

Classification of Urticaceae based on morphology and phylogenetic inference

1 ALEXANDRE K. MONRO^{1,2,*}, OLIVIER MAURIN¹, LONG-FEI FU³, TOM WELLS⁴, MELANIE WILMOT-
 2 DEAR¹, JULIET BEENTJE¹, D.J. NICHOLAS HIND¹, IB FRIIS⁷, YI-GANG WEI³, GRACE BREWER¹,
 3 ROBYN COWAN¹, STEVEN DODSWORTH^{1,5}, JIA DONG⁶, NIROSHINI EPITAWALAGE¹, IZAI A.B.
 4 SABINO KIKUCHI^{1,8}, ISABEL LARRIDON¹, ALISON MOORE¹, HERVÉ SAUQUET⁹, JACQUIE UJETZ^{2,10},
 5 ZENG-YUAN WU¹¹, FELIX FOREST¹, WILLIAM J. BAKER¹, ELLIOT GARDNER^{12,13,14}

1. ROYAL BOTANIC GARDENS, KEW, TW9 3AE, UNITED KINGDOM

2. LIFE SCIENCES DEPARTMENT, THE NATURAL HISTORY MUSEUM, LONDON, SW7 8BD

3. GUANGXI KEY LABORATORY OF PLANT CONSERVATION AND RESTORATION ECOLOGY IN
 KARST TERRAIN, GUANGXI INSTITUTE OF BOTANY, GUANGXI ZHUANG AUTONOMOUS
 REGION AND CHINESE ACADEMY OF SCIENCES, GUILIN 541006, CHINA

4. DEPARTMENT OF PLANT SCIENCES, OXFORD UNIVERSITY, OX1 3RB, UK

5. SCHOOL OF BIOLOGICAL SCIENCES, UNIVERSITY OF PORTSMOUTH, PORTSMOUTH PO1 2DY,
 UK

6. ROYAL BOTANIC GARDENS, EDINBURGH, EH3 5NZ, SCOTLAND

7. NATURAL HISTORY MUSEUM OF DENMARK, UNIVERSITETPARKEN 15, DK-2100,
 COPENHAGEN Ø, DENMARK

8. DEPARTMENT OF BOTANY, UNIVERSITY OF BRITISH COLUMBIA, VANCOUVER, BC V6T 1Z4,
 CANADA

9. NATIONAL HERBARIUM OF NEW SOUTH WALES (NSW), ROYAL BOTANIC GARDENS AND
 DOMAIN TRUST, SYDNEY, AUSTRALIA

10. DEPARTMENT OF INFECTIOUS DISEASE, IMPERIAL COLLEGE, LONDON W2 1PG, UK

11. GERMPLASM BANK OF WILD SPECIES, KUNMING INSTITUTE OF BOTANY, CHINESE
 ACADEMY OF SCIENCES, KUNMING 650201, CHINA

12. CASE WESTERN RESERVE UNIVERSITY, DEPARTMENT OF BIOLOGY, 2080 ADELBERT ROAD,
 CLEVELAND, OHIO 44106, USA (CURRENT AFFILIATION)

13. THE MORTON ARBORETUM, 4100 IL-53, LISLE, ILLINOIS 60532, USA

14 SINGAPORE BOTANIC GARDENS, NATIONAL PARKS BOARD, 1 CLUNY ROAD, 259569,
 SINGAPORE

Abstract

The Urticaceae (ca. 2600 species) were first formally recognized by Jussieu in the 18th century and last comprehensively monographed by Weddell in the 19th century. Since Weddell's work, family delimitation has been modified and many genera described in a fragmented manner. Over the past two decades, numerous molecular studies have supported the inclusion of Cecropiaceae within Urticaceae and identified paraphyly in several genera, notably *Laportea*, *Urera*, *Boehmeria*, *Parietaria*, *Pellionia*, and *Pouzolzia*. However, few studies have translated these molecular insights into a revised taxonomy.

This study aimed to provide a robust, updated classification for Urticaceae by: a) increasing taxon and genomic locus sampling through the integration of newly generated sequence data with previously published datasets; and b) incorporating morphological data to support a revised delimitation of tribes and genera, and to establish a new linear sequence for the family. We also sought to identify remaining taxonomic challenges.

Using Sanger and Angiosperms353 sequence data, we constructed a phylogenetic framework for 57 out of 59 currently accepted genera. We also assessed the phylogenetic informativeness of 57 morphological characters by mapping them onto the phylogeny.

Our analyses support the delimitation of 61 monophyletic genera and an infrafamilial classification comprising seven tribes, two of which we describe as new: Myriocarpeae and Leukosykeae. We provide a revised linear sequence for the family. Our classification reinstates several names previously treated as synonyms (*Fleurya*, *Leptocnide*, *Margarocarpus*, *Polychroa*, *Scepocarpus*, *Sceptrocnide*), places several genera in synonymy (*Hemistylus* and *Rousselia* under *Pouzolzia*; *Hesperocnide* under *Urtica*; *Gesnoulina* and *Soleirolia* under *Parietaria*), and proposes the recognition of two new genera, *Muimar* gen. nov. and *Pouzolziella* gen. nov., to accommodate *Boehmeria nivea* and *Pouzolzia australis*, respectively.

Mapping morphological characters onto the phylogeny indicates that while most states are homoplastic at the family level, their combination is valuable for recognizing genera. Geographic character mapping suggests a high degree of spatial conservatism at the genus rank. Our dated ultrametric tree suggests an origin for Urticaceae in Indomalaya during the mid-Cretaceous, followed by establishment in the Laurasian boreotropical flora and subsequent dispersal to the neotropics and Africa.

Once classified within an evolutionary framework we believe that the Urticaceae represent a valuable study system in evolutionary biology for investigating transitions across biomes, the drivers of floral trait evolution, and intrinsic speciation mechanisms.

New tribes.—Leukosykeae, Myriocarpeae

New genera. —*Muimar*, *Pouzolziella*

Keywords. Rosales, Cecropiaceae, linear sequence, tribal classification, generic delimitation, *Polychroa*, *Margarocarpus*, *Leptocnide*, *Sceptrocnide*

6 Introduction

According to the last conspectus (Friis, 1989) of the family, the Urticaceae Juss. comprise ca 900 species grouped into 48 genera. With the inclusion of the Cecropiaceae, as supported by several studies (see taxonomic history below) and a revised assessment of species numbers the Urticaceae currently comprises 54 genera and 2,625 species (Christenhusz & Byng, 2016) making it a large flowering plant family (Willis, 2017). Approximately two-thirds of the species diversity of the family is accounted for by two species-rich genera, *Pilea* with ca 715 spp (Monro, 2004) and *Elatostema* with ca 800 spp (Fu, Wei & Monro, pers obs). Urticaceae are found in all major plant biogeographic regions and biomes except for Antarctica. Greatest species and genus diversity is observed in the wet and moist tropics and subtropics at elevations between 500 and 2000 masl in mountainous landscapes, especially those associated with karst. Urticaceae include hemi-epiphytes (*Poikilospermum*), herbs (Boehmeriaceae, Elatostemateae, Parietarieae, Urticeae), vines (Urticeae), shrubs (Boehmeriaceae, Elatostemateae, Parietarieae, Urticeae) and trees (Boehmeriaceae, Cecropiaceae, Urticeae). The tribes can be crudely divided into disturbance-adapted taxa that are common in early, to mid-succession (including riparian) vegetation and agricultural landscapes (Boehmeriaceae, Cecropiaceae, Parietarieae, Urticeae), and deep-shade climax vegetation specialists (Elatostemateae) (Wu et al., 2018). The main economic uses of the family are as a fibre (*Boehmeria nivea*, *Dendrocnide* spp., *Girardinia diversifolia*, *Obetia tenax*, *Scepcarpus* spp. (Wells et al., 2021), *Touchardia latifolia*, *Urtica dioica* (Sfiligoj Smole et al., 2019), with minor medicinal (Bansal et al., 2012) (Lin et al., 1998) (Modarresi Chahardehi et al., 2010), and occasional nutritional use (Diazgranados et al., 2020). *Cecropia*, locally dominant in low to mid elevation early succession forest in the Neotropics represents an important food source for several mammal and bird species of importance for habitat conservation (sloths, toucans, bats) (Charles-Dominique, 1986; Dejean et al., 2012; Lobova et al., 2003)

Urticaceae flowers begin development as bisexual, unisexuality being achieved by the much slower pace of development of one of the sexes, whose vestiges are retained as staminodes or pistilodes. The former may play a role in achene dispersal within the Elatostemateae. Within the tribe Parietarieae and Forrskaoleae, however, there is a notable trend to bisexuality. The Parietarieae include both truly bisexual flowers (*Parietaria officinalis*) and flower-like inflorescences. For example, in *Forrskaolea*, pistillate and staminate flowers are borne in reduced flower-like inflorescences, the male flowers being reduced to a single stamen and tepal in the process. Within all other tribes, flowers and most inflorescences are unisexual, or where inflorescences are bisexual, they do not form flower-like configurations.

The Urticaceae have ‘dry’ stigmas, pollen accessing the pistil via papillae whose morphology does not vary across the family and which appear almost identical to those found in *Arabidopsis* (Edlund, 2004). There is, however, great variation in pistil morphology (Fig. 1), and this has played an important role in genus delimitation (Blume, 1857; Weddell, 1854, 1856, 1869). For example, the sister tribes Elatostemateae and Urticeae are characterised by pin-cushion shaped pistils over which the stigma papillae are uniformly spread; in contrast most members of the Boehmerieae mostly have extended pistils over which stigma papillae may be uniformly distributed or restricted to a specific surface; both types of pistil are exhibited in the Parietarieae. This contrasts with relatively uniform male flower- and stamen- morphology across the family, where the male sepal is characterised by a sub-apical appendage that may be equal in length to the sepal or reduced to a ridge. The ovaries are functionally unicarpellate but begin development bicarpellate, occasionally giving rise to bi-ovulate gynoecia. The fruit are achenes which are usually associated with the vestiges of the perianth or a modification of the pedicel or bracts that in many cases are fleshy and/ or brightly coloured.

49

50 [Figure 1]

51 History of Urticaceae circumscription

The main revisions of the family are summarised in Table 1. The Urticaceae were first described as a coherent group by Jussieu (Jussieu, 1789), as the order Urticae [Urticales], whose circumscription included genera now assigned to the Cannabaceae, Moraceae and Urticaceae together with a small number currently assigned to the Caryophyllaceae (*Pteranthus*), Monimiaceae (*Ambora* [*Tambourissa*], *Hedycarya*) and Rubiaceae (*Theligonum*). Urticae genera were assigned to three subgroupings based on ovule and embryo disposition. Of these groupings, the second corresponds moderately well to the Urticaceae as currently circumscribed (APG IV) (The Angiosperm Phylogeny Group, 2016), with the exceptions of *Morus*, *Artocarpus*, *Cannabis* and *Theligonum*. Later, Gaudichaud ((Gaudichaud, 1830), see Conn & Hadiah (Conn & Hadiah, 2009) for a detailed discussion) treated Jussieu’s Urticae as a family, ‘les Urticées’ which he subdivided into three un-named groupings of unspecified rank, between family and tribe, based on ovule position and embryo anatomy. Gaudichaud’s subdivisions were largely incongruent with Jussieu’s classification. Gaudichaud recognized eleven tribes within these three groupings: i. Elatostemateae, ii. Urereae, iii. Boehmerieae, iv. Parietarieae, v. Forsskaoleae, vi. Cecropieae, vii. Celtideae, viii. Cannabineae, ix. Broussonetieae, x. Moreae, and xi. Ficeae, of which i-vi correspond to the Urticaceae as currently circumscribed (APG IIV). As was the case with Jussieu’s classification, Gaudichaud included several genera that are now assigned to other families (Gunneraceae, Pipemaceae, Lacistemataceae and Gnetaceae).

Between 1854 and 1869 Weddell published three revisions of the Urticaceae (1854, 1856, 1869). These remain, to this day, the most comprehensive, detailed and thoughtful discussions of the family and its circumscription. Weddell (Weddell, 1856) divided the Urticaceae into five tribes (Urereae, Procridae =Elatostemateae, Boehmeriae, Parietariae and Forsskaoleae) based on the number of divisions in the staminate and pistillate perianths, the presence or absence of stinging hairs, the degree of fusion and symmetry of the pistillate perianth, stigma morphology and the prominence of bracts within the inflorescence. Weddell's circumscriptions were congruent with both Jussieu's (Jussieu, 1789) and Gaudichaud's (Gaudichaud, 1830), the main difference being that he restricted the family circumscription to the first five of Gaudichaud's tribes, Elatostemateae to Forsskaoleae, thereby excluding the Cecropiae. Weddell's 1854 revision ((Weddell, 1854)) recognized 34 genera and renamed the Elatostemateae tribe Lecantheae (Conn & Hadiah, 2009). In 1856 (Weddell, 1856) Weddell recognized 39 genera, maintained the same five tribes and again changed the name of the Elatostemateae, this time to Procridae. In 1857 ((Blume, 1857)) Blume published a parallel revision of the Urticaceae in ignorance of Weddell's 1856 classification and this resulted in a number of now superfluous generic names (see the footnote to the title page of Blume 1857 (Blume, 1857)). Blume did not include a tribal or equivalent classification of the genera and like Weddell, excluded the Cecropiae from his circumscription of the family. In 1869 (Weddell, 1869) Weddell published his final revision of the family in DeCandolle's *Podromus systematis naturalis regni vegetabilis*, increasing the number of genera to 43 but maintaining his 1856 tribal arrangement.

Except for the subtribes, it is very much Weddell's classification (Weddell 1856), characterised by five tribes and the exclusion of the Cecropiae, that has been followed by subsequent authors for the rest of the 19th and 20thC (Bentham & Hooker, 1883) (Engler, 1894) (Berg, 1973, 1978a) (Friis, 1989)(see Table 1). Friis (Friis, 1989) followed the same subdivisions but included the diagnostic characters of pistillode ejecting the achene or not and of the pistillode pubescent or not. The exception being Corner (Corner, 1962) and Chew (Chew, 1963) who maintained the Cecropiae within the Urticaceae. Early phylogenetic analysis of morphological characters (Humphries & Blackmore, 1989) (Fig. 14.1) also suggested a monophyletic grouping of Urticaceae, *Poikilospermum* and Cecropiae (as Cecropiaceae) but it was not until the 21stC, and the analyses of DNA sequence data that authors again began to question the exclusion of the Cecropiae (Datwyler & Weiblen, 2004; Hadiah et al., 2008; Monro, 2006; Wu et al., 2013) and in the 2003 APG II, after nearly 180 years, the Cecropiae returned to their position within the Urticaceae.

100

101 [Add in review of molecular phylogenetic contribution relevant to taxonomy]

From Weddell's treatments onwards, a number of genera have remained problematic with respect to their tribal placement. These include *Myriocarpa*, which was tentatively placed within the Boehmeriaceae by Weddell (Weddell, 1869); *Touchardia*, whose position in the Boehmeriaceae has been questioned by Friis (Friis, 1989), *Poikilospermum*, variously included (Bentham & Hooker, 1883; Engler, 1894; Weddell, 1869) and excluded (Berg, 1978a; Friis, 1989) from the Urticaceae, and *Metatrophis*, initially ascribed to the Moraceae (Brown, 1935)(Brown 1935) but which Florence (Florence, 1997) proposed should be included in the Urticaceae. These have to some extent been resolved through the analysis of DNA sequence data (Datwyler & Weiblen, 2004; L. Fu et al., 2022; Hadiyah et al., 2008; Kim et al., 2015a; Monro, 2006; Sytsma et al., 2002; Wells et al., 2021; Wu et al., 2013). In addition, approximately 1/4 of the genera (*Urera*, *Meniscogyne*, *Elatostema*, *Elatostematoides*, *Laportea*, *Pellionia*, *Procris*, *Achudemia*, *Arborella*, *Pouzolzia*, *Boehmeria*, *Parietaria* and *Leukosyke*) have been shown to be para- or polyphyletic (Chen, 1982; Kim et al., 2015b; Monro, 2006; Schüßler et al., 2019; Tseng et al., 2019; Wells et al., 2021; Wu et al., 2013).

