A PHYLOGENY AND REVISED CIRCUMSCRIPTION FOR KAIROA (MONIMIACEAE), WITH THE DESCRIPTION OF A NEW SPECIES FROM PAPUA NEW GUINEA

SUSANNE S. RENNER1 AND WAYNE N. TAKEUCHI2

Abstract. Kairoa endressiana is described from limestone environments in Papua New Guinea’s (PNG) southern region. According to chloroplast and nuclear DNA sequences, the novelty is closely allied to Faika and Kairoa, two genera previously regarded as monotypic. In recognition of these molecular findings, Kairoa is redefined by one nomenclatural transfer and by the addition of K. endressiana. A key to the three species is presented, together with updated maps of their geographic distributions. Color photographs are provided for all currently accepted taxa.

Keywords: Faika, Kairoa, Mollinedioideae, Monimiaceae, New Guinea

Monimiaceae (Laurales) is a pantropical clade of 195–200 species and 26 genera (Philipson, 1993; Renner, 1998, 1999; Whiffin, 2007; Peixoto and Pereira-Moura, 2008). The family’s present distribution includes Central and South America (ca. 30 spp. in 5 genera), tropical Africa (the monotypic Xymalos Baill.), Madagascar-Mascarenes (63 spp. in 3 genera), Réunion-Mauritius (the monotypic Monimia Thouars), Sri Lanka (the monotypic Hortonia Wight), New Caledonia (10 spp. in 2 genera, including the monotypic Kibaropsis Vieill. ex Jérémie), New Zealand (1 sp.), Australia (26 spp. in 8 genera, including the monotypic Austromatthaea L. S. Sm., Hemmanta Whiffin, and Endressia Whiffin nom. illeg. [the name Endressia is preempted by the Apiaceae genus Endressia J. Gay, published in 1832]), and the Malesian region (a center of diversity with ca. 84 spp. and 10 genera of which 2 are monotypic). Owing to their remarkable fossils and contemporary disjunctions, the Monimiaceae have historically served as a focal group for biogeographic study (references in Renner, 2005).

In his revision of the family for the Malesian region, Philipson (1986) accepted eight genera for New Guinea, consisting of Faika Philipson (1 sp.), Kairoa Philipson (1 sp.), Kibara Endl. (36 spp.), Lauterbachia Perkins (1 sp.), Levieria Becc. (7 spp.), Palmeria F. Muell. (11 spp.), Steganthera Perkins (16 spp.), and Wilkiea F. Muell. (1 sp.). Three of these genera (Faika, Kairoa, and Lauterbachia) were regarded as monotypic and endemic to New Guinea. Most of the Papuasian species have traditionally been assigned to the Mollinedioideae, a subfamily distinguished by pistillate receptacles with a detachable upper part (circumscissile), and including several poorly understood taxa of uncertain affinity. With the taxonomic adjustments effected below, New Guinea Monimiaceae are now composed of 76 species in 7 genera, by far the most diverse of the family’s geographic stations.

MATERIALS AND METHODS

DNA extraction and sequencing followed the trnL-F and ITS primers and polymerase chain reaction (PCR) protocols in Renner and Won (2001). Total genomic DNA was isolated from silica-dried leaves or from herbarium specimens with a commercial plant DNA extraction kit, following the manufacturer’s manual. PCR reaction products were purified with a PCR clean-up...
kit, and cycle sequencing was performed with the BigDye Terminator cycle sequencing kit on an ABI Prism 3100 Avant automated sequencer (Applied Biosystems, Foster City, California, USA). Sequences were edited and aligned in Sequencher (4.6; Gene Codes, Ann Arbor, Michigan, USA). The aligned plastid DNA matrix comprises 512 nucleotides of the trnL-F intergenic spacer and 784 nucleotides of the nuclear ribosomal RNA internal transcribed spacer (ITS) region. Accession numbers for all other sequences used for the analyses are given in Renner (in prep.). The Monimiaceae family dataset includes all but two of the currently accepted genera of Monimiaceae, and 51 of the 195–200 species. Rooting was on Hernandiaceae and Monimiaceae, based on Renner and Chanderbali (2000). Maximum likelihood (ML) analyses and bootstrap searches were performed using RAXML (Stamatakis et al., 2008, http://phylobench.vital-it.ch/raxml-bb/) and the GTR + G + I model. Model parameters were estimated over the duration of specified runs. Since there were no differences between the chloroplast (cp) and nuclear (nc) topologies receiving ML bootstrap support above 75%, the cp and nc datasets were combined into a single matrix of 1294 nucleotides.

