921; PRFw 24259, (= Uw 10949); PRFw 10913, (= Uw 10948); *Webster & Hyland 18879* (DAV).

Piranhea longepedunculata Jablonski. Leaf: *Breteler 4969* (US). Wood: *Breteler 4970*, MAD-SJRw 55650, (= Uw 12254) (MER, US); *Breteler 5096*, USw 35682, (= Uw 12306, MAD-SJRw 55702) (MER, NY, U, US, WAG).

Piranhea trifoliata Baill. Leaf: *Krukoff 5924* (US); *Steyermark 86615* (US). Wood: *Capucho 493*, USw 22377 (= Aw 4526, MADw 30166, MAD-SJRw 23457) (F, IAN); *Ducke s.n.*, USw 31485 (MAD); *Krukoff 6163*, USw 7524 (US).

Podocalyx loranthoides Klotzsch. Leaf: *Bernardi 1675* (NY); *Froés 21543* (NY); *Krukoff 811* (NY); *Williams 14480* (US). Wood: *Wurdack & Adderley 42795*, MADw 22429 (= MAD-SJRw 54246) (NY, US).

Pseudanthus divaricatissimus (Muell. Arg.) Benth. Leaf: *Constable 53354* (US); *Ingram s.n.* (NSW). Woody twig: *Constable 53354* (US); *Ingram s.n.* (NSW).

Pseudanthus orientalis F. v. Muell. Leaf: *Clemens 44092* (US); *Wilson 639* (US). Woody twig: *Clemens 44092* (US).

Pseudanthus ovalifolius F. v. Muell. Leaf: *Beauglehole & Orchards 30452* (NSW); *Muir 906* (US). Woody twig: *Beauglehole & Orchards 30452* (NSW); *Muir 906* (US).

Pseudanthus pimelioides Sieb. ex Spreng. Leaf: *Boorman s.n.* (US); *Clemens 42750* (US). Woody twig: *Boorman s.n.* (US); *Clemens 42750* (US); *Constable NSW 55972* (NSW).

Scagea depauperata (Baill.) McPherson. Leaf: *Franc 1642a* (US).

Scagea oligostemon (Guillaum.) Airy Shaw. Leaf: *Guillaumin & Baumann-Bodenheim 11808* (US); *McKee 2352* (US); *McKee 2651* (US).

Stachyandra merana (Airy Shaw) A. Radcliffe-Smith. Leaf: *Baron 6431* (K); *Capuron 23335-5F* (K).

Stachyandra viticifolia (Airy Shaw) A. Radcliffe-Smith. Leaf: *Capuron 20975 SF* (K). Wood: *Capuron 1914.R.4*, CTFw 9069 (TAN).

Stachyandra sp. Wood: *Belin 218.R.6*, CTFw 13786 (TAN).

Stachystemon axillaris George. Leaf: *Blackwell & Griffin 3132* (PERTH).

Stachystemon brachyphyllus Muell. Arg. Leaf: *George 12928* (PERTH).

Stachystemon polyandrus (F. Muell.) Benth. Leaf: *Hnatiuk 761262* (PERTH).

Stachystemon vermiculare Planch. Leaf: *Pritzel s.n.* (US); *Royce 5207* (PERTH).

Tetracoccus dioicus Parry. Leaf: *Moran 13170* (US); *Terrell & Gordon 4004* (US); *Webster & Hildreth 7478* (DAV). Wood: *Campbell 21484* (RSA).

Tetracoccus fasciculatus (Wats.) Croizat var. *fasciculatus*. Leaf: *Johnston 7783* (GH, US); *Webster, 21221* (DAV). Wood: *Johnston 7783*, Aw 23748 (GH, US).

Tetracoccus fasciculatus (Wats.) Croizat var. *hallii* (Brandegee) Dressler. Leaf: *Webster & Hildreth 7460* (DAV); *Wiggins 6617* (US). Wood: *Webster & Hildreth 7460* (DAV).

Tetracoccus ilicifolius Coville & Gilman. Leaf: *Gilman s.n.* (US); *Gilman 2181* (US). Wood: *Gilman 2181* (US).

Voatamalo eugenioides Capuron ex Bosser. Wood: *SF 198 R 259*, (= CTFT 13816, Uw 23104); *SF 5327 R 4* (= CTFT 15079, Uw 23105).

Whyanbeelia terrae-reginae Airy Shaw & Hyland. Leaf: *Irvine 1399* (K). Wood: *Hyland 7945* (K).

APPENDIX 2. Previous anatomical literature on Oldfieldioideae. Comprehensive works abbreviated as follows: G = Gaucher (1902); S = Solereder (1908); MC = Metcalfe & Chalk (1950).

Androstachys Prain. Anonymous (1909); MC; Bolza & Keating (1972); Rao & Raju (1985); Alvin (1987); Alvin & Rao (1987); Dahlgren & van Wyk (1988).

Austrobuxus Miquel (often reported as "*Longetia*," see below). Rothdauscher (1896); G; Dehay (1935); Math-ou (1940); Heimsch (1942); MC; Bamber (1974); Rao & Raju (1985).

Celaenodendron Standley. Record (1928); Record (1938); Record & Hess (1943); Hayden (1977).

Croizatia Steyerm. Levin (1986).

Dissiliaria F. Mueller. MC; Dehay (1935); Bamber (1974); Rao & Raju (1985).

Hyaenanche Lambert & Vahl. Pax (1884); G; S; Dehay (1935); Assailly (1954).

Longetia Baillon. Much published anatomical information on "*Longetia*" pertains to *Austrobuxus nitidus* (= *Longetia malayana*); there appears to be no previous anatomical study of *Longetia buxoides* (Baill.) Airy Shaw.

Micrantheum Desfontaines. Pax (1884); G; S; MC; Rao & Raju (1985).

Mischodon Thwaites. G; Gamble (1922); Heimsch (1942); MC; Raju (1984); Rao & Raju (1985).

Neoroepera Mueller Arg. Rothdauscher (1896).

Oldfieldia Bentham. Stone (1904); MC; Assailly (1954); Lebacq & Dechamps (1964); Bolza & Keating (1972); Hayden (1977); Rao & Raju (1985).

Paradrypetes Kuhlm. Milanez (1935); Araujo & Mattos Filho (1984); Levin (1986); Mennega (1987).

Petalostigma F. Mueller. Froembling (1896); Rothdauscher (1896); G; S; Dehay (1935); MC; Bamber (1974); Rao & Raju (1985).

Picrodendron Planchon. Hayden (1977) (q.v. for earlier references); Hakki (1985); Rao & Raju (1985).

Piranhea Baillon. Dehay (1935); Record (1938); MC; Hayden (1977); Pyykkö (1979); Roth (1981); Worbes (1989).

Pseudanthus Sieber ex Sprengel. Pax (1884); G; S; Rao & Raju (1985).

Stachystemon Planchon. Pax (1884); G; MC.

Tetracoccus Engelman ex Parry. Heimsch (1942); MC.