The taxonomic challenge

Weddell (Weddell, 1856: 4) wrote in the introduction to his monograph of the family: "... there is no plant family where the species are more variable, none, in other words, where it is more difficult to recognise the species and even the genera by a simple inspection of appearance ...". This, to some extent, has been reflected by the abundant homoplasy amongst the characters traditionally used to delimit taxa (Kim et al., 2015c; Tseng et al., 2019; Wells et al., 2021; Wu et al., 2015) in the family but despite this Weddell's 19thC classifications (Weddell, 1854, 1856, 1869) the tribal classification remains little changed to this day.

The Urticaceae have been consistently recovered as sister to the Moraceae within a subclade of the Rosales that also comprises Ulmaceae and Cannabaceae (Stevens, 2017). The first published phylogeny of relationships within the Urticaceae was that of Friis (Friis, 1989: Fig. 16.9A). This suggested a partially resolved phylogeny with five tribes arranged in an unresolved trichotomy: the Urticeae united by stinging hairs, the Elatostemateae (as Lecantheae) by the staminodes actively ejecting the achene from the fruit and the Boehmeriaceae, Parietarieae and Forsskaoleae united by the presence of a lanate or pilose pistillode. Sytsma *et al.* (Sytsma et al., 2002) published the first phylogeny based on analyses of DNA sequence data which suggested the inclusion of *Poikilospermum* in the Urticaceae. This was followed by Datwyler *et al.* (Datwyler & Weiblen, 2004) whose analysis of DNA data suggested the inclusion of the Cecropiaceae into the Urticaceae, and by Monro (Monro, 2006) who confirmed the inclusion of *Poikilospermum* within the Urticaceae, suggesting its placement within the Urticeae. In 2008, Hadiyah *et al.* (Hadiyah et al., 2008) confirmed the inclusion of the Cecropiaceae and the placement of *Poikilospermum* and proposed the placement of *Myriocarpa* within the Elatostemateae. In 2013, Wu *et al.* (Wu et al., 2013) with the most comprehensive sampling of genera and genomes to date recovered four monophyletic groups broadly congruent with Friis's 1989 phylogeny except for the inclusion of the Cecropiaceae as sister to the

Boehmeriaceae, Parietariaceae and Forsskaoleae. From 2013 there has been support for an Urticaceae comprising five tribes (Z. Y. Wu et al., 2013: Fig. 2) which corresponds closely to Gaudichaud's 1830 classification (Gaudichaud, 1830) but differs from those of Weddell (Weddell, 1854, 1856, 1869) and Friis (Friis, 1989) with respect to the inclusion of the Cecropiaceae. Despite the increased taxon sampling by Wu et al. (Wu et al., 2013) and the resolution of some of the basal branches in the phylogenies, many clades were recovered with weak support. For example, Huang *et al.* (Huang et al., 2019) were unable to resolve the relationship between species of *Urera* in the Urticeae clade despite the inclusion of data from four chloroplast regions and increased taxon sampling. Wells *et al.* (Wells et al., 2021), however, were able to resolve this node through the application of Angiosperms353 nuclear sequence data (Johnson et al., 2019a).

Morphological diagnosis of the Urticaceae

The exclusion of the morphologically distinct Conocephaloideae (*Cecropia*, *Coussapoa*, *Pourouma*, *Musanga*, and *Myrianthus*) from the Urticaceae simplified the diagnosis of the family although it left the status of the former ambiguous (Corner, 1962). Jussieu (Jussieu, 1789) had originally circumscribed the Urticaceae based on the arrangement of flowers in the inflorescence and the basal and orthotropous (upright) position of the ovule in the ovary. Gaudichaud (Gaudichaud, 1830) employed a similar circumscription delimiting the Urticaceae by the presence of an upright ovule, initially attached at both its ends to the ovary wall and the embryo in the achene being reversed. With the exclusion of the Cecropiaceae, additional diagnostic characters included elastic and simultaneously reflexing stamens (Friis, 1989), non-amplexicaulous and simple leaf laminae and the presence of cystoliths in the leaf lamina. With the inclusion of the Cecropiaceae into the Urticaceae (Datwyler & Weiblen, 2004; Hadiyah et al., 2008; Monroe, 2006; Sytsma et al., 2002; Wu et al., 2013), however, previously used diagnostic characters to distinguish the family from the fig family, Moraceae, (erect orthotropous ovule, absence of amplexicaulous stipules) are lost leaving only the absence of a white latex.

Morphological basis for higher classification in Urticaceae

Several transitions to perennality of height (trees, shrubs, lianas), fusion of inflorescence branches, fusions of the perianth, arrangement of the stigma and fleshy fruits have made the application of morphological characters to generic and tribal delimitation problematic (Monroe, 2006; Wells et al., 2021; Wu et al., 2018). For example, the absence of a visible perianth tube can be the product of its fusion to the carpel, as in *Astrothalamus* and *Oreocnide*, or a product of its complete reduction, as in *Phenax*. Similarly, some characters, such as caudiform versus capitate stigma types, that are relatively constant within genera, can both occur within the same *Parietaria* inflorescence, or different species of *Poikilopsernum*. The availability of DNA sequence data has therefore been of great help in revising generic and tribal delimitation and of course in evaluating the phylogenetic informativeness of morphological characters.

Gaudichaud, Blume, Benthams and Weddell were generally in agreement with respect to the characters to be used for generic delimitation although they occasionally disagreed as to their interpretation. Weddell (Weddell, 1856) is the most expansive of the authors with respect both to character selection and interpretation, making frequent reference to how decisions were made by himself and contemporary authors (Blume, Benthams, Gaudichaud) in his introductory chapters and the ‘Obs.’ sections after each genus and we have relied heavily on this work.

Aims

The aim of this study was to establish a fully resolved and strongly supported hypothesis of phylogenetic relationship for all genera within the Urticaceae, and to use these to propose a revised and stable tribal classification that could form the basis of a linear sequence for the family. In the process we sought to evaluate the monophyly of the genera and phylogenetic informativeness of the morphological characters that have defined genera and tribes to date.

Materials & Methods

Our strategy was to use four data sources iteratively and reciprocally, to inform the application of tribal and genus names, an approach successfully applied to the Urticeae (Wells et al., 2021) and Elatostemateae (L. Fu et al., 2022). These data sources were: Sanger sequence data for up to eight non-coding plastid (chloroplast) and one coding (18S) nuclear region (data source 1), used to evaluate the monophyly of genera and inform taxon sampling for Angiosperms353 targeted enrichment (HybSeq) data of up to 350 nuclear genes (data source 2) (Johnson et al., 2019b), which in turn was used to evaluate relationships between genera and assess the phylogenetic informativeness of morphology (data source 3) and geography (data source 4). In light of assessments of their phylogenetic informativeness, the morphological and geographical data were then used to redelimit the genera in conjunction with a nomenclatural review, which was subsequently translated into taxonomic actions (see Taxonomy section).

Taxon sampling

For all data sets we sampled all the genera recognized by Friis (Friis, 1989) as belonging to the Urticaceae and by Berg (Berg, 1978a) as belonging to Cecropiaceae. In addition, we included genera described, or allocated to the family since that time, *Haroldiella* J. Florence (Florence, 1997), *Metatrophis* F.Br. (Florence, 1997), and *Zhengyia* T.Deng, D.G.Zhang & H.Sun (Deng et al., 2013). *Metapilea* W.T.Wang and *Parsana* Parsa & Maleki were excluded from this study as their taxonomic status is doubtful (see below) and herbarium material was not available for sampling.

We also sampled putative unrecognized genera recovered in previous studies (Kim et al., 2015c; Tseng et al., 2019; Wells et al., 2021; Wu et al., 2013, 2015). These included *Boehmeria nivea* L., *Laportea aestuans* (L.) Chew, *L. alatipes* Hook. f. *L. bulbifera* (Siebold & Zucc.) Wedd., *L. canadensis* (L.) Wedd., *L. cuspidata*

(Wedd.) Friis, *L. floribunda* (Baker) Leandri, *L. interrupta* (L.) Chew, *L. humblotii* (Baill.) Friis, *L. mooreana* (Hiern) Chew, *L. ovalifolia* (Schumacher & Thonn.) Chew, *L. peduncularis*, *L. ruderalis* (G. Forst.) Chew, *Pellionia tsoongii* (Merr.) Merr., *Pouzolzia rugulosa* (Wedd.) Acharya & Kravtsova (as *Boehmeria rugulosa* in Wu et al. (Wu et al., 2018)), *Pouzolzia sanguinea* (Blume) Merr., *Pouzolzia calophylla* W.T. Wang & C.J. Chen, and *Procris repens* (Lour.) B.J. Conn & Hadiah.

We verified accession determination using type collections housed at BM and K, complemented by images of type collections available through Global Plants (<https://plants.jstor.org/>), the Muséum National d'Histoire Naturelle, Paris (<https://science.mnhn.fr/institution/mnhn/collection/p/item/search>), The Linnean Herbarium of the Swedish Museum of Natural History (<http://linnaeus.nrm.se/botany/fbo/welcome.html.en>), Naturalis Bioportal (<https://bioportal.naturalis.nl/?language=en>) and the Natural History Museum of Denmark digitalized assets (<http://www.daim.snm.ku.dk/search-in-types>). As many of the type assignments in these portals are erroneous, we used the original published descriptions (protologues) to verify type status.

For Sanger sequencing

For the collection of Sanger sequence data we aimed to sample at least three species from each putative genus. Where a genus was monospecific, a single accession was used. Outgroups were chosen based on a phylogeny of the Rosales (L. B. Zhang & He, 2011) and 14 genera selected from the Ulmaceae, Cannabaceae and Moraceae.

We combined sequence data from previous studies (Wu et al., 2013, 2015) and fully vouchered accessions on NCBI GenBank with newly generated data. We generated additional sequences for 21 ingroup taxa using herbarium collections at BM, HAJB and K, focussing on genera that were absent in previous studies (*Musanga*, *Cypholophus*), poorly sampled (*Hemistylus*, *Rousselia*, *Obetia*, *Nothocnide*, *Myrianthus*, *Gyrotaenia*, *Phenax*) or problematic in previous analyses (*Boehmeria*, *Laportea*, *Pouzolzia*, *Urera*).

Angiosperms 353 sequencing

We sampled one accession of all monophyletic groupings recovered in previous studies that could be equated to the rank of genus. This resulted in a total of 111 accessions. *Trema orientale* (Cannabaceae) and six species of Moraceae were selected as outgroups.

Data generation

DNA extraction and amplification for Sanger sequencing

Total genomic DNA was mostly isolated from silica-gel dried or fresh leaves, with some from herbarium material supplied by BM and K. All material was extracted using the CTAB method (Doyle, 1987) with minor modifications. PCR was conducted in a total volume of 25 µL containing 2.5 µL 10× PCR buffer,

2.5 μ L MgCl₂ (25 mM), 2.0 μ L dNTP mixture (2.5 mM), 0.75 μ L each primer (10 μ M), 0.125 μ L Taq polymerase (5 U/ μ L) (TaKaRa, Dalian, China), 1–2 μ L template DNA (containing 5–50 ng genomic DNA), and finally distilled deionized water to give a final volume of 25 μ L. The PCR profiles for *trnL-trnF*, *rpl14-rps8-infA-rpl36*, *matK*, *rbcL*, ITS included an initial denaturation step at 94 °C for 1 min, followed by 30 cycles of 50 s at 94 °C, 1 min at 52 °C (55 °C for ITS), 80 s at 72 °C and a final extension at 72 °C for 10 min. The PCR parameters for 18S were as follows: a 97 °C initial hot start for 4 min, followed by 35 cycles of 94 °C for 30 s, 52 °C for 30 s, 72 °C for 70 s, finished with an extension step of 7 min at 72 °C. The PCR conditions for *matR* were below: initial denaturation at 95 °C for 3 min, 16 cycles of 20 s at 94 °C, 40 s at 65 °C, and degrade 1 °C per cycle, 90 s at 72 °C. Additionally, 20 cycles of 20 s at 94 °C, 40 s at 50 °C, 90 s at 72 °C, and with a final extension period of 5 min at 72 °C. The purified PCR products were directly used for cycle sequencing with the ABI Prism BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, California, USA) following the manufacturer's recommendations. Both strands of the resulting products were sequenced by using an ABI 377 and ABI 3730xl and automated sequencer ((Applied Biosystems, Foster City, California, USA)).

Target-enrichment DNA extraction & library preparation

Targeted sequencing data was generated as part of the Plant and Fungal Trees of Life (PAFTOL) project at RBG Kew. DNA extractions were performed using a modified CTAB protocol (Doyle and Doyle, 1987) and purified using AMPure XP beads (Beckman Coulter, Indianapolis, IN, USA). Purified DNA extracts were run on a 1.5% agarose gel to assess the average fragment size. Samples with very low concentration (not visible on a 1.5% agarose gel), were assessed on a 4200 TapeStation System using Genomic DNA ScreenTapes (Agilent Technologies, Santa Clara, CA, USA). The quality of the DNA was evaluated based on agarose gel and TapeStation images and were then quantified using a Qubit® 3.0 Fluorometer (Life Technologies, Carlsbad, CA, USA). DNA samples with the average fragment sizes above 350 bp were sonicated using a Covaris M220 Focused-ultrasonicator with Covaris microTUBES AFA Fiber Pre-Slit Snap-Cap (Covaris, Woburn, MA, USA) with varied shearing times depending on the DNA fragment size profile, to obtain an average of 350-bp insert sizes. Dual-indexed libraries for Illumina® sequencing were prepared using the DNA NEBNext® Ultra II Library Prep Kit at half the recommended volume, with Dual Index Primers Set 1, NEBNext® Multiplex Oligos for Illumina® (New England BioLabs, Ipswich, MA, USA). Quality of libraries were evaluated on an Agilent Technologies 4200 TapeStation System using High Sensitivity D1000 ScreenTape (Agilent Technologies, Santa Clara, CA, USA). Libraries were subsequently quantified using a Qubit® 3.0 Fluorometer. Equimolar (10 nM) libraries were pooled and a total of 1 μ g DNA in each pool was enriched using the target capture kit Angiosperms-353 v1, Catalog #308196; (Johnson et al., 2018) following the manufacturer's protocol v4 (4.0; <http://www.arborbiosci.com/mybaits-manual>). Hybridizations were performed at 65 °C for 28–32 hrs in a Hybex™ Microsample Incubator and using red Chill-out™ Liquid Wax (Bio-Rad, Hercules, CA, USA) to prevent evaporation. Enriched products were amplified from the bait-bound templates, with

KAPA HiFi 2X HotStart ReadyMix PCR Kit (Roche, Basel, Switzerland) for 10 cycles. PCR products were then cleaned using the QIAquick PCR purification kit (Qiagen). Products were quantified with a Qubit™ 3.0 Fluorometer and in some cases reamplified (and repurified) a second time between 3 and 8 cycles due to low DNA concentrations. Final products were run on an Agilent Technologies 4200 TapeStation System using High Sensitivity D1000 ScreenTape to assess quality and average fragment size. Two pools of 25 hybridised libraries each, were multiplexed together and sequenced on an Illumina MiSeq with v2 (300-cycles, 150 bp paired-end reads) and v3 (600-cycles, 300 bp paired-end reads) chemistry (Illumina, San Diego, CA, USA) at the Royal Botanic Gardens, Kew.

Sampling of morphological characters

Following Scotland et al.'s (Scotland et al., 2003) discussion on the best way to integrate morphological and molecular data in a phylogenetic context we evaluated the congruence of each morphological character state with nodes on a fully resolved ultrametric Hyb-Seq phylogenetic tree with the aim of identifying phylogenetically informative characters. For the purpose of coding morphological characters for use in phylogenetic analyses, Hawkins *et al.* (Hawkins et al., 1997) demonstrated that morphological characters and character states should be distinguished and treated separately, which we did using a two-step process whereby, (i) a comparative study of organismal variation was used to define discrete characters, and (ii) those characters were partitioned and coded as different states that were assigned to the analysed taxa. The character states were then mapped onto a fully resolved ultrametric phylogenetic tree and their distribution across the tree used to classify them as informative or not at any particular rank according to Scotland (Scotland, 1992).