Taxonomic descriptions refer to the character states on exsiccatae, except when otherwise noted. The term “receptacle,” applied to the monimiaceous flower, is used in the sense of Philipson (1986, 1993; i.e., as being equivalent to “hypanthium” or “floral cup”). Photographs were taken with a Canon EOS-350D or with a professional grade EOS-5D.

RESULTS

A maximum likelihood phylogeny from combined chloroplast and nuclear data (Fig. 1) shows that Kairoa endressiana Takeuchi & Renner (described below as a new species) is closest to Kairoa suberosa Philipson and Faika villosa Philipson (treated here as Kairoa villosa (Philipson) Renner & Takeuchi). The three species form a well-supported clade that is sister to Kibara (the latter represented in the sampling by its type species, Kibara coriacea (Bl.) Tul., and two congeners).

Since monotypic genera contain no information about relationships, the classification of New Guinea Monimiaceae can be improved with the transference of Faika to Kairoa. In conformity to the data presented below, Kairoa is thus redefined by the inclusion of Faika, and K. endressiana is described as a new addition to the enlarged genus. Kairoa remains endemic to the New Guinea mainland, but is now seen as being more widely distributed across the island and with occurrences on the Austrocratonic shelf or its margins.

In the remainder of this paper the proposed changes are formally established with an amended description of Kairoa, a key to the species, and a complete description for K. endressiana.

TAXONOMIC SYNOPSIS


Monoecious or dioecious shrubs. Vegetative indument villous, woolly, hirtellous, or absent. Branchlets terete to complanate, older parts often corky, periderm deeply furrowed or ± smooth. Leaf-blades usually elliptic, base obtuse-cordate, margins toothed, apex acute-acuminate. Staminate inflorescence axillary; flowers solitary, cymose, or racemose; pedicels 0–5 mm; bracts minutely deltate or conspicuously foliaceous; receptacles globose to discoid, circumscissile, glabrous outside, hairy inside; tepals 2–5 pairs, with or without thickened glands, hyperstigma apparently absent; carpels 8–150+, styles rudimentary or prolonged. Fruits consisting of monocarps in a capitate arrangement, drupaceous; receptacle accrescent; monocarps ovoid-oblongoid, inserted on stalk-like projections from the receptacle or not, congested; epicarp sericeous, hirsute, or glabrous, black.

**KEY TO THE SPECIES OF KAIROA**

1a. Dioecious shrubs; vegetative parts conspicuously hirsute, laminae chartaceous; stamens ca. 25, dispersed over all interior surfaces of the receptacle. ........................................... *Kairoa villosa*

1b. Monoecious shrubs; vegetative parts glabrous, woolly, or subappressedly-hairy (but not patently hirsute); laminae thick, coriaceous or firm; stamens 2–4 or >100, inserted on the receptacle floor. ...................... 2

2a. Leaf venation prominent on upper side; pistillate flowers fascicled, ca. 5 mm pedicellate at anthesis, bracts minute, ca. 1 mm long; staminate flowers 15–20 mm pedicellate, stamens >100, anthers dehiscing on 2 longitudinal stomia. ........................................... *Kairoa suberosa*

2b. Leaf venation deeply impressed on upper side; pistillate flowers solitary, subsessile or at most to 2 mm pedicellate, conspicuously bracteate, primary bracts foliaceous, to 29 × 6 mm; staminate flowers subsessile, stamens 2 or 4, anthers dehiscing on a single ∩-shaped peripheral stomium. ........................................... *Kairoa endressiana*


_Haec species a congeneris bracteis femineis magnis usque ad 29 × 6 mm inflorescentis masculinis racemiformibus parvis usque ad 11 × 9 mm floribus masculinis tantum 2–4-staminatis distinguitur._