Due to the large number of Urticaceae ingroup taxa for which character coding was required, we used a two-stage iterative approach to morphological sampling. The first stage comprised the evaluation of the phylogenetic informativeness of a 'long list' of 73 morphological characters drawn from the discussions of Weddell (Weddell, 1856), Friis (Friis, 1989), Monro *et al.* (Monro et al., 2015), Wells *et al.* (Wells et al., 2021, Urticeae), Kim *et al.* (Kim et al., 2015a, Urticeae), Treiberg *et al.* (Treiber et al., 2016, Cecropiaceae), Tseng *et al.* (Tseng et al., 2019, Elatostemateae) and Wu *et al.* (Wu et al., 2018) and the first authors own field and herbarium experience of the family. 'Long list' characters evaluated, and their states are listed in Table S1. Phylogenetic informativeness was assessed visually by reconstructing ancestral states (see 'Ancestral state reconstructions' below) across the HybSeq ultrametric (dated) tree (Wells et al., 2021). We selected characters which were informative for at least one node equivalent to the rank of tribe in the phylogeny. Once evaluated in this way, we selected 21 morphological characters for evaluation on the combined Sanger - Target-enrichment data tree, to which we added an additional morpho-ecological character, 'fruit fleshy' versus 'fruit not fleshy' (Table 2, character #21) to reflect a bird facilitated dispersal syndrome (Bolmgren & Eriksson, 2005).

Sampling and analysis of geographical characters

Phylogenetic relationships have been consistently shown to be closely aligned with geography within the Urticaceae (Wells et al., 2021; Wu et al., 2013, 2018), and for this reason we included geographic distribution as a phylogenetic character in our analysis. We used the following Ecozones as defined by Olson & Dinerstein (Olson & Dinerstein, 2002), Afrotropic (Af), Australasia (Au), Indomalaya (In), Nearctic (Na), Neotropic (Nt), Pacific Islands (Pf), and Palearctic (Pr). Distribution data was gathered from specimen labels. A Dispersal-Extinction-Cladogenesis (DEC) analysis was carried out using BioGeoBears (Matzke, 2013), allowing a maximum of two areas per node, on 32 CPU threads.

Phylogenetic analyses

Sanger sequence alignment and phylogenetic analysis

Sanger sequences were initially aligned using MAFFT with manual adjustments made in Bioedit v7.2 (Hall, 2011)

Estimates of support.

We adopted the same criteria of in BI, ML and MP analyses as Tseng & al. (Tseng et al., 2019): “For MP and ML analyses, 70–79%, 80–90%, and 90–100% bootstrap supports were considered as weak, moderate, and strongly supported, respectively, and values lower than 70% were considered as providing insufficient support. For BI analyses, the posterior probabilities of <0.9, 0.9–0.94, 0.95–0.99, and 1.0 were considered as providing no, weak, moderate, and strong support, respectively”.

HybSeq sequence assembly and phylogenetic analysis

We trimmed reads using Trimmomatic v.0.36 (ILLUMINACLIP: TruSeq3-PE.fa:2:30:10 HEADCROP:3 LEADING:30 TRAILING:25 SLIDINGWINDOW:4:25 MINLEN:20) (Bolger et al., 2014) and assembled them with HybPiper 1.2, which produces gene-by-gene, reference-guided *de novo* assemblies (Johnson et al., 2016), using the reference described by Johnson & al. (Johnson et al., 2019b). To ensure good alignment across the entire family, all analyses were carried out on exonic sequences only, the default output for HybPiper. For each gene, we first discarded sequences shorter than 25% of the average length for the gene. We aligned each gene with MAFFT v.7.453 (Katoh & Standley, 2013) and used trimAl v.1.4 (Capella-Gutiérrez et al., 2009) to trim columns containing more than 75% gaps. An initial set of gene trees was inferred using FastTree, and these were used to prune outlier sequences using TreeShrink. We then ran trimAl once more using the same parameters as before, mainly to remove any all-gap columns resulting from the removal of outlier sequences. We used IQ-TREE to estimate a maximum-likelihood tree for each gene under the best-fit model, with 1000 ultrafast bootstrap replicates, collapsing nodes with less than 30% support using TreeCollapserCL4 (Hodcroft, 2013). We then used ASTRAL-III, a summary-coalescent method, to estimate a species tree from all gene trees estimating node support

using local posterior probability (LPP), which reflects quartet tree concordance. Alignment, trimming, and estimation of gene trees were parallelized using GNU Parallel v.20191122 (Tange, 2018).

Combined analysis of Sanger and HybSeq data

We combined the Sanger and HybSeq data sets to generate a supertree as follows. First, Sanger loci were assembled from off-target reads in HybSeq samples using HybPiper, with select sequences from the Sanger data set used as references. Sanger loci were then aligned in three sets: (1) Elatostemateae; (2) Boehmerieae, Urereae, and Urticeae; and (3) Cecropieae. To ensure correct placement of the sub-clades, the Sanger loci assembled from the HybSeq samples were included in all three sets of alignments. Each set of alignments was merged to create a supermatrix, and a maximum-likelihood tree was inferred using IQ-TREE. The resulting three trees were then combined with the HybSeq gene trees, and ASTRAL was run on the entire set to infer a supertree.

Divergence time estimation

For the ASTRAL HybSeq tree (Fig. 3), branch lengths in substitutions per site were estimated on a supermatrix of all loci using RAxML (Stamatakis, 2014) under the GTR+CAT model, with 100 bootstrap replicates. The resulting trees were used to infer a set of 100 time-calibrated trees using treePL (Smith & O'Meara, 2012). Fossil age constraints were derived from the angiosperm calibration dataset of (Ramírez-Barahona et al., 2020), updated for this study. Specifically, the following minimum age constraints were imposed based on fossils: crown Boehmerieae, 41.2 Ma (Collinson, 1989); stem *Boehmeria*, 23.03 Ma (Takhtajan, 1982); stem *Pilea*, 23.03 Ma (Takhtajan, 1982); stem Urticeae, 48.7 Ma (DeVore et al., 2020). Outgroup constraints included stem Artocarpeae (Collinson, 1989), 64 Ma; stem Dorstenieae, 33.9 Ma (Chandler, 1961); stem Ficeae, 56 Ma (Chandler, 1963); and crown Moraceae, 47.8 Ma (Chandler, 1963). Full details for these age constraints are provided in Supplementary Data X. The maximum age of the tree (Moraceae+Urticaceae crown) was constrained to 81.7–93.3 Ma based on Zhang *et al.* (Q. Zhang et al., 2019). Parameters for treePL were optimized following Maurin (Maurin, 2020). 95% HPD of age estimates were summarized on the maximum likelihood tree using TreeAnnotator.

The HybSeq+Sanger supertree (Fig. 5) was calibrated as follows. To calculate branch lengths in substitutions (for later use in estimating divergence times), the sub-clade Sanger alignments were combined using MAFFT –merge, and then all HybSeq and Sanger loci were combined into a supermatrix. We then used IQ-TREE to infer branch lengths on the existing supertree based on the supermatrix, under the best-fit model for each locus. We then ran treePL on this tree, using the age constraints and parameter optimization method described above.

Nomenclatural review

With the aim of underpinning a stable classification, a review of the classifications of Jussieu (Jussieu, 1789), Gaudichaud (Gaudichaud, 1830), Blume (Blume, 1857), Weddell (Weddell, 1869), Bentham & Hooker (Bentham & Hooker, 1883), Engler (Engler, 1894) and Friis (Friis, 1989) was undertaken (Table 1). This was accompanied by a review of all the genus names assigned to the Urticaceae and Cecropiaceae, their generotypes and their types. Names were sourced from Jussieu (Jussieu, 1789), Gaudichaud (Gaudichaud, 1830), Blume (Blume, 1857), Weddell (Weddell, 1869), Bentham & Hooker (Bentham & Hooker, 1883), Engler (Engler, 1894), Friis (Friis, 1989) and Deng (Deng et al., 2013), from The World Checklist of Vascular Plants (Govaerts et al., 2021). For each genus name the original publication was located and checked. Generotypes were sourced from Index Nominum Genericorum (Farr & Zijlstra, 1996), verified using the Biodiversity Heritage Library (<http://www.biodiversitylibrary.org/>) and Botanicus (<http://www.botanicus.org/>). The validity and priority of names was undertaken in accordance with Articles 6, 20, 21, 38 and 40 of the Shenzhen International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018).

Generic and tribal delimitation

As with any rank, tribes provide a means of subdividing a larger group into smaller ones whilst highlighting coinciding patterns and discontinuities in morphology and evolution. They can also make the identification process more manageable. As in Wells *et al.* (Wells et al., 2021) and Fu *et al.* (L. Fu et al., 2022), we aimed to provide a classification in which tribes and genera are morphologically diagnosable and monophyletic. The justification for this is that we want to deliver a classification which supports identification both *in situ* or in biological collections, is predictive and also provides an evolutionary framework that supports the generation and testing of evolutionary hypotheses. We therefore sought to avoid taxa that could only be diagnosed using molecular data or proposing groupings that were recovered as poly- or para- phyletic with strong support. This approach was problematic where genera recovered as para- or polyphyletic were well-defined by unique combinations of morphological characters. For example, the genera *Pouzolzia* and *Laportea* are both fairly easy to recognise based on characters of habit, leaves, perianth, and fruit, but both have been recovered as paraphyletic ((Kim et al., 2015c; Wells et al., 2021; Wu et al., 2018)). In these circumstances we looked for additional morphological characters and used the pronounced phylogeographic signal within the family (Huang et al., 2019; Wells et al., 2021; Wu et al., 2018) to inform our decision-making. Where a taxon recovered as paraphyletic, comprising several monophyletic groupings which co-occur in the same biogeographic domain and were morphologically indistinguishable, then we would consider such a situation intractable and not propose any taxonomic action.

409

410 *Linear sequence of the tribes and genera*

411 A phylogeny is essentially a three-dimensional representation of putative relationships, branches at each
412 node being free to rotate around each other (Haston et al., 2007). Conversion to a two-dimensional
413 sequence is, however, frequently needed for the physical organisation of biological collections, or printed
414 lists in monographs, catalogues, and field guides. By using a systematic arrangement that incorporates
415 basic information of relationships, the resulting arrangement or sequence adds significant value to the
416 uses of the collection (Funk, 2003) and, in theory, stability of the classification, assuming that estimates of
417 relationships are correct. Converting a three-dimensional organisation of information into a two-
418 dimensional one requires some arbitrary decisions around the ordering of terminals at a node. For
419 example, Haston *et al.* (Haston et al., 2007) decided to place first the terminal with the fewer number of
420 taxa in a rotating node.

421 Because we are proposing a tribal classification, we have opted to align the order of the linear sequence
422 with the existing status-quo (Friis, 1989; Weddell, 1869), whilst respecting the hierarchy of relationships
423 recovered by the phylogenetic analyses. Where arbitrary decisions needed to be made between two genera
424 at a node then we used the approach of Haston (Haston et al., 2007) and (Christenhusz et al., 2011) to
425 place the clade with the smaller number of extant species first, which at least may facilitate the
426 identification-by-matching process in the herbarium.

427 **Missing sequence data**

428 A single genus sampled for the Sanger sequence data set that is absent from the Angiosperms353
429 sequence dataset, *Neodistemon* (Boehmeriaceae). A single genus sampled for the Angiosperms353 sequence
430 data is absent from the Sanger sequence data, *Metatrophis* (Parietariaceae) (Appendix 1).

431

432

433

434 Results

435 Taxon sampling

436 We obtained Sanger sequence data for a total of 532 ingroup and seven outgroup accessions, and HybSeq
437 data for 82 ingroup and 6 outgroup accessions (Fig S1 . plot of the loci against a phylogram).

438 Phylogenetic analyses

439 Sanger sequence data

440

441 Fig. 2

442

443 [Figure 2. Bayesian analysis of the Sanger sequence dataset constrained by the topology of an ASTRAL
444 analysis of the Angiosperms353 HybSeq low copy nuclear gene dataset. Clades 1 and 2 represent the first
445 order subdivision of the family. Clades A to G represent lower order subdivisions corresponding to
446 tribes. Values above branches are bootstrap percentage above 75. Red asterisks indicated branches with
447 high support where genera were not recovered as monophyletic.]

448 The combined analyses of Urticaceae Sanger sequence data (Fig. 2) divides into two strongly supported
449 (PP=1), clades, Clades 1 & 2). Clade 1 comprises all of the ingroup taxa from the Cecropiaceae,
450 Boehmeriaceae, Forsskaoleae and Parietariae *sensu* Friis (1989) (with the exception of *Gyrotaenia*, *Myriocarpa*
451 and *Touchardia*); and Clade 2 comprises all of the taxa in the Urticeae and Elatostemateae, with the
452 addition of *Gyrotaenia*, *Myriocarpa*, *Poikilospermum*, and *Touchardia*. Clades 1 and 2 are subsequently
453 subdivided into five (Clades IA-D1, D2) and three (Clades IIE-G) strongly supported (PP=100)
454 subclades respectively (see Fig 1a-e), each of which can be morphologically delimited (see below).

455 Within Clade 1 (Boehmeriaceae, Cecropiaceae, Forsskaoleae, Parietariae) we recovered accessions of
456 *Leukosyke*, *Maoutia* and *Gibbsia* (Clade D) as sister to the Cecropiaceae (Clade C), with *Maoutia* recovered as
457 polyphyletic with respect to *Gibbsia* with strong support. The Boehmeriaceae (Clade A) and Cecropiaceae
458 were recovered as moderately supported (90%, 88% respectively), whilst the Forsskaoleae (Clade B) were
459 recovered with weak support (BS 57%), and the Parietariae (Clade B) excluding *Rousselia* and *Hemistylus*)
460 with strong support (100%). *Sarcochlamys* was recovered sister to *Boehmeria nivea* with strong support
461 (BS100%).

462 Within the Boehmeriaceae, *Pouzolzia* was recovered as polyphyletic (*Gonostegia*, *Neodistemon*, *Rousselia*,
463 *Hemistylus*) and paraphyletic (*P. australis*, *P. calophylla*, *P. elegans*, *P. poeppigiana*, *P. rubricaulis*, *P. rugulosa*, *P.*

sanguinea). *Pipturus* was recovered as polyphyletic (*Nothocnide mollissima*, *Pouzolzia elegans*). *Boehmeria* was recovered as paraphyletic (*B. nivea*, *B. virgata*) and polyphyletic (*Cypholophus*).

Within the Forsskaoleae (Clade B), *Australina* was recovered as polyphyletic with respect to *Droguetia* and *Metatrophis*. Within the Parietariae (Clade B), *Parietaria* was recovered as polyphyletic with respect to *Gesnouinia* and *Soleirolia*.

Within the Cecropieae (Clade C), the accession of *Musanga* was recovered within *Cecropia* with strong support (100%), and one of four accessions of *Pourouma* was recovered within *Cecropia* accessions but with weak support (50%).

Within Clade 2, *Gyrotaenia* and *Myriocarpa* (Clade F) were recovered as sister to Elatostemateae (Clade E), with *Myriocarpa* polyphyletic with respect to *Myriocarpa* with strong support (BS 100%). Within the Urticeae (Clade G), *Laportea* was recovered as paraphyletic, forming four groups sister to *Nanocnide* (weak support), *Touchardia* (strong support), within *Obetia* (strong support) and an unplaced grouping (strong support). Within the Elatostemateae, *Procris repens* was recovered sister to a clade comprising all accessions of *Procris* and *Elatostema penninerve*, *E. bulbiferum* and *E. filicinum*, the latter rendering *Elatostema* polyphyletic with respect to *Elatostematoides* and *Procris*.

Angiosperms353 low copy nuclear gene data

Fig. 3.

Urticaceae divide into two strongly supported clades, Clade I) comprising all of the ingroup taxa from the Cecropiaceae, Boehmeriaceae, Forsskaoleae and Parietariae (PP 1.0; QS 73.32), with the exception of *Gyrotaenia*, *Myriocarpa* and *Touchardia*, and Clade 2) comprising all of the taxa in the Urticeae and Elatostemateae (sensu Friis 1989) (PP1.0, QS 93.67) with the addition of *Gyrotaenia*, *Myriocarpa*, *Touchardia* and the unplaced genus *Metatrophis* (Florence 1997).

Clade I divides into four strongly supported subclades corresponding to the tribes Cecropieae (Fig. 3, C, PP 1.0, QS 95.1), Forsskaoleae + part of the Parietariae (Fig. 3, B, PP 1.0; QS 56.49), Boehmeriaceae (Fig. 3, A, PP 1.0, QS 45.67) and a clade (Fig. 3, D, PP 1.0, QS 89.72) comprising *Gibbsia*, *Leukosyke*, *Maoutia* and *Sarcochlamys*. The Parietariae sensu Friis (1989) was recovered as paraphyletic, the genera *Hemistylus* and *Rousselia* being recovered within a clade comprising mostly *Pouzolzia* species (Fig. 3, 'Pouzolzia I', PP 1.0, QS 79.75).

Clade 2 divides into three strongly supported subclades corresponding to the tribes Urticeae (Fig. 3, G, PP 1.0, QS 96.16), Elatostemateae (Fig. 3, E, PP 0.91, QS 39.95) and a clade comprising the genera *Gyrotaenia* and *Myriocarpa* (Fig. 3, F, PP 1.0, QS 97.95), the latter clade being recovered as sister to the Elatostemateae (PP 1.0, QS 58.82).

In addition, we found evidence of paraphyly for *Boehmeria*, *Pouzolzia*, *Pellionia* and *Laportea*. *Boehmeria* species were recovered in three positions in the tree, 1) sister to *Archiboehmeria* + *Astrothalamus* + *Debregeasia* (Fig. 3, 'Boehmeria II', PP 1.0, QS 89.17), 2) sister to *Cypholophus* (Fig. 4, 'Cypholophus', PP 1.0, QS 99.08), and 3) sister to *Phenax* (PP 0.99, QS 41.58). *Pouzolzia* was recovered in four positions in the tree, 1) sister to a clade comprising *Neraudia*, *P. australis*, *Pipturus* and *Nothocnide* (Fig. 3, 'Pouzolzia III', PP 1.0, QS 58.02) within a clade comprising *Neraudia*, *Pipturus* and *Nothocnide* (Fig. 3, 'Pouzolzia II', PP 1.0, QS 70.52), 3) sister to *Gonostegia* (weakly supported, Fig. 3, 'Pouzolzia IV', PP 0.76, QS 38.05), and 4) in a clade comprising *Rousselia* and *Hemistylus* (Fig. 3, 'Pouzolzia I', BS 100%, 100/99.36).

Pellionia was recovered in four positions (Figs 2.3, 4.3), 1) within *Elatostema* (Fig. 2.3, BS 100%), 2) sister to *Procris*, *Elatostematoides*, *Elatostema* and two un-named clades (Fig. 2.3, BS 800%) (*Pellionia repens*), 3) sister to *Elatostematoides* (Fig. 2.3, BS 100%) (*Pellionia tsoongii*), and 4) sister to *Procris* (Fig. 2.3, BS 100%) (*Pellionia brachyceras*, *Elatostema penninerve*).

Laportea was recovered in five positions in the tree, 1) sister to *Girardinia* (Fig. 3, 'Laportea II' PP 0.83, QS 38.16) or a clade comprising *Nanocnide*, *L. cuspidata*, *Zhengyia*, *Hesperocnide* & *Urtica* (Fig. 3, 'Laportea I' PP 1.0, QS 40.95), 2) sister to *Nanocnide japonica* (Fig. 3, 'Laportea I', BS 1.0, QS 64.88), 3) sister to a clade comprising *Obetia* & *L. humblotii* (Fig. 3, 'Laportea IV', PP 1.0, QS 90.08), 4) sister to *Obetia* (Fig. 3, 'Laportea III', PP 1.0, QS 52.12), and 5) sister to *Touhardia* (Fig. 3, 'Laportea V', PP 1.0, QS 95.32).

We also recovered the unplaced genus, *Metatrophis* sister to *Droguetia* within Clade B (Fig. 3, PP 0.97, QS 46.12).

Combined analysis of Sanger and HybSeq data

Fig. 4

[Fig. 4.1-4.3 Time-calibrated supertree of Sanger sequence and Angiosperms353 HybSeq low copy nuclear gene datasets. Clades 1 and 2 represent the first order subdivision of the family. Clades A to G represent lower order subdivisions corresponding to tribes.]

The supertree recovers major groupings (Clades 1 & 2, A through to G) congruent with the Angiosperms353 ASTRAL tree.

Conflict between Sanger and HybSeq data

Combined Sanger and HybSeq data

Comparing topologies recovered by analyses of the Sanger *versus* Angiosperms353, sequence data (Figs. 2.1, 2.2 & 3) we identified three genera whose position was both strongly supported and in conflict between the respective datasets.

Sarchochlamys

In the Angiosperms353 sequence analyses *Sarchochlamys* is recovered within the Leukosykeae with strong support (Fig. 3, PP 1.0, QS 89.72). Within the Sanger data analyses, *Sarchochlamys* is recovered within the Boehmerieae (Fig. 2.1, PP 1.0, BS 100%).

Laportea canadensis

In the Angiosperms353 sequence analyses, *Laportea canadensis*, and sister *Laportea* species, is recovered within the Urticaeae and sister to *Girardinia* (Fig. 3: Laportea II, PP 0.83, QS 38.16). In the Sanger data analyses (Fig. 2.2), however, *Laportea canadensis* is recovered sister to a clade comprising *Laportea* accessions recognised as *Fleurya*, *Urera*, *Poikilospermum*, *Touchardia*, *Obetia* and *Scepcarpus* (BS 100%), which is itself recovered sister to *Girardinia*.

Phylogenetic informativeness of morphological characters

Reconstructions of 22 morphological phylogenetically informative characters and 73 states useful for the delimitation of tribes and genera are shown in Fig. S3. Of these, all were recovered as homoplastic at the scale of family or tribe. In combination, however, character states were useful in delimiting both tribes and genera. For example, the combination of stem releasing an exudate (character state 2), amplexicaulous stipules (character state 8), and absence of a pistillode (character state 10) distinguished the putative tribe Cecropieae from all other tribes. The unique combinations of character states which delimit the proposed tribes and genera are listed below (Taxonomy section).

Our results, therefore, in combination with phylogenetic analyses, enable the recognition of seven major phylo-morphological groupings (A to G, Fig. 3, 4 & 5).

Divergence time estimates and ancestral area reconstruction

Table 3 summarises the stem ages for all Urticaceae generic level groupings. Figure 3 presents divergence time estimates for the Angiosperms353 dataset and Figure 5 a time calibrated ASTRAL tree with reconstructed ancestral areas predictions.

We propose a stem age of 105–118 million years and a crown age of 93–93.3 million years for the Urticaceae. Of the seven major phylo-morphological groupings, four, Urticeae, Elatostemateae, Boehmeriaceae, Forsskaoleae and Parietariaceae (Fig. 3 (clades A to E) are proposed to have originated at the end of the Cretaceous Period (Maastrichtian). Clade F (*Myriocarpa*, *Gyrotaenia*) is proposed to have originated in the Cretaceous (Fig. 3); Clade C (Cecropiaceae) in the Oligocene (clade C, Fig. 3); and clade D (*Gibbsia*, *Maoutia*, *Leukosyke* and *Sarcochlamys*) in the Eocene (D, Fig. 3).

Our results suggest that most genera originated in the Eocene, followed by the Miocene.

Fig. 5

[Figure 5. Ancestral area estimates projected onto a time-calibrated supertree of Sanger sequence and Angiosperms353 HybSeq low copy nuclear gene datasets. Clades A to G represent lower order subdivisions corresponding to tribes.]

We recover a strong geographical signal within our analyses. Indomalaya is recovered as the most likely ancestral area for six of the seven major phylo-morphological groupings: that comprise *Gibbsia* + *Maoutia* + *Leukosyke* + *Sarcochlamys* clade; the Cecropiaceae, Boehmeriaceae, Urticeae, and Elatostemateae. The Palearctic was recovered as the most likely ancestral area for the Parietariaceae. In contrast, the higher-order clades into which the tribes group lack strong geographical structure, several biogeographic regions being equally probable ancestral areas. Within tribes there is also major geographical structure. For example, within the Cecropiaceae, *Pourouma*, *Coussapoa* and *Cecropia* represent a monophyletic group of ancestrally neotropical taxa; within the Parietariaceae, *Didymodoxa*, *Australina*, *Metatrophis* and *Droguetia* form a monophyletic group of Afrotropical taxa; within the Urticeae, *Obetia* (plus sister unplaced *Laportea* segregate) and *Scopocarpus* form a monophyletic group of Afrotropical taxa; and all of the extant taxa in the Myriocarpeae comprise neotropical taxa. Of the 53 taxa delimited as genera, 51 (96%) were recovered as having an ancestral area restricted to a single biogeographical region and most of these to Indomalaya. Exceptions were *Forsskaolea*, *Laportea* V (*Fleurya*), *Boehmeria*, *Elatostema*, *Fleurya*, *Pilea*, *Phenax*, *Poikilospermum*, *Pouzolzia* and *Urtica*. Of the exceptions, only *Fleurya* occurred in non-adjacent regions (Neotropics + Afrotropics, Pacific). Within species-rich genera that occurred across more than one biogeographic region (*Elatostema*, *Pilea*, *Urtica*) only *Urtica* was not recovered to have strong geographical phylostructure.

590

591 Discussion

592 We were able to obtain a well resolved and strongly supported phylogeny for the Urticaceae that included
 593 all genera and ca 1/3 of the species. We found that the Angiosperms353 low copy nuclear data provided a
 594 well resolved and strongly supported backbone phylogeny of the Urticaceae, which when used as a
 595 constraint on a combined analysis with Sanger sequence data provided a robust framework for testing the
 596 monophyly of the genera, organising these into tribes, reconstructing morphological character ancestral
 597 states and allowing the identification of monophyletic morphological groups. This enabled us to recognise
 598 53 groupings at the rank of genus and based on our evaluation of morphology and phylogenetic
 599 relationships we arrange these into seven tribes and provide a linear arrangement. The lack of resolution
 600 of previous studies may have resulted from a reliance on plastome sequence data (Gonçalves et al., 2019;
 601 Rokas et al., 2003), and or, less complete taxon-sampling.

602 Experimental Error

603 *Phylogenetic informativeness of morphological characters*

604 Establishing hypotheses of homology for Urticaceae genera can be challenging due to the reduced nature
 605 of the flowers, on which much of past classifications were based, which can result in convergence in
 606 character states and or saturation of morphological space (Lee & Palci, 2021), leading to systematic errors
 607 in their coding and interpretation (Dávalos et al., 2014). Because we evaluated phylogenetic
 608 informativeness across the whole family (Fig. S3), morphological characters that would have been
 609 recovered as informative (plesiomorphic, apomorphic) within a subset of the Urticaceae may be classed as
 610 uninformative (homoplastic non-homologous) in the context of the whole family. The converse,
 611 however, would not be true, a character recovered as homoplastic in a subset of the tree could not be
 612 recovered as synapomorphic across broader tree. Our approach is therefore very conservative and
 613 character states that we have recovered as non-homologous at the family level should not be ignored by
 614 future studies focussing on subsets of the family.

615 Tribal classification

616 Weddell's tribal classification, based on Jussieu's (Jussieu, 1789), Gaudichaud's (Gaudichaud, 1830) and
 617 his own detailed and comprehensive reviews of the genera (Weddell, 1856, 1869), later updated by Friis
 618 (Friis, 1989), is largely congruent with recent family-level phylogenies of the Urticaceae. The exceptions
 619 are the Cecropieae (Figs 4 & 5, Clade C) and two clades, one comprising the Indomalayan genera,
 620 *Gibbsia*, *Leukosyle*, *Maoutia* and *Sarchochlamys* (Figs 4 & 5, Clade D, Leukosykeae); the other, the
 621 neotropical genera, *Myriocarpa* and *Gyrotaenia* (Figs 4 & 5, Clade F, Myriocarpeae). Weddell's classification
 622 of the family into five tribes is intuitive and using a small number of morphological traits it is easy to

place taxa within it. For these reasons we have decided to adapt Weddell's classification rather than replace it. To do so we propose two new tribes, the Leukosykeae, restricted to Indomalaya, and the Myriocarpeae, restricted to the neotropics.

Weddell (Weddell, 1856) had placed *Leukosyke* (as *Missiessya*), *Maoutia* and *Myriocarpa* (*Gyrotaenia* and *Gibbsia* had yet to be described) within the Boehmerieae subtribe Maoutieae based on the absence of a perianth in the female flowers (Weddell, 1856: 341). *Sarcochlamys* was placed in another subtribe of the Boehmerieae, together with several other genera, based on the female flowers having a perianth comprising free parts and a weakly succulent fruit. We recovered the Maoutieae, excluding *Myriocarpa* and with the addition of *Sarcochlamys*, as sister to the Cecropieae (Fig. 4, Clade C), and both as sister to a clade comprising Boehmerieae (Fig. 4, Clade A) + Parietarieae (Fig. 4, Clade B) + Forsskaoleae (Fig. 4, Clade B). Our evaluation of the phylogenetic informativeness of perianth absence suggests that the absence of perianth is homoplastic at this rank, occurring in *Australina*, *Didymodoxa*, *Droguetia*, *Forsskaolea*, *Maoutia* and *Phenax*. Our options were to place the genera in this clade into the Cecropieae or to propose a new tribe. We chose the latter, under the name Leukosykeae as these taxa are morphologically distinct from the Cecropieae, having non-amplexicaulous stipules, stipules not enclosing another clearly visible iteration of leaf and stipule, and possessing visible cystoliths in their leaf laminae.

Myriocarpa and *Gyrotaenia* were recovered as sister to the Elatostemateae (Figs 2.3, 4.2, 5, Clades E & F), and both as sister to the Urticeae (Figs 2.3, 3, 4.2 Clade G). *Myriocarpa* and *Gyrotaenia* are morphologically distinct from the *Elatostemateae* by their tree habit, the release, when cut, of a semi-opaque exudate from the stem that oxidises dark grey or black, conspicuous stipule scars, and the absence of subapical appendages in the male flowers. The two genera share the presence of fusiform cystoliths with the *Elatostemataeae*, and conspicuous stipules and staminate flowers lacking subapical appendages with the Urticeae. We could have placed *Myriocarpa* and *Gyrotaenia* within an expanded *Elatostemateae*, or combined the *Elatostemateae* with the Urticeae tribes, or recognised them as a distinct grouping. We chose the latter option as either combination of taxa would have resulted in tribes that were very heterogenous and a challenge to delimit morphologically, and very difficult to diagnose in the field or herbarium.

The Forsskaoleae and Parietarieae were recovered as sister to each other (Figs 2.1, 3, 4.1, Clade B). Friis (Friis, 1989) expressed doubts as to their monophyly and indeed we recovered *Rouselia* and *Hemistylus* as embedded within the Boehmerieae. Schüßler *et al.* (Schüßler *et al.*, 2019) showed clearly that *Parietaria* is polyphyletic with respect to *Gesnouinia* and *Soleirolia* and we have included them in *Parietaria* (see discussion on genus delimitation in the Taxonomy section below). The Parietarieae is therefore reduced to a single genus (*Parietaria*). Both Forsskaoleae and Parietarieae share complex and atypical flower arrangements for the Urticaceae. *Parietaria* includes species with truly bisexual flowers whilst the Forsskaoleae, are characterised by genera with flower-like inflorescences or flower clusters approximating

to bisexual flowers (see Fig. S3: Trait 19), and associated with this, a transition to male flowers reduced to a single stamen (see Fig. S3 Trait 16). Both tribes are characterised by the presence of uncinata (hooked) hairs (see Fig. S3 Trait 4), one or no stipule (see Fig. S3 Trait 7), bisexual inflorescences (see Fig. S3 Trait 19), and an association with xeric environments. Given these shared characteristics we decided to combine the two tribes.