Understory shrubs (1–)2–3 m in height, monoecious. _Stems_ erect, outer bark fuliginous, ± smooth, not corky. _Branchlets_ complanate, (1.5–)2.5–4.0(–6.0) mm wide, persistently lanuginose, virgate, firm, ± nodose; surfaces brumnescent (or nigrescent), striate, lacking abscission scars; periderm crustaceous, elenticellate; internodes (1.5–)3.0–8.0(–13.0) cm. _Leaves_ opposite, distichous, obliquely spreading, sometimes unequal; _petioles_ 4–10 × 2–4 mm, planoconvex, channelled above, indument as on branchlets; _leaf-blades_ linear-elliptic (or linear-lanceolate), (9.5–)12.7–29.0(–34.5) × 2.1–7.3 (–8.8) cm, firm-coriaceous, dry-textured, conspicuously rugose, bullate; surfaces nitid or opaque, epunctate under reflected and transmitted light, adaxially olivaceous, strigulose,

glabrescent, abaxially tawny-brown, subapressedly hairy; lamina base obtuse to obscurely cordulate; margins serrate-spinulose; apex acute or acuminate, mucronulate at the top; venation reticulate-brochidodrome, secondaries 10–15 per side, (1–)11–39 (–48) mm apart, at the lamina center diverging 55–80˚ from costae, arcuate, supramedially and inframarginally confluent, the commissural looping nerves disposed in two ranks, inner rank stronger, partial intersecondary veins numerous; reticulum irregular, coarsely areolate, conspicuous; midribs bifacially prominent, higher order veins impressed (or planate) on upper side, strongly raised beneath. Staminate inflorescence axillary from defoliate nodes, condensed, racemiform, 9–11 × 6–9 mm, axil thirtelous; primary bract ovate-lanceolate, 2.5–3.6 × 1.0–1.7 mm, spirally inserted on rachises, persisting, adaxially smooth, abaxially striguliform-hairy. Staminate flowers (measurements from immature spirit-preserved material) 3–7 together; secondary bracts paired, inserted at the base of a 2 mm pedicel, appressed, narrowly trullate, 1.8–2.5 × 0.8–1.0 mm, enclosed by the subtending primary bract; receptacle ovoid, 3.2–4.0 × 3.0–3.8 mm, obscurely 4-angled, red or black, gradually tapering to the pedicel, exterior surfaces glabrous, occasionally set with 1–2 tertiary (receptacle) bracts, interior surfaces pilosulous on the flat base of the vault; tepals 2–3-seriate, obtuse, eglandular; stamens 2 or 4, equal, erect; filaments ≤0.2 mm long, laxly pilosulous; anthers ovoid-oblongoid, ca. 1.2 × 0.8 mm, dehiscing on a vertical ∩-shaped peripheral stoma nium; staminodes absent. Pistillate flowers (measurements from anthetic spirit-preserved material) solitary, inserted between leaf nodes, subsessile or to 2 mm pedicellate, apparently protogynous; primary bracts foliaceous, linear-elliptic, ovate-lanceolate, or obovate, (7–)10–18 (–29) × 4–6 mm, denticulate, induplicative, adaxially glabrescent, abaxially stri gulose; secondary bracts paired, appressed to receptacles, acuminate, 3.0–3.5 × 1.0–1.5 mm, indument as for primary bracts; receptacle globose-obovoid, 4.0–5.0 × 4.5–5.0 mm, circumscissile, red, proximally strigulose on the outer side, pilose on the inside; tepals 4-seriate, obtuse, the innermost pair largest, hyperstigma not seen; carpels 8–15 (–21), conoid, 1.5–2.0 × 0.5–0.9 mm, pilose, evenly tapered to an acute summit, style poorly defined. Fruits from foliate nodes, monocarps capitately arranged; peduncle 2–5 × 1–2 mm (or absent); receptacle globuliform-discoid, (2–)4–8 mm across, weakly accrescent, fuscous, shaggy, margins recurved or not; monocarps 1–14 (–21), ellipsoid-oblongoid, 12–14 × 7–9 mm, inserted on stalk-like projections from the receptacle or not; epicarp laxly sericeous, glabrescent, verruculose, crustaceous, black; stigmatic residue umbonate, 0.2–0.7 mm long; seed single, ellipsoid, 10.9–12.2 × 6.2–6.7 mm, slightly compressed, rugose-scorbiculate, dull brown; endosperm copious, white, no ruminations; embryo linear, erect, ca. 1/2 the seed length.