The Cecropiaceae is delimited as proposed, albeit at the rank of family, by Berg (Berg, 1978b), with the exception of *Poikilospermum*, which was recovered by us, and several previous studies as within the Urticeae (Huang et al., 2019; Kim et al., 2015c; Monro, 2006; Wells et al., 2021; Wu et al., 2013). The remaining tribes remain unchanged as summarised by Friis (Friis, 1989). For a morphological delimitation of the tribes see the ‘Key to the Tribes’ and circumscriptions of the tribes below (Taxonomy section).

Phylogeography

Whilst not the main focus of this study we feel that it is worth noting the strong geographical signal across the Urticaceae (Fig. 5), which may contradict the proposed role of long-distance dispersal (LDD) (Wu et al., 2018) in the diversification of the Urticaceae. Patterns of relationships and stem ages of the genera and clades recovered by us suggest (Fig. 5) a boreotropical distribution with divergence along Laurasian dispersal routes, coupled with relatively slow dispersal, resulting in an Indomalayan centre of origin for the taxa ancestral to most of the tribes and many of the genera, with continent-restricted tropical distributions for the terminal genera, in Indomalaya, Africa or the neotropics. For example, the ancestral taxon to the Urticeae likely diverged in the Cretaceous in Indomalaya, but the present-day resulting genera now all have distributions restricted to a single biogeographic region, with the exception of the cosmopolitan genus *Urtica* (Fig. 5, Table 3).

Our results support a scenario whereby the Urticaceae originated in Indomalaya during the mid Cretaceous (Figs 4 & 5), becoming well represented in the Laurasian boreotropical flora (Dick & Pennington, 2019), dispersing from there to the neotropics and Africa during this time and subsequently becoming fragmented as the world cooled and tropical climates receded towards the equator during the Oligocene. The latter is supported by our recovery of the Afrotropics and neotropics as Upper Eocene / Oligocene / Miocene ancestral area for the stem node of several genera: *Cecropia*, *Coussapoa*, *Discocnide*, *Gyrotaenia*, *Musanga*, *Myrianthus*, *Myriocarpa*, *Obetia*, *Pourouma*, and *Scepcarpus*. Exceptions to this scenario are the proposed Paleocene, Lower Eocene or mid Eocene and Afrotropical origin for the Parietarieae and Forsskaoleae (Fig. 5).

The delimitation of genera

In his ‘Théorie élémentaire de la botanique’, De Candolle (Candolle, 1813) wrote: “il résulte qu'un jour les limites des familles seront beaucoup mieux prononcées que celles des genres, et que ceux-ci ne pourront être établis définitivement qu'après les familles elles-mêmes ; pour le moment il en est tout autrement, [translation: it follows that one day family limits will be much better articulated than those of genera, whose limits will only be definitively established after the families themselves; for the moment it is quite different, ...]. This is clearly the case with the Urticaceae at the present time, the integration of molecular data demonstrates many genera to be poly- and para- phyletic and in the process disrupting the morphological groupings developed by taxonomists over the last two centuries.

Adopting the criteria of monophyly and morphological diagnosability we recognize 53 genera within the Urticaceae. With the inclusion of the Cecropiaceae (five genera) and *Zhengyia* (Deng et al., 2013) into the family, this represents no increase on the total of 48 genera recognized by Friis (Friis, 1989). The delimitation of the genera, however, differs significantly with respect to *Boehmeria*, *Elatostema*, *Laportea*, *Neraudia*, *Parietaria*, *Pouzolzia*, with *Fleurya*, *Gonostegia*, *Leptocnide*, *Margarocarpus*, and *Spectrocnide* being resurrected, and two new genera, *Muimar* and *Pouzolziella* being described (see Taxonomy section).

A linear sequence for the genera

By aligning our linear sequence as much as possible with those used to organise herbarium collections ((Bentham & Hooker, 1883; Friis, 1989; Weddell, 1869), whilst reflecting phylogenetic relationships we seek to propose a sequence that will minimise the number of curatorial changes required should it be used for collections’ management. The major differences to existing sequences (Bentham & Hooker, 1883; Friis, 1989; Weddell, 1869) will be the establishment of the Myriocarpeae and their placement prior to the *Elatostemateae*; the placement of the Parietarieae between the *Elatostemateae* and the Boehmerieae. The establishment of the Leukosykeae does not affect the linear sequence as the genera that comprise it were placed at the end of the Boehmerieae, which they now follow. The re-delimitation and arrangement of many genera in the Boehmerieae, however, will lead to a number of changes: *Cypholophus* is incorporated into *Boehmeria*, *Muimar* is described (formerly *Boehmeria*) and placed adjacent to *Archiboehmeria*, *Leptocnide* and *Margarocarpus* (both formerly *Pouzolzia*) are resurrected and placed adjacent to *Gonostegia* and *Neraudia* respectively, *Pouzolziella* (formerly *Pouzolzia*) is described and placed prior to *Pipturus*. The sequence within the remaining tribes is, however, little affected: in the Urticeae, *Poikilospermum* and *Touchardia* are included and placed adjacent to *Fleurya* and *Laportea* sensu Chew is split into four resurrected genera. In the Parietarieae, *Metatrophis* is included and placed adjacent to *Droguetia*.

Opportunities for future research

The aim of our research was to provide not only a stable classification but an evolutionary framework to facilitate further research in the family. We feel that the Urticaceae offers many exciting opportunities to

ask broader taxonomic and evolutionary questions, and that in this respect the family has been overlooked. Of these we would like to highlight the following:

Transitions across biomes

Our dated estimations of ancestral states (Fig. S2) suggest that transitions from herbaceous to woodiness and non-fleshy to fleshy fruits occurred synchronously several times (Fig. S2, traits 2 & 21) in the diversification of the Urticaceae. Wells *et al.* (Wells et al., 2021), proposed that such a transition in the Urticaceae may have been associated with major biome shifts and specifically the colonisation of closed-canopy forest. Closed canopies would have required lineages to increase in height to reach direct sunlight, either by becoming trees or lianas, or to adapt to the reduced light levels in the forest understory. Fleshy fruit would have enabled animal dispersal of the seeds. Within the Urticaceae both strategies can be observed. For example, the tree and liana genera such as *Dendrocnide* and *Scepcarpus*, or the deep shade specialists, *Elatostema* and *Pilea*. Fleshy fruit, however, are largely restricted to large shrubs and trees.

The shift to an arborescent habit and fleshy fruits occurred several times. Notably, during the upper Cretaceous / lower Palaeocene for the Cecropieae, arborescent Urticaceae and *Oreconide*, the time at which closed canopy forests are proposed to have first developed (Carvalho et al., 2021). This was also the time at which there was a shift from mid / late successional vegetation to early successional vegetation by the Cecropieae, and *Cecropia* is now one of the dominant ecological pioneer tree species in the Neotropics. It was also the epoch during which the Elatostemateae shifted to deep shade habitats, characterised by succulent herbaceous habit and distichous heteromorphic leaves. Taxa in these genera, notably *Pilea* and *Elatostema* are common components of the tropical montane forest groundstory, and in southeast Asia of the twilight zone in caves (Monro et al., 2018).

Within the Parietarieae there has been a shift to dry biomes, all of the genera included here being associated, or have species associated with deserts and xeric shrublands, the stem of this clade was also dated to the Cretaceous / lower Palaeocene.

We believe that the above warrant further study, incorporating greater taxon and trait sampling and that doing so would make a valuable contribution to macro-ecological studies that seek to address biome shifts and the origin of the forest biome.

Identifying the drivers of floral morphology

There are two aspects of floral morphology that merit greater study, the trend towards gynomonoecy in the *Parietarieae* (Fig. S2, trait 19), and the great variation in stigma morphology and associated degree of sepal fusion (Figure I).

The trend to bisexuality within the Parietarieae clade is noteworthy because it is restricted to this clade and has resulted in truly gynomonoecious flowers in *Parietaria*. We did not, however, recover bisexual inflorescences as ancestral in this clade (Fig. S2, trait 19) and so the most parsimonious explanation for it would be that it represents a shared response to a common driver. The observation that all taxa in the clade share a perennial herbaceous habit and an association with xeric, often rock environments may indicate an environmental rather than biological driver. Bertin & Kerwin (Bertin & Kerwin, 1998) in their study of gynomonoecy in *Aster* found no association with environmental or physiological variables and concluded that gynomonoecy could be a mechanism for reducing pollen-pistil interference or attracting pollinators. Gregg (Gregg, 1975), however, suggested that gynomonoecy could be a strategy for prioritising seed production in high light environments, whereby plants take advantage of abundant light and airflow to maximise seed production at the expense of pollen production.

We found some correlation between sepal fusion and pistil extension, taxa where the sepals are fused to form a tubular perianth having extended pistils, whilst those with divided free sepals generally lack extended pistils (FigS2, trait 12 & 17). The association of extended pistils and tubular flowers is well documented in animal pollinated flowers ((doi: 10.2307/annurev.ecolsys.34.011802.30000015, <https://doi.org/10.3732/ajb.0900182>) but less so in wind-pollinated species, especially where gynoeceous. The broad variation in perianth and pistil morphology across the Urticaceae, combined with morphological arrangement characteristic of zoophily may suggest such a mechanism of pollination in ancestral lineages

Species documentation in Boehmeria and Cecropia

Our findings of strong phylogeographic structure within Urticaceae suggest that *Boehmeria*, which includes many species with broad geographical ranges and morphological variation (e.g. *B. virgata* occurs in 32 countries and has 14 varieties, (Wilmot-Dea & Friis, 2013)) likely harbours many more species, many of which could be considered cryptic, than currently recognised. For this reason, a DNA-first approach involving much greater taxon sampling followed by an evaluation of the phylogenetic informativeness of morphological characters is a priority.

The genus *Cecropia* comprises ca 63 species of pioneer tree species. Species delimitation, however, is unstable (Berg et al., 2005) and based on relatively few collections, often of a single sex. A lack of collections is due to the fact that the species are dioecious, but it is not obvious, combined with their occupation by aggressive stinging ants that can undermine the enthusiasm of the most stoic collector. *Cecropia* are, however, important components of neotropical tropical forest, both because of their role as pioneer species, but also as important sources of food for many large frugivorous birds and mammals (Stevenson et al., 2015). A stable and comprehensive classification will thus have a broad impact on the science of ecology.

Intrinsic drivers of speciation and substrate as drivers of speciation in the *Elatostemateae*

The two genera where species radiations have unequivocally occurred are *Pilea* (ca 715 spp versus sister genus *Lecanthus*, 5spp), and *Elatostema* (ca 700 spp, versus sister genus, *Elatostematoides*, ca 20 spp). Both are characterised by high numbers of point-endemics, especially on limestone and ultramafic substrates. For example, in the case of *Elatostema*, 184 out of 280 species native to China are associated with and mostly restricted to limestone substrates (Wang, 2014). We have found evidence that the colonization of limestone has occurred very rarely within *Elatostema* and that it is associated with species radiation, apomixis and increased rates of diversification (Fu et al. *in prep.*). Both *Pilea* and *Elatostema* occupy shaded microhabitats in montane forest and have wind-pollinated flowers and poorly mechanically dispersed seeds. As such they seem ill-suited for dispersal and vulnerable to allopatry. A study by (Fu et al., 2017) based on a small sample of limestone associated species suggested that 1/3 of the species reproduce by apomixis and this is also suggested to be the case in *Pilea* (L. Fu et al., 2022). Apomixis can provide a mechanism whereby founding individuals can colonise new habitats, reproduce, disperse and benefit from sexual isolation (Hörandl, 2010) enabling well-adapted lineages to persist. .

Conclusion

We use a combination of Sanger sequence data from the plastome, 353 low copy nuclear genes and morphology to revise the classification of the Urticaceae and delimitation of many of the genera. We aimed to do so by recognising groupings where monophyly and morphological discontinuities coincide. This resulted in the recognition of seven tribes, two of which we describe here as new, 53 genera, two of which we describe here as new, and a linear sequence for the family. Our analyses suggest strong congruence between geography and phylogenetic signal. We also identify several foci for future research and suggest that the family could be of value in researching several broader questions in evolutionary biology.

Taxonomy

Tribal arrangement and linear sequence of the *Urticaceae*

Fig 6

Urticeae Lam. & DC. (1806: 184). Fig. 6.

Urtica

Zhengyia

- 819 *Sceptrocnide* (*Laportea* cuspidata clade)
- 820 *Nanocnide*
- 821 *Laportea* (*Laportea* canadensis clade)
- 822 *Girardinia*
- 823 *Discocnide*
- 824 *Dendrocnide*
- 825 *Obetia*
- 826 *Scepcarpus*
- 827 *Urera*
- 828 *Poikilospermum*
- 829 *Touchardia*
- 830 *Fleurya* (*Laportea* II)

- 831 **Myriocarpeae** tribe nov., A.K.Monro, I. Friis & Wilmot_Dear. Type: *Myriocarpa* Benth., Bot. Voy.
- 832 Sulphur 168. t. 55. 1844. Fig. 7.

- 833 *Myriocarpa*
- 834 *Gyrotaenia*

- 835 **Elatostemateae** Gaudich. (1830: 493). Fig. 8

- 836 *Elatostema*
- 837 *Elatostematoides*
- 838 *Procris*
- 839 *Polychroa* (*Pellionia repens*)
- 840 *Lecanthus*
- 841 *Achudemia*
- 842 *Pilea*

- 843 **Parietarieae** Gaudich. (1830: 501). Fig. 9.

- 844 *Parietaria*
- 845 *Forsskaolea*
- 846 *Didymodoxa*
- 847 *Australina*
- 848 *Metatrophis*
- 849 *Droguetia*

- 850 **Boehmerieae** Gaudich. (1830: 499). Fig. 10.

- 851 *Oreocnide*
852 *Phenax*
853 *Boehmeria*
854 *Pouzolziella* gen. nov.
855 *Pipturus*
856 *Neraudia*
857 *Margarocarpus*
858 *Pouzolzia*
859 *Leptocnide*
860 *Gonostegia*
861 *Chamabainia*
862 *Muimar* gen. nov.
863 *Archiboehmeria*
864 *Astrothalamus*
865 *Debregeasia*
- 866 **Leukosykeae** tribe nov., A.K.Monro, I. Friis & Wilmot_Dear. Type: *Leukosyke* Zoll. & Moritzi, Syst.
867 Verz.: 100. 1845. Fig. 11.
- 868 *Leukosyke*
869 *Sarcochlamys*
870 *Maoutia*
871 *Gibbsia*
- 872 The tribal name is derived from “syce”, Greek for “fig tree”. If treated as Latin and following the third
873 declension, it should be declined as a consonant in singular nominative and in singular genitive -is:
874 Leukosyke (genitive singular => Leukosykeis; tribal name ==> Leukosykeae).
- 875
- 876 **Cecropieae** Gaudich. (1830: 506). Fig. 12.
- 877 *Cecropia*
878 *Pourouma*
879 *Coussapoa*
880 *Musanga*
881 *Myrianthus*
882

883 Key to the tribes

- 884 1. Stipules amplexicaulous and conical, enclosing a well-formed leaf which itself encloses
885 another well-formed stipule; cystoliths absent from mesophyll; secondary veins of leaf
886 laminae parallel, conspicuously closely and regularly spaced **Cecropieae**
- 887 1. Stipules not amplexicaulous or amplexicaulous, where amplexicaulous (*Zhengyia*) not
888 conical and not enclosing a well-formed leaf; cystoliths present in the mesophyll (only
889 visible in dried material); secondary veins of leaf laminae parallel or not, conspicuously
890 closely and regularly spaced or not 2
- 891 2. Shrubs or small trees; trichomes present, trichomes neither hooked or with bulbous
892 bases; fruit fleshy, **achene and ovary borne at an angle to the main axis of the**
893 **perianth**, broadest above the midpoint (exception: *Maoutia*); Indomalaya, Australasia,
894 Oceania **Leukosykeae**
- 895 2. Shrubs, trees, *lianas*, *hemi-epiphytes* or *herbs*; trichomes present or absent, where
896 present trichomes not hooked or hooked, with or without bulbous bases; fruit fleshy or
897 not, **achene and ovary aligned with the main axis of the perianth**, broadest below the
898 midpoint (exceptions: *Chamabainia*, *Phenax*, *Debregeasia*, *Pipturus*); Palearctic,
899 Afrotropics, Indomalaya, Australasia, Oceania, Nearctic or Neotropics 3
- 900 3. Stems not releasing an exudate when cut, plant with **hooked trichomes** and never with
901 a bulbous base; pistillode pubescent 4
- 902 3. Stems releasing a clear or weakly opaque exudate when cut, or not; plant **with**
903 **trichomes not hooked** and with or without a bulbous base; pistillode glabrous 5
- 904
- 905 4. Stipules two at each node, occasionally one (*Astrothalamus*, *Debregeasia*,
906 *Margarocarpus sanguinea*, *Neraudia*, *Pouzolzia*); inflorescences, or at least flower-
907 clusters unisexual (rarely some *Boehmeria* species with some bisexual clusters also present), never
908 forming reduced flower-like structures **Boehmerieae**
- 909 4. Stipules one at each node, or absent (*Parietaria*, *Metatrophis*); inflorescences or flowers
910 bisexual, often forming a reduced flower-like structure (*Australina*, *Didymodoxa*,
911 *Droguetia*, *Forsskaolea*) **Parietarieae**
- 912 5. Stems releasing a clear or weakly opaque exudate when cut; **cystoliths in the**
913 **mesophyll punctiform, or occasionally elliptic**; some of the trichomes on stem and
914 or leaf or inflorescences with a bulbous base or not (*Poikilospermum*, *Scepcarpus*,
915 *Touchardia*) but where not then always a tree or vine; female sepals unequal or
916 completely fused forming a tube **Urticeae**

- 917 5. Stems releasing a clear or weakly opaque exudate when cut, or not, where releasing a
918 clear exudate male inflorescence racemose; **cystoliths in the mesophyll fusiform**;
919 trichomes on stem and or leaf or inflorescences never with a bulbous base; female
920 sepals equal or not (*Pilea*), never completely fused to form a tube 6
- 921 6. Herbs, occasionally shrubs or epiphytes, never trees; **stem not releasing exudate**
922 **when cut**; male inflorescence paniculate or capitate, rarely racemose (*Achudemia*
923 *myriantha*), **male flower sepals bearing a subapical appendage**; Palearctic,
924 Afrotropics, Indomalaya, Australasia, Oceania, Nearctic, or Neotropics
925 **Elatostemateae**
- 926 6. Woody shrubs or small trees; **stems releasing clear exudate when cut**; male
927 inflorescence racemose; **male flower sepals not bearing a subapical appendage**;
928 Neotropics **Myriocarpeae**
929
- 930 **Keys to genera**
- 931 *Urticeae*
- 932 1. Trees or hemi-epiphytes; **leaves entire or weakly and irregularly sinuate** 2
933 1. Herbs, shrubs, or trees; **Leaves toothed, lobed or laciniate** 5
- 934 2. Plant bearing trichomes with bulbous bases, or not; Inflorescence a branched panicle, the
935 female sepals free for most of their length, never tubular ***Dendrocnide***
- 936 2. Plant often glabrous, where pubescent, lacking trichomes with bulbous bases, the female
937 inflorescence one or more densely capitate and often brightly coloured heads, the female
938 sepals fused for all or most of their length forming a tube ***Poikilospermum***
- 939 3. Cystoliths fusiform 3
940 3. Cystoliths punctiform 5
- 941 4. Herbs; stems not woody; stipules intrapetiolar, undivided; perianth not fleshy in fruit
942 ***Nanocnide***
- 943 4. Trees, shrubs or lianas; stems woody; stipules interpetiolar, divided, at least at apex;
944 perianth fleshy in fruit ***Urera***
- 945 5. Climbers or repent herbs ***Scepocarpus***
946 5. Herbs, trees or shrubs 6
- 947 6. Trees 7
948 6. Shrubs or herbs 9

- 949 7. Afrotropics; leaves deeply lobed, lacinate or profoundly serrate, where serrate teeth of
950 fully developed leaves ≥ 5 mm, cystoliths punctiform ***Obetia***
- 951 7. Indomalaya, Australasia or Oceania; leaf margin toothed, teeth < 5 mm deep,
952 cystoliths punctiform or fusiform 8
- 953 8. Hawaii; glabrous; inflorescence ***Touchardia***
- 954 8. Indomalaya, Australasia or Oceania (but not Hawaii); pubescent or glabrous,
955 where pubescent hairs strongly *Urticating* ***Dendrocide***
- 956 9. Stipules amplexicaulous and leaf-like ***Zhengyia***
- 957 9. Stipules never amplexicaulous, never leaf-like 10
- 958 10. Stipules intrapetiolar (borne in axis of petiole) 11
- 959 10 Stipules interpetiolar (borne at the side of the petiole) 12
- 960 11. Leaves alternate, < 30 cm tall, single undivided stipule at each node
- 961 ***Nanocnide***
- 962 11. Leaves opposite, > 20 cm tall, two stipules at each node ***Urtica***
- 963 12. Leaves serrate and deeply divided, lobed, lacinate or undivided; at least some
964 trichomes > 5 mm; female sepals 3, partially fused ***Girardinia***
- 965 12. Leaves serrate, never deeply divided, lobed, lacinate; trichomes ≤ 5 mm; female
966 sepals 4, free 13
- 967 13. Female inflorescence raceme-like, unbranched or with < 4 branches; filaments
968 partially adnate to the adjacent sepal; sepals equal or longer than the achene in
969 fruit ***Sceptrocide***
- 970 13. Female inflorescence a branched panicle with > 4 branches; filaments not adnate
971 to the adjacent sepal; sepals shorter than the achene in fruit 14
- 972 14. Stipule scars inconspicuous; pedicels of female flowers articulated; stigma
973 capitate or sub-caudiform; male sepals partially fused (at base) ***Fleurya***
- 974 14. Stipule scars conspicuous; pedicels of female flowers not articulated; stigma
975 caudiform; male sepals free ***Laportea***
- 976
- 977 ***Myriocarpeae***
- 978 1. Laminae not asperous; female inflorescences few branched and raceme-like, > 6 cm in
979 length; female flowers with a foot-shaped stigma; no part of infructescence fleshy
- 980 ***Myriocarpa***

- 981 1. Laminae asperous; female inflorescences not raceme-like, < 6 cm in length; female
 982 flowers with a penicillate stigma, peduncle branches becoming fleshy in fruit
 983 *Gyrotaenia*
 984
- 985 *Elatostemateae*
- 986 1. Leaves opposite or spirally arranged; Palearctic, Afrotropics, Indomalaya, Australasia,
 987 Oceania, Nearctic or Neotropics 2
 988 1. Leaves alternate or opposite, where opposite one of the leaves in each pair minute and
 989 soon lost, never spirally arranged; Palearctica, Afrotropics, Indomalaya, Australasia,
 990 Oceania, but never Nearctic or Neotropics 4
- 991 2. Achene bearing a crescent-shaped protuberance; Indomalaya *Lecanthus*
 992 2. Achene bearing a crescent-shaped protuberance; Palearctic, Afrotropics, Indomalaya,
 993 Australasia, Oceania, Nearctic or Neotropics 3
- 994 3. Male and female flowers 5-parted; Palearctic, Indomalaya *Achudemia*
 995 3. Male and female flowers 2-, 3- or 4-parted; Palearctic, Afrotropics, Indomalaya,
 996 Australasia, Oceania, Nearctic or Neotropics *Pilea*
- 997 4. Stipules intrapetiolar (borne in axis of petiole); female flower sepals equal, inflorescence
 998 bracts absent; peduncle fleshy in fruit; achene surface smooth *Procris*
 999 4. Stipules interpetiolar (borne at the side of the petiole); female
 1000 flower sepals equal or unequal, inflorescence bracts present; peduncle not fleshy in fruit;
 1001 achene surface ornamented, never smooth 5
- 1002 5. Male inflorescence symmetrical; female inflorescence a panicle, not involucre
 1003 *Polychroa*
 1004 5. Male inflorescence asymmetrical; female inflorescence involucre or not 6.
- 1005 6. Stem succulent; leaves 3-nerved or penninerved, female inflorescence involucre,
 1006 achene not compressed *Elatostema*
 1007 6. Stem woody or succulent; leaves 3-nerved, female inflorescence not involucre,
 1008 achene compressed *Elatostematoides*
- 1009 *Lenkoseae*
- 1010 1. Stipules not forked; female inflorescence fused to form a coral-like structure, bearing
 1011 > 1000 flowers, flowers sessile *Sarcochlamys*
 1012 1. Stipules forked; female inflorescence a panicle, partially fused or not, but never fully fused

1013	or forming a coral-like structure, bearing < 1000 flowers, flowers sessile female flowers	
1014	pedicellate	2
1015	2. Stipule scars conspicuous; male and female inflorescences once dichotomously	
1016	branched, comprising two tight heads bearing < 500 flowers	<i>Leukosyke</i>
1017	2. Stipule scars inconspicuous; male and female inflorescences branched dichotomously	
1018	once or more, or paniculate, where dichotomously branched flowers borne in loose	
1019	clusters and not tight heads	3
1020	3. Filaments inflexed in bud; female inflorescence involucrate, bearing <50 flowers, stigma	
1021	sessile; achene compressed	<i>Gibbsia</i>
1022	3. Filaments not inflexed in bud; female inflorescence not involucrate, bearing > 50 flowers,	
1023	stigma stalked; achene not compressed	<i>Maoutia</i>
1024	<i>Cecropieae</i>	
1025	1. Afrotropics, Indomalaya	2.
1026	1. Neotropics	4
1027	2. Stipules not enclosing another shoot iteration; leaf margin prominently serrate	
1028		<i>Myrianthus</i>
1029	2. Stipules enclosing another shoot iteration which itself includes a visible stipule; leaf margin	
1030	entire or irregularly sinuate	3
1031	3. Leaves palmately compound, petiolules winged; male inflorescence a panicle of fused	
1032	capitae	<i>Musanga</i>
1033	3. Leaves palmately lobed; male inflorescence a fascicle of spadices	<i>Cecropia</i>
1034	4. Leaves palmately lobed; female and male inflorescence a fascicle of fused spadices	
1035		<i>Cecropia</i>
1036	4. Leaves palmately lobed or entire; female inflorescence paniculate, male inflorescences	
1037	paniculate or spicete, flowers borne in capitae, panicles or spikes	5
1038	5. Hemi-epiphytes; both female and male flowers borne in fused capitae borne on	
1039	dichotomously branching panicles	<i>Coussapoa</i>
1040	5. Trees or hemi-epiphytes; both female and male flowers free, borne in compact	
1041	irregularly branched panicles or spikes	<i>Pourouma</i>

1042	<i>Parietarieae</i>	
1043	1. Shrubs; leaves subcoriaceous, lanate below; male sepals lacking a sub-apical	
1044	appendage; Afrotropics, Palearctic, Oceania	2
1045	1. Herbs; leaves membranous to chartaceous; glabrous or pubescent below but never	
1046	lanate; male sepals with a sub-apical appendage; Afrotropics, Indomalaya, Australasia	3
1047	2. Cystoliths fusiform; stipules absent; Oceania (Austral Islands)	<i>Metatrophis</i>
1048	2. Cystoliths punctiform; stipules present; Afrotropics, Palearctic	<i>Forsskaolea</i>
1049	3. Stipules absent; leaf margin entire	<i>Parietaria</i>
1050	3. Stipules present; leaf margin crenate, serrate or entire	4
1051	4. Cystoliths punctiform; stipules two at each node; inflorescence bracts fused almost to	
1052	apex forming involucre	<i>Droguetia</i>
1053	4. Cystoliths punctiform or fusiform; stipule one at each node; inflorescence bracts free	5
1054	5. Cystoliths punctiform, Afrotropics, Indomalaya	<i>Didymodoxa</i>
1055	5. Cystoliths fusiform or oblongiform, Australasia (Australia, New Zealand)	<i>Australina</i>
1056	<i>Boehmerieae</i>	
1057	1. Achenes associated with a fleshy structure derived from the perianth, pedicel or peduncle;	
1058	Afrotropics, Indomalaya, Australasia, Oceania	2
1059	1. Achenes not associated with a fleshy structure derived from the perianth, pedicel or	
1060	peduncle	6
1061	2. Infructescence a panicle with the fused sub-terminal and terminal branches, resembling a branching	
1062	coral; Southeast Asia (Borneo, Philippines).	<i>Astrothalamus</i>
1063	2. Infructescence a panicle or fascicle, where paniculate, branches not fused. Afrotropics,	
1064	Indomalaya, Australasia, Oceania	3
1065	3. Stem not releasing a clear or greyish exudate when cut; hooked hairs present at shoot	
1066	tips, petiole, lamina or inflorescence; tree or shrub; Oceania (Hawaii)	<i>Neraudia</i>
1067	3. Stem releasing a clear or greyish exudate when cut; hooked hairs absent, or glabrous	
1068	from any part of plant; tree, vine or shrub; Afrotropics, Indomalaya, Australasia, Oceania	4
1069	4. Fruit bright orange or red; only persistent stigma visible	<i>Debregeasia</i>

- 1070 4. Fruit white, pale grey or cream; most or some part of achene clearly visible, stigma
1071 visible or not 5
- 1072 5. Trees or shrubs; stipule scars inconspicuous; female flowers pedicellate, perianth
1073 accrescent; infructescence clearly branched or sessile, fruit borne in compact heads
1074 bearing < 10 units; achene broadest at or below midpoint *Oreocnide*
- 1075 5. Trees, shrubs or vines; stipule scars conspicuous; female flowers sessile, perianth not
1076 accrescent; infructescence unbranched or sessile, fruit borne in compact heads bearing
1077 >15 units; achene broadest above midpoint *Pipturus*
- 1078 6. Achene white, cream or pale brown, shiny 7
- 1079 6. Achene brown, dark brown or black, shiny or matt 11
- 1080 7. Single undivided stipule associated with each leaf; leaf lamina toothed or entire; male sepals with
1081 subapical appendages or not 8
- 1082 7. Two stipules associated with each leaf; leaf lamina toothed; male sepals bearing a
1083 sub-apical appendage 9
- 1084 8. Stipules intrapetiolar; leaf lamina toothed; male flowers with subapical appendages; female flower
1085 with stigma articulated; achene bilaterally asymmetrical *Margarocarpus*
- 1086 8. Stipules interpetiolar; leaf lamina entire or toothed; male sepals lacking subapical appendages;
1087 female flower with stigma not articulated; achene bilaterally symmetrical *Pouzolzia*
- 1088 9. Stipules broader than long; leaf lamina toothed; fruit surface neither ribbed nor
1089 winged; achene bilaterally asymmetrical *Leptocnide*
- 1090 9. Stipules longer than broad; leaf lamina toothed or entire; fruit surface ribbed or
1091 winged; achene bilaterally symmetrical 10
- 1092 10. Stipules scars conspicuous; lamina toothed; pubescence never comprising hooked
1093 hairs; male flowers sessile; Australasia (Lord Howe Islands, Kermadec Islands)
1094 *Pouzolziella*
- 1095 10. Stipules scars inconspicuous; lamina toothed or entire; pubescence comprising
1096 hooked as well as not hooked hairs, sometimes hooked hairs restricted to
1097 inflorescence or young stems; male flowers pedicellate *Pouzolzia*
- 1098 11. Leaf margin entire; achene shiny, easily detached from the perianth in fruit 12

- 1099 11. Leaf margin toothed; achene not shiny **13**
- 1100 12. Leaves alternate or opposite, where opposite alternate leaves also present, leaves
- 1101 one or two at each node; lateral ‘primary’ veins extending $\frac{1}{2}$ to $\frac{3}{4}$ the lamina length;
- 1102 achene brown *Pouzolzia*
- 1103 12. Leaves opposite, two or three at each node; lateral ‘primary’ veins extending the full
- 1104 length of the lamina, including the apex; achene black *Gonostegia*
- 1105 13. Hooked hairs absent from plant; stipules intrapetiolar **14**
- 1106 13. Hooked hairs present on leaves, young stems, inflorescences or perianth; stipules
- 1107 interpetiolar **15**
- 1108 14. Leaves lanate below; female perianth fused, extending for most of the length of the
- 1109 flower, hairs borne only on one side of the stigma; male flowers sessile, sepals not
- 1110 bearing sub-apical appendages; achene subcompressed, bilaterally symmetrical
- 1111 *Muimar*
- 1112 14. Leaves pubescent but never lanate below; female perianth absent; hairs borne the
- 1113 full circumference of the stigma; male flowers pedicellate, sepals bearing sub-apical
- 1114 appendages; achene compressed, bilaterally asymmetrical *Phenax*
- 1115 15. Small herbs; female flowers borne in paniculate cymes; stigma capitate, male
- 1116 flowers solitary, achene broadest above the midpoint *Chamabainia*
- 1117 15. Shrubs, small trees or herbs; female flowers in compacted paniculate cymes that
- 1118 appear fasciculate; stigma extended, liguliform, corkscrew-like or filiform; male
- 1119 flowers borne in paniculate or fused cymes; achene broadest below or at the
- 1120 midpoint **16**
- 1121 16. Leaves alternate or opposite; female and male flowers borne in sessile, dense
- 1122 fascicle-like cymes either along the stem or along modified branches; stigma
- 1123 corkscrew-like or filiform, hairs borne the full length of the extended stigma
- 1124 *Boehmeria*
- 1125 16. Leaves alternate; female and male flowers borne in capitae in paniculate cymes;
- 1126 stigma ligulate, hairs borne the full length of the extended stigma *Archibohmeria*

1127 Synopsis of the genera

1128 URTICEAE. Fig. 6.

1129

1130 1. *Urtica* L. in Sp. Pl. 2: 983. 1753 – Type (designated by Green, 1929): *Urtica dioica* L.