Eponymy: the epithet recognizes Prof. Peter K. Endress (Institut für Systematische Botanik, Universität Zurich), a systematist, morphologist, and important contributor to our knowledge of floral evolution.

Additional specimen examined: PAPUA NEW GUINEA. Southern Highlands Province: Strickland drainage, Tualapa bivouac, limestone forest along fast-flowing stream, 05°17'07"S, 142°29'44"E, 1050 m, 12 July 2008, W. Takeuchi & D. Ama 24034 (A, BO, CANB, L, LAE, M).

Distribution: known only from the type locality in the upper Strickland basin (Fig. 4).

Habitat and ecology: dark understories in limestone forest at 1050–1140 m.

Phenology: flowering and fruiting in July.

Conservation status: data deficient (DD). Most of the Strickland basin and adjoining districts are still poorly known. With further exploration Kairoa endressiana may prove to be more common than suggested by current evidence. The other species of Kairoa have been recorded from widely dispersed localities and are classifiable as “Near Threatened” (NT) under the updated IUCN criteria (IUCN Standards and Petitions Working Group, 2008).

Kairoa endressiana is easily identified by its solitary pistillate flowers with exceptionally large primary bracts. In congeners, the bracts (when present) are minute and scale-like. Although Kairoa suberosa has staminate inflorescences of similar form, the racemes of K. endressiana are considerably smaller (e.g., flowers are 1.5–2.0 cm pedicellate in K. suberosa, but subsessile in K. endressiana). Both the female and male inflorescences of the new species also differ in gross structure from K. villosa. Table 1 provides a compilation of contrasting attributes between the three species of Kairoa.

Philipson (1980) reported the geographic range of *Kairoa suberosa* as being confined to Morobe and Northern Provinces (Fig. 6), inadvertently omitting Milne Bay Province from the documented distribution. Shortly after Philipson’s publication, C. E. Carr 12152 (LAE) was identified from Central Province, placing the then-monotypic genus across the Central Dividing Ranges and into PNG’s southern region. The epithet in *Kairoa suberosa* is a reference to the corky periderm on older wood, a feature shared by *Kairoa villosa* but not by *K. endressiana*.

Unlike other Peninsular endemics (i.e., restricted to the New Guinea “tail” from south Morobe to Milne Bay Province), *Kairoa suberosa* occurs on both sides of the Salamaua contact, a major tectonic boundary between the Markham-Ramu basin and the Peninsula proper (see Pigram and Davies, 1987; Davies et al., 1997). Other endemics (e.g., *Cyathealamoureuxii* Takeuchi, *Freyecinetia takeuchii* Huynh, *Gardeniakamialiensis* Takeuchi, *Guioa grandifoliola* Welzen, *Hypserpa ademae* Takeuchi, *Nastus schlechteri* (Pilger) Holttum, *Schraderaschlechteri* (Valton) Puff, Buchner & Greimler, and *Zanthoxylum novoguineense* Hartley) are found only to the east of the Salamaua boundary.

3. *Kairoa villosa* (Kaneh. & Hatus.) Renner & Takeuchi, comb. nov. Fig. 7–8.


Philipson (1985) established the monotypic genus *Faika* from five collections centered on the Bird’s Neck region of Irian Jaya. The distribution specified in the diagnosis has since been expanded with the addition of new locality records from the Bewani Mts. (LAE 56531); Bomberai Peninsula (*W. Takeuchi et al. 16076*), Foja Mts. (*W. Takeuchi et al. 20714, 20841*), and the April River of PNG (*Takeuchi and Renner, 2002*). The taxon’s currently known range is shown in Fig. 8.

**DISCUSSION**

The family Monimiaceae has an unusually wide range of floral morphologies (Endress, 1980, 1992; Endress and Lorence, 1983). In the era before sequencing technology, perceived discontinuities in floral variation (e.g., in stamen numbers and stomatal arrangements inside the
Table 1. Summary of differentiating attributes for the taxa currently included in *Kairoa*.

<table>
<thead>
<tr>
<th>KAIROA ENDRESSIANA</th>
<th>KAIROA VILLOSA (FAKA)</th>
<th>KAIROA SUBEROSA</th>
</tr>
</thead>
<tbody>
<tr>
<td>known only from the type locality in Southern Highlands Province, PNG</td>
<td>known from scattered localities in northern New Guinea, mainly in Irian Jaya</td>
<td>known from many localities in Peninsular PNG, mainly on the northern side</td>
</tr>
<tr>
<td>monoecious shrubs 1–3 m tall; stems smooth</td>
<td>dioecious shrubs 1–4 m tall; stems conspicuously corky, periderm deeply furrowed</td>
<td>monoecious shrubs 0.5–5.0 m tall; stems conspicuously corky, periderm deeply furrowed</td>
</tr>
<tr>
<td>vegetative parts lanuginose or appressedly hairy</td>
<td>vegetative parts hirsute</td>
<td>vegetative parts glabrous or pubescent</td>
</tr>
<tr>
<td>leaf-blades coriaceous; linear-elliptic (or linear-lanceolate), 9.5–34.5 × 2.1–8.8 cm; base obtuse to cordulate; margins serrate, spinulose; apex mostly acuminate</td>
<td>leaf-blades chartaceous; oblong-elliptic, 21–44 × 4.5–13 cm; base cordate; margin repand to remotely serrate; apex acute-apiculate to subcuspidate</td>
<td>leaf-blades coriaceous or firm; elliptic, oblong, or lanceolate-oblong, to 45 × 17 cm; base cuneate to cordate; margin entire, callose-denticulate, or fiercely toothed; apex acute</td>
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<tr>
<td>male inflorescence from nodes lacking attached leaves, racemose, 3–7-flowered</td>
<td>male inflorescence from leaf axils, 1(–3)-flowered</td>
<td>male inflorescence from leaf axils, subracemose, to 24-flowered</td>
</tr>
<tr>
<td>male flowers obvoid, 3.2–4.0 × 3.0–3.8 mm, glabrous outside, pilosulous inside; pedicels 2 mm long; bracts numerous (through 2–3 orders), primary bracts to 3.6 × 1.7 mm; tepals 4–6</td>
<td>male flowers ellipsoid-obvoid, ca. 5.5–7.0 × 3.5–4.0 mm, bifacially glabrous; subsessile; bracts lax, 1–2 mm long; tepals 6</td>
<td>male flowers initially globose, ca. 18 mm diam., rupturing and irregularly lobed after expansion, bifacially glabrous; pedicels 15–20 mm long; bracts absent or with 1–2 inserted on pedicels, 1.0 mm long; tepals 8</td>
</tr>
<tr>
<td>stamens 2 or 4, in opposed pairs; anthers ovoid-oblongoid, ca. 1.2 × 0.8 mm, dehiscing on a single □-shaped peripheral stomium</td>
<td>stamens ca. 25, dispersed over interior surfaces of the vault; anthers oblongoid, 1.0–1.5 × 0.3–0.6 mm, opening on 2 longitudinal stomia</td>
<td>stamens &gt;100, dispersed over the receptacular floor; anthers oblongoid, 1.0 × 0.5 mm, opening on 2 longitudinal stomia</td>
</tr>
<tr>
<td>female inflorescence between the leaf nodes; bracts conspicuous, to 29 × 6 mm</td>
<td>female inflorescence from leaf axils; bracts deltate, ca. 1.5 mm long</td>
<td>female inflorescence from leaf axils; bracts narrowly cuneate, 1–2 mm long</td>
</tr>
<tr>
<td>female flowers solitary; pedicels to 2 mm long; receptacle globose-obvoid, 4.0–5.0 × 4.5–5.0 mm, circumsessile, proximally strigulose outside, pilose inside; tepals in 4 pairs; carpels usually 8–15, conoid-acute, to 2.0 × 0.9 mm, pilose</td>
<td>female flowers solitary; subsessile; receptacle turbinate, ca. 7 × 8 mm, circumsessile, externally glabrous, internally setulose; tepals ca. 5 pairs; carpels 70+, attenuate, 3.0–4.5 × 0.5–0.7 mm, hirtellous on the lower 1/3</td>
<td>female flowers ± fasciculate; pedicels ca. 5 mm long; receptacle globose to discoid depending on maturation, 5–8 mm diam., circumsessile, externally glabrous, internally hirtellous on vault floor; tepals 4; carpels to ca. 150 or more, linear-conoid, 1.5–2.0 × 0.2–0.3 mm, muricate</td>
</tr>
</tbody>
</table>