1131 = *Hesperocnide* Torr. in Pacif. Rail. Rep. iv. 139. 1856 – Type: *Hesperocnide tenella* Torr.

1132 **Species and distribution:** 70 spp., global.

1133 **Notes:** *Hesperocnide* has been repeatedly recovered within *Urtica* (Wu & al., 2013; Kim & al., 2015). As

1134 one of its two species lack a combination with *Urtica*, we make it here.

1135 *Urtica tenella* (Torr.) A.K.Monro **comb. nov.** $\equiv$ *Hesperocnide tenella* Torr. in Pacif. Rail. Rep. Whipple,

1136 Bot. 4(5; 4): 139. 1857. Holotype: USA, California, Napa valley, April 25 1853, *Bigelow s.n.* (NY barcode

1137 NY00284326; isotypes, K barcode K000708597, GH barcode GH 00035109).

1138

1139 2. *Zhengyia* T.Deng, D.G.Zhang & H.Sun in Taxon 62: 94. 2013 – Type: *Zhengyia shennongensis* T.Deng,

1140 D.G.Zhang & H.Sun.

1141 **Notes** $\square$ Indomalaya; 1 sp.

1142

1143 3. *Sceptrocnode* Maxim. in Bull. Acad. Imp. Sci. Saint-Petersbourg 22: 238. 1876 – Type: *Sceptrocnode*

1144 *macrostachya* Maxim. in Bull. Acad. Imp. Sci. Saint-Petersbourg 22: 240. 1876.

1145 *Sceptrocnode cuspidata* (Wedd.) A.K.Monro & I. Friis **comb. nov.** $\equiv$ *Laportea cuspidata* (Wedd.)

1146 Friis in Kew Bull. 36: 156. 1981. $\equiv$ *Girardinia cuspidata* Wedd. in Prodr. [A. P. de Candolle] 16(1): 103.

1147 1869 – **Lectotype (designated here):** China, Pekin [Beijing], R.P. *David 21* [2278] (P barcode

1148 P06816094; isotype: P barcode P06816093).

1149 *Sceptrocnode interrupta* (L.) A.K.Monro & I. Friis **comb. nov.** $\equiv$ *Laportea interrupta* (L.) Chew

1150 in Gard. Bull. Singapore 21: 200 (1965). $\equiv$ *Schychowskyia interrupta* (L.) W.Wight in Contr. U.S. Natl. Herb.

1151 9: 371 (1905). $\equiv$ *Boeberia interrupta* (L.) Willd. in Sp. Pl., ed. 4, 4: 340 (1805) $\equiv$ *Urtica interrupta* L. in Sp.

1152 Pl.: 985 (1753). – **Lectotype** (selected by Corsi *et al.* 1999 ??): "Habitat in India." [India], Herb. Hermann

1153 3: 1, No. 336 (BM barcode BM-000594643).

1154 **Notes** $\square$ Indomalaya; 1 spp.

1155 Molecular studies have consistently recovered *Laportea* as paraphyletic (Kim et al., 2015c; Wells et al.,

1156 2021; Wu et al., 2013). Whilst the taxa are morphologically similar, they may be distinguished based on

1157 combinations of stipule, inflorescence, stigma and fruit characters as summarised in Table 4.

[Table 4. Diagnostic characters for *Sceptrocnide*, *Laportea*, *Fleurya* and Madagascan *Obetia* previously ascribed to *Laportea*.]

4. *Nanocnide* Blume in Mus. Bot. 2: 154. 1856 – Type: *Nanocnide japonica* Blume in Mus. Bot. 2: 155. 1856. Type: Blume, *Mus. Bot.* 2: t. 17. 1856.

Notes □ Indomalaya, Palearctic; 3 sp.

5. *Laportea* Gaudich. in Voy. Uranie: 498. 1830, nom. cons. – Type: *Laportea canadensis* (L.) Wedd. in Ann. Sci. Nat. Bot., sér. 4. 1: 181. 1854. ≡ *Urtica canadensis* L. in Sp. Pl. 2: 985. 1753.

Oblixilis Raf. in Fl. Tellur. 3: 49. 1837 – **Lectotype (selected here)**: *Oblixilis canadensis* (L.) Raf. in Fl. Tellur. 3: 49. 1837.

Urticastrum Heist. ex Fabr. in Enum.: 204. 1759, nom. rej.

Sclepsion, Raf., ined.

Notes □ Nearctic, Palearctic, Afrotropics, Indomalaya; ca 5 spp. Several studies have consistently recovered *Laportea* as paraphyletic across the Urticeae tribe (Kim et al., 2015c; Wells et al., 2021; Wu et al., 2013). Whilst the taxa are morphologically similar, they may be distinguished based on combinations of stipule, inflorescence, stigma and fruit characters as summarised in Table 4.

We recovered as paraphyletic (*Laportea* I — V, Figs 3 & 4). Four of these groupings had also been recovered by previous authors (Kim et al., 2015c; Wells et al., 2021; Wu et al., 2018). To some extent, the paraphyly of *Laportea* is an artefact of Ohwi's (Ohwi, 1936) decision to combine *Sceptrocnide* and *Laportea*, and Chew's (Chew, 1965) decision to combine *Fleurya* and *Laportea*. *Laportea* I, II and V (, Figs 3 & 4) can be diagnosed morphologically based on inflorescence, flower and fruit morphology (Table 4, also the see key to the Urticeae below). We therefore decided to revert to the earlier delimitations of these genera, resulting in groupings that are congruent with morphology, monophyly and geography. In the case of *Laportea* IV (*L. humblotii*) a morphological review suggested that it can be considered congeneric to *Obetia*, notably in the shared development of a large papery fruit.

6. *Girardinia* Gaudich. in Voy. Uranie: 498. 1830 – Type: *Girardinia leschenaultiana* Decne. in Voy. Inde 152. 1844 – **Lectotype (selected here)**: India, *Leschenault 54* (P barcode P00601956).

Notes □ Palearctic, Afrotropics, Indomalaya; 2 spp.

1189

1190 **7. *Discocnide*** Chew in Gard. Bull. Singapore 21: 207. 1965 – Type: *Discocnide mexicana* (Liebm.) Chew in

1191 Gard. Bull. Singapore 21: 208. 1965 – Holotype: Mexico, *Liebmanna* 14222 (C barcode C10017123)

1192 = *Discocarpus* Liebm., Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh., ser. 2, 2: 308.

1193 1851, nom. illegit., non *Discocarpus* Klotzsch (1841: 201).

1194 **Notes** □ Neotropics; 1 sp.

1195

1196 **8. *Dendrocide*** Miq. in Pl. Jungh. 29: 1851 – Type: *Dendrocide costata* Miq. in Pl. Jungh. 30: 1851.

1197 **Notes** □ Indomalaya, Australasia; ca 36 spp.

1198

1199 **9. *Obetia*** Gaudich. in Voy. Bonite, Bot., Atlas: t. 82. 1844 – Type: *Obetia ficifolia* Gaudich. in Voy. Bonite,

1200 Bot., Atlas: t. 82. 1844.

1201

1202 ***Obetia floribunda*** (Baker) A.K. Monro & T. Wells, **comb. nov.** ≡ *Laportea floribunda* (Baker) Leandri

1203 in Ann. Inst. Bot.-Géol. Colon. Marseille 7–8: 24. 1950 ≡ *Pilea floribunda* Baker in Bull. Misc. Inform.,

1204 Kew 1897: 280. 1897 – Holotype: Madagascar, Tanala, Ambohimombo, *F. Major* 270 (K barcode

1205 K000242862; isotypes: G barcode G00023431, G barcode G00023542)]

1206 ***Obetia humblotii*** (Baill.) A.K. Monro & T. Wells, **comb. nov.** ≡ *Laportea humblotii* (Baill.) Friis in

1207 Nordic J. Bot. 2: 233. 1982. ≡ *Ureia humblotii* Baill. in Bull. Mens. Soc. Linn. Paris 1: 479. 1885 –

1208 **Lectotype (selected here)**: Madagascar, Antsianaka, *M. Humblot* 484 (P barcode P06457704;

1209 isoelectotypes: LD barcode LD1216815, P barcode P06457701, P barcode P06457702, P barcode

1210 P06457703).

1211 ***Obetia oligoloba*** (Baker) A.K. Monro & T. Wells, **comb. nov.** ≡ *Laportea oligoloba* (Baker) Friis in

1212 Nordic J. Bot. 2: 233. 1982. ≡ *Ureia oligoloba* Baker in J. Linn. Soc., Bot. 20: 265. 1883 – **Lectotype**

1213 **(selected here)**: Madagascar (Centre) [Imerina], R. Baron s.n. ‘Aug. 1881’ (K barcode K000242866;

1214 isoelectotypes: K barcode K000242863, P barcode P00524247, P barcode P00435850).

1215 ***Obetia perrieri*** (Leandri) A.K. Monro & T. Wells, **comb. nov.** ≡ *Laportea perrieri* Leandri in Ann. Inst.

1216 Bot.-Géol. Colon. Marseille 7–8: 20–21. 1950 – **Lectotype (designated here)**: Madagascar, Diego-

1217 Suarez Province, l’Ankarana limestone plateau, *H. Humbert* 18884, (P barcode P00435843; isoelectotypes: P

1218 barcode P00435842, P barcode P00435841).

1219 **Notes** □ Afrotropics; 12 spp. Madagascan species ascribed to *Laportea* exhibit the combination of stipules

1220 adjacent to the petiole base, leaves with ‘box’ venation and fruit with papery rather than fleshy sepals.

1221 Two representatives of this group (*L. humblotii* (Baill.) Friis, *L. floribunda* (Baker) Leandri) were included in

this study and recovered as congeneric or sister to *Obetia*. Morphological examination of *Obetia* species, *L. humblotii*, *L. oligoloba* (Baker) Friis, *L. perrieri* Leandri suggests that they could be considered congeneric with *Obetia* which we propose here. The presence of intrapetiolar stipules and absence of cystoliths and urticating hairs in *L. floribunda*, however, suggests that it differs from *Obetia* and the other Madagascan species ascribed to *Laportea* by Chew. Further research may conclude that *L. floribunda* represents a distinct and undescribed genus but in the present classification we have included it in *Obetia*.

10. *Scepcarpus* Wedd. in Prodr. [A. P. de Candolle] 16: 98. 1869 – Type: *Scepcarpus mannii* Wedd. in Prodr. [A. P. de Candolle] 16: 98. 1869.

Notes □ Afrotropics; ca 15 spp. Distinguished from *Urera* by the asymmetrical pistillate inflorescences, pistillate sepals fused to a greater degree and Afrotropical distribution (Wells & al., 2021).

Scepcarpus acuminatus (Poir.) T.Wells & A.K.Monro in Mol. Phylogenet. Evol. 158: 12. 2021. ≡ *Urera acuminata* (Poir.) Gaudich. ex Decne., Nouv. Ann. Mus. Hist. Nat. 3: 490. 1834. ≡ *Urtica acuminata* Poir., Encycl. [J. Lamarck & al.] Suppl. 4. 226. 1816. Validation of *Scepcarpus acuminatus* (Poir.) T.Wells & A.K.Monro described in Molec. Phylogen. Evol. 158: 12. 2020.

Scepcarpus keayi (Letouzey) T.Wells & A.K.Monro **comb. nov.** ≡ *Urera keayi* Letouzey in Adansonia, n.s., 7: 299. 1967. **Lectotype (designated here):** Ivory Coast, Lamé (40 km NE of Abidjan), 6 November 1958, *A.J.M. Leenwenberg 1901* (WAG barcode WAG0003460; isotypes: K barcode K000242888, WAG barcode WAG0003461, WAG barcode WAG0003462, WAG barcode WAG0003463).

11. *Urera* Gaudich. in Voy. Uranie: 496. 1830, nom. cons. – Lectotype (selected by Britton & P.Wilson. in Scient. Surv. Porto Rico 1: 243, 1924): *Urera baccifera* (L.) Gaudich. ex Wedd. in Ann. Sci. Nat. Bot., ser. 3, 18: 199. 1852 ≡ *Urtica baccifera* L. in Sp. Pl., ed. 2, 2: 1398. 1763.

Urera subgenus ***capitata*** [add authors] **subgen. nov.** Type: *Urera capitata* Wedd., Ann. Sci. Nat., Bot. sér. 3, 18: 201 (1852). Validation of *Urera* subgen. *Capitata* T.Wells & A.K.Monro described in Molec. Phylogen. Evol. 158: 14. 2020.

Notes □ The African species have been placed in the resurrected genus *Scepcarpus* (see above), and the Hawaiian species moved to *Touchardia* (below) as proposed by Wells & al. (Wells et al., 2021). Last monographed by Weddell (1856).

- 1254 **12. *Poikilospermum*** Zipp. ex Miq. in Ann. Mus. Bot. Lugduno-Batavi 1: 203. 1864 – Type:
- 1255 *Poikilospermum amboinense* Zipp. ex Miq. in Ann. Mus. Bot. Lugduno-Batavi 1: 203. 1864.
- 1256 = *Conocephalus* Blume in Bijdr. Fl. Ned. Ind.: 483. 1825 – Type: *Conocephalus suaveolens* Blume in
- 1257 Bijdr. Fl. Ned. Ind.: 483. 1825.
- 1258 = *Balansaephytum* Drake in Bull. Soc. Bot. France 43: 82. 1896 – Type: *Balansaephytum tonkinense*
- 1259 Drake in Bull. Soc. Bot. France 43: 82. 1896.
- 1260 = *Conocephalopsis* Kuntze in Revis. Gen. Pl. 3: 136. 1898, nom. nud.
- 1261 **Notes** □ Indomalaya, Australasia; 27 spp. Mainly hemi-epiphytes. Morphologically very similar to
- 1262 *Touchardia*. Last monographed by Chew (Chew, 1963).
- 1263
- 1264 **13. *Touchardia*** Gaudich. in Bot. Voy. Bonite: t. 94. 1844 – Type: *Touchardia latifolia* Gaudich. in Bot.
- 1265 Voy. Bonite: t. 94. 1844.
- 1266 ***Touchardia kaalae*** (Wawra) T.Wells & A.K. Monro, **comb. nov.** ≡ *Urera kaalae* Wawra in Flora 57: 542.
- 1267 1874.
- 1268 **Notes** □ Nearctic (Hawaii); 3 spp.
- 1269
- 1270 **14. *Fleurya*** Gaudich. in Voy. Uranie: 497. 1830 – Lectotype (designated by Britton & Millspaugh, 1920:
- 1271 106): *Fleurya paniculata* Gaudich. in Voy. Uranie: 497. 1830.
- 1272 = *Schychowskyia* Endl. in Ann. Wiener Mus. Naturgesch. 1: 187. t. 13. 1836 – Type: *Schychowskyia*
- 1273 *ruderalis* (G. Forst.) Endl. in Ann. Wiener Mus. Naturgesch. 1: 187. t. 13. 1836 ≡ *Urtica ruderalis* G. Forst.
- 1274 in Fl. Ins. Austr. 66. 1786.
- 1275 = *Parsana* Parsa & Maleki in Fl. Iran [Parsa] Suppl. Gén.: 548. 1952.
- 1276 **Notes** □ Afrotropic, Indomalaya, Australasia; 4 spp. Chew (Chew, 1965) cited the genotype as *Fleurya*
- 1277 *spicata* Gaudich., but a genotype had already been designated by Britton & Millspaugh (1920).
- 1278 Molecular studies have consistently recovered *Laportea* as paraphyletic (Kim et al., 2015c; Wells et
- 1279 al., 2021; Wu et al., 2013). Whilst the taxa are morphologically similar, they may be distinguished based on
- 1280 combinations of stipule, inflorescence, stigma and fruit characters as summarised in Table 4.
- 1281
- 1282 MYRIOCARPEAE. Fig. 7.
- 1283 **15. *Myriocarpa*** Benth. in Bot. Voy. Sulphur: 168. t. 55. 1844 – Type: *Myriocarpa stipitata* Benth. in Bot.
- 1284 Voy. Sulphur: 168. t. 55. 1844 – Type: Bot. Voy. Sulphur: t. 55. 1844. **Epitype (selected here):**
- 1285 Colombia, Chocó, Nuquí, *A. Gómez* 451 (HUA; isoeotype: MO).

Notes □ Neotropics; ca 14 spp. The Sanger molecular data presented here suggests that *Myriocarpa* may be polyphyletic with respect to *Gyrotaenia*. The two taxa are united by spike-like racemes but are morphologically distinct, *Myriocarpa* having long filament-like extended infructescences and dry fruit, *Gyrotaenia* having short (< 5 cm) infructescences and fleshy fruit. We have decided to maintain the taxa as distinct until additional samples have been analysed.

16. *Gyrotaenia* Griseb. in Pl. Wright. 1: 174. 1860 – Type: *Gyrotaenia myriocarpa* Griseb. in Pl. Wright. 1: 174. 1860.

Notes □ Neotropics; 5 spp. see above.

ELATOSTEMATEAE. Fig. 8

17. *Elatostema* J.R.Forst. & G.Forst. in Char. Gen. Pl., ed. 2. [105]. 1776. nom. con., typ. cons. (Sprague, 1929; Cambridge Code 1930: 70. 1988) – Type: *Elatostema sessile* J.R. Forst. & G. Forst. in Char. Gen. Pl., ed. 2.: 106. 1776. Type: Char. Gen. Pl., ed. 2., p. 53. 1776.

= *Langeveldia* Gaudich. in Voy. Uranie: 494. 1830 – Type: *Langeveldia acuminata* (Poir.) Gaudich. in Voy. Uranie: 495. 1830 ≡ *Procris acuminata* Poir. in Encycl. [J]. Lamarck & al.] 5(1): 629. 1804. Type: [Indonesia] Isle du Java, *Commerson s.n.* (P-JU 16858!, P barcode P00663015).

Notes □ Afrotropics, Palearctic, Indomalaya, Australasia; ca 700 spp.

A clade comprising *Pellionia brachyceras*, *Elatostema penninerve*, *Elatostema filicinum* and *Elatostema bulbiferum* were recovered sister to *Procris* in our supertree of Sanger and Angiosperms353 data (Fig. 4.3). This clade comprises penninnerved leaved species that possess nanophylls, and female flowers whose sepals lack a sub-apical appendage that are in these respects different from *Elatostema* and species described under *Pellionia*, and similar to *Procris* (L. Fu, 2021; Wang, 2016). This clade differs from *Procris* in the absence of the subglobose capitate female inflorescence that is the main diagnostic character for the genus. The generic type of *Pellionia* (*P. elatostematoides*) shares the combination of penninnerved leaves and the presence of nanophylls, and should maybe be moved to this clade, which would then be named as *Pellionia*, and excluded from *Elatostema*, to which it was moved by Tseng et al. (Tseng et al., 2019). Material of *P. elatostematoides* has not, however, been sampled for sequence data by this or previous studies and so whilst we hypothesise that were it to be sequenced it would be recovered within this clade, in the absence of the molecular data we have left it un-named.

1318

1319 18. *Elatostematoides* C.B. Rob. in Philipp. J. Sci., C, 5: 497. 1911 – Type: *Elatostematoides manillense*
1320 (Wedd.) C.B. Rob. in J. Sci., C, 5: 501. 1911.

1321 *Elatostematoides tsoongii* (Merr.) A.K.Monro **comb. nov.** ≡ *Elatostema tsoongii* (Merr.) H. Schroet. in
1322 Repertorium Specierum Novarum Regni Vegetabilis, Beihefte 83(2): 21. 1936. ≡ *Pellionia tsoongii* (Merr.)
1323 Merr. in Lingnan Science Journal 6(4): 325. 1928. ≡ *Polychroa tsoongii* Merr. in Philipp. J. Sci. 21: 493.
1324 1922. Lectotype (designated here): China, Kwangtung Province [Guangdong], Tung Sing, June 22 1918,
1325 K.K. Ts'oong 1870 (PE)

1326 **Notes** □ Indomalaya, Australasia; ca 20 spp. Outside of the Philippines, *Elatostematoides* has been
1327 considered congeneric with *Elatostema* (Rodda & al., 2020) but based on Tseng & al.'s (Tseng et al., 2019)
1328 molecular phylogeny and morphological revision of the delimitation of *Elatostema* is recognized as a
1329 distinct genus here.

1330

1331 19. *Procris* Comm. ex Juss. in Gen. Pl. 403. 1789, nom. cons. – Type: *Procris cephalida* Comm. ex Poir. in
1332 Encycl. [J. Lamarck & al.] 5(1): 629. 1804, nom. cons.

1333 *Sciophila* Gaudich., Voy. Uranie, Bot.: 493. 1830, nom. illegit., non Wibel 1799.

1334 **Notes** □ Afrotropics, Indomalaya, Australasia; ca 20 spp.

1335

1336 20. *Polychroa* Lour. in Fl. Cochinch. 2: 559. 1790 – Type: *Polychroa repens* Lour. in Fl. Cochinch. 2: 559.
1337 1790. ≡ *Elatostema repens* (Lour.) Haller f. in Ann. Jard. Bot. Buitenzorg 13: 316. 1896 ≡ *Pellionia repens*
1338 (Lour.) Merr. in Lingnan Sci. J. 6(4): 326. 1928 ≡ *Procris repens* (Lour.) B.J.Conn & Hadiah in Gard. Bull.
1339 Singapore 63(1-2): 160. 2011 – Type: *J. de Loureiro s.n.*, China] (type material not traced). **Neotype**
1340 **(selected here)**: China, Hainan, Lam Ko District, LinFa Shan, Siu Shui Kau, W.-T. Tsang 262 (Lingnan
1341 University #15761) (K).

1342

1343 **Notes** □ Indomalaya; 1 sp. We have recovered *Polychroa* as sister to a clade comprising both *Elatostema*,
1344 *Elatostematoides* and *Procris* (Fig. xx), whilst previous studies (Fig. X, Tseng et al., 2019; Z. Y. Wu et al.,
1345 2013) recover it as sister, and so potentially congeneric with *Procris*. Morphologically *Polychroa* is distinct
1346 from *Elatostema* and *Procris* in its repent habit, the presence of prominent orange-brown papery stipules
1347 and the non-capitate / receptaculate pistillate inflorescences. Of note are the very few known collections
1348 bearing female inflorescences or infructescences.

1349 We could not locate any material at BM corresponding to a type collection (Merrill, 1935; Wajer,
1350 pers. comm. 2021) and so designate a neotype from the type locality.

- 1351
- 1352 **21. *Lecanthus*** Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 187. 1854 – Lectotype (designated by Hutchinson
- 1353 in Gen. Fl. Pl. 2: 186. 1967), *Lecanthus nightii* Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 187. 1854. nom. illeg.
- 1354 =*Meniscogyne* Gagnep. in Bull. Soc. Bot. France 75: 99. 1928 – Type: *Meniscogyne thorelii* Gagnep. in
- 1355 Bull. Soc. Bot. France 75: 99. 1928 – **Lectotype (designated here)**: Laos, *Thorel 2391* P barcode
- 1356 P00602029).
- 1357
- 1358 **Notes** □ Afrotropics, Indomalaya; 5 spp.
- 1359
- 1360 **22. *Achudemia*** Blume in Mus. Bot. Lugd.-Bat. 2: 57. 1856. Type: *Achudemia javanica* Blume in Mus. Bot.
- 1361 Lugd.-Bat. 2: 57. 1856.
- 1362 =*Smithiella* Dunn. in Bull. Misc. Inform., Kew 1920: 210, 1920 – Generitype: *Smithiella myriantha*
- 1363 Dunn., nom. illeg., non *Smithiella* H. Perag. & Perag. ≡ *Aboriella* Bennet in Indian Forester 107: 437, 1981
- 1364 ≡ *Dunniella* Rauschert in Taxon 31: 562, 1982 – **Lectotype (designated here)**: India, *Burkill 37636* (K
- 1365 barcode K000708616).
- 1366 **Notes** □ Palearctic, Indomalaya; five spp. We believe that the type material of *Metapilea* may be of an
- 1367 immature *Achudemia boniana* specimen (see L. Fu et al., 2022). Due to the sampling policy of the
- 1368 herbarium where the type collection is stored it is not possible to sample this material for DNA and so its
- 1369 status and position remain unknown.
- 1370
- 1371 **23 *Pilea*** Lindl. in Coll. Bot. ad t. 4. 1821, nom. cons. – Type: *Pilea muscosa* Lindl., nom. illeg. superfl. =
- 1372 *Parietaria microphylla* L. = *Pilea microphylla* (L.) Liebm.
- 1373 *Adicea* Raf. in First Cat. Gard. Transylv. Univ.: 13. 1824, nom. nud.
- 1374 *Adicea* Raf. ex Britton & A. Br. in Ill. Fl. N. U.S. 1: 533. 1896. nom. illeg., homonym.
- 1375 =*Adike* Raf. in New Fl. 1: 63. 1836 – Type: *Adike pumila* (L.) Raf. in New Fl. 1: 63. 1836.
- 1376 =*Chamaecnide* Nees & Mart. ex Miq., in Martius Fl. Bras. 4: 203. 1853 – Type: *Chamaecnide*
- 1377 *microphylla* Nees ex Miq.
- 1378 =*Dubrueilia* Gaudich. in Voy. Uranie: 495. 1830 – Type: *Dubrueilia peploides* Gaudich. – **Lectotype**
- 1379 **(designated here)**: Hawaii, *Gaudichaud s.n.* (P, barcode P00636991).
- 1380 =*Haroldiella* J. Florence in Fl. Polynésie française 1: 218. 1997 – Type: *Haroldiella sykesii* J. Florence
- 1381 in Fl. Polynésie française 1: 221. 1997.

- 1382 =*Neopilea* Leandri in Ann. Mus. Colon. Marseille, sér. 6, 7-8: 46. 1950 – Type: *Neopilea*
1383 *tsaratananensis* Leandri.
- 1384 =*Sarcopilea* Urb. in Symb. Antill. 7: 201. 1912. Genetype: *Sarcopilea domingensis* Urb. – **Lectotype**
1385 **(designated here)**: Dominican Republic, *Tuerckeheim 3392*, (BR barcode BR0000005623624).
- 1386 **Notes** □ Afrotropics, Palearctic, Indomalaya, Australasia (absent from Australia and New Zealand),
1387 Nearctic, Neotropics; ca 715 spp. The delimitation of *Pilea* and a subgeneric classification was recently
1388 proposed by Fu & al. (L. Fu et al., 2022).
- 1389 PARIETARIEAE. Fig. 9.
- 1390 **24. *Parietaria*** L. in Sp. Pl. 2: 1052. 1753. Type: *Parietaria officinalis* L. in Sp. Pl. 2: 1052. 1753.
- 1391 =*Freirea* Gaudich. in Voy. Uranie: 502. 1830 – **Lectotype (selected here)**: *Freirea australis* Nees
1392 in Pl. Preiss. 1: 638. 1845 – **Lectotype (designated here)**: Australia, *Preiss 2399* (MEL 115271;
1393 isoelectotypes: L barcode L0420597, LD barcode LD1513730, LE barcode LE00011441, LE barcode
1394 LE00011442, LE barcode LE00011455, MEL barcode MEL115373).
- 1395 =*Thaumuria* Gaudich. in Voy. Uranie: 502. 1830 – **Lectotype (designated here)**: *Thaumuria cretica*
1396 Gaudich. ex Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 210. 1854 ≡ *Parietaria cretica* L. in Sp. Pl. 2: 1052.
1397 1753.
- 1398 =*Soleirolia* Gaudich. in Voy. Uranie: 504. 1830. Type: *Soleirolia repens* Kuntze in Revis. Gen. Pl. 2:
1399 633. 1891. ≡ *Parietaria soleirolii* (Req.) Spreng. in Syst. Veg. ed. 16, 4(2): 318 (1827).
- 1400 =*Gesnoulia* Gaudich. in Voy. Uranie: 502. 1830. Type: *Gesnoulia arborea* (L. f.) Gaudich. in Voy.
1401 Uranie: 502. 1830 ≡ *Boehmeria arborea* (L.f.) Desf. in Tabl. École Bot., ed. 3: 348. 1829 ≡ *Parietaria arborea*
1402 (L.f.) L'Hér. in J. Phys. Chim. Hist. Nat. Arts 33: 55. 1788 ≡ *Urtica arborea* L.f. in Suppl. Pl.: 417. 1782 –
1403 **Lectotype (designated here)**: Spain, *Masson s.n.* (BM barcode BM000829399).
1404
- 1405 **Notes** □ Global; 26 spp. *Parietaria* was recovered as polyphyletic (Schüßler et al., 2019) *Parietaria* was
1406 recovered as polyphyletic with respect to the island endemics *Gesnoulia* and *Soleirolia* (Fig. 3 & 4.1). The
1407 main differences between these three genera according to Friis and Weddell (Friis, 1989; Weddell, 1856),
1408 relate to habit and flower sexuality. *Parietaria* comprising pantropical erect or suberect herbs with bisexual
1409 flowers; *Gesnoulia*, a large woody shrub with unisexual flowers, endemic to Macaronesia; and *Soleirolia*, a
1410 minute creeping herb with unisexual flowers and winged fruits, endemic to Corsica in the Mediterranean.
1411 A closer evaluation of the taxa reveals a number of shared morphological characters such as, an absence
1412 of stipules, prominently bracteate inflorescences and the bracts associated with pistillate flowers forming
1413 tubular lobed involucre that transform markedly in fruit. Applying our criteria for genus delimitation,
1414 therefore, we treat all three genera as *Parietaria*.

1415

1416 *Parietaria debilis* G.Forst. and *P. officinalis* are remarkable in the Urticaceae for being
1417 gynomonoecious, bearing unisexual and bisexual flowers, which can be found on the same inflorescence,
1418 and which have dimorphic stigmas and fruiting perianths. Gynomonoecy has only been documented in a
1419 few *Parietaria* species but understanding how it is determined could enable the elaboration of testable
1420 hypotheses on the evolution of monoecy in the Urticales. *P. debilis* (including *P. pensylvanica*) is notable for
1421 its global distribution which encompasses temperate climates in both the temperate and tropical latitudes
1422 of the southern and northern hemispheres.

1423

1424 **25. *Forsskaolea*** L. in Orobalsamum: 17. 1764 $\equiv$ *Chamaedryfolia* Kuntze in Revis. Gen. Pl. 2