**NOTE:** Character profiles extracted from type descriptions and refined by examination of annotated herbarium specimens.
**Figure 5.** *Kairoa suberosa* Philipson. **A,** circular inset, left, staminate inflorescence; **B,** rectangular inset, right, mature fruits with apical monocarps removed, showing the accrescent receptacle; **C,** severed section of main stem with the characteristically fissured and corky bark. All from *W. Takeuchi & D. Ama 17008.*

**Figure 6.** Island of New Guinea showing the distribution of *Kairoa suberosa* Philipson. **A,** geographic range as given in Philipson (1980); **B,** collection locality for *C. E. Carr 12152* (Koitaki, Central Province).

receptacle) were used as a basis for erecting a relatively large number of small genera (see Perkins and Gilg, 1901; Philipson 1980, 1985). These genera can now be reevaluated with contemporary data, although some, such as Parakibara Philipson, are still known only from the type collection. The status of Lauterbachia Perkins is particularly problematic. No specimens of L. novoguineensis Perkins have been obtained since the loss of its type in World War II. Based on more abundant flowering material, it is clear that androecium characteristics are poorly suited for generic separation. Within the Kairoa clade, staminal number and arrangement are diagnostic only at the species level.

Although other features of the androecium are not as significant as previously supposed, Kairoa can be distinguished from the genera morphologically closest to it (i.e., Kibara, Steganthera) by the form and dehiscence of the anthers. In Kairoa the anther cells open vertically on both sides (in K. endressiana the stoma can be confluent across the top), while in Kibara and Steganthera the dehiscence is horizontal. Kibara and Steganthera also have squat or rotund stamens (more broad than long), thus at pollen release the anthers have the appearance of an open clamshell. In Kairoa, the anther cells are decidedly longer than broad and clearly erect. Especially since the principal features of the androecium (e.g., staminal number and disposition) cannot be maintained as a basis for generic separation, it is ironic that lesser attributes like anther dehiscence should remain as apparent distinctions. Unfortunately the current generic concepts are obscured and complicated by an acute lack of information on many aspects of Monimiaceae biology. For example, although germination patterns have proven of discriminatory value elsewhere in the family (A. Ford, pers. comm.), virtually nothing is known of the New Guinea plants with respect to their development from seed. Critical observations on hyperstigmas (see Endress, 1979, 1980) are also a potential source of new insights. The presence (or absence) of stigmatic or receptacle exudates has never been confirmed by Papuasian investigators even though the hyperstigma is a major lead in Philipson’s (1986) generic key. Future nomenclatural adjustments cannot be discounted as long as obvious information gaps remain unaddressed.

Phylogenetic relationships in the Mollinedioideae will not be easy to unravel, primarily because herbarium documentation of Papuasian Monimiaceae is collectively inadequate for DNA-based evaluation of generic circumscriptions. Existing collections are disproportionately biased toward fruiting specimens that are less useful than flowering material in terms of key taxonomic characters. In contrast to the brightly colored fruits (see Romanov et al., 2007), anthetic flowers are small, inconspicuous, and have a misleading resemblance to immature buds (Philipson, 1984). Even experienced field botanists seem unaware of the unisexual nature of the inflorescence, and of the critical necessity in obtaining mature flowers from both sexes. Except for Philipson’s own gatherings, none of the collections cited by him make any reference (on their labels) to internal floral structures, or even to whether a plant is monoecious or dioecious. The paucity of diagnostic information is a major impediment for herbarium-based studies. As in other Papuasian families where specialist collecting is needed, further progress will depend on the participation by field workers cognizant of taxonomic issues. Judging from the anticipated constraints to future inquiry, a satisfactory knowledge of the biology and morphology of Papuasian Monimiaceae is still many years away.

LITERATURE CITED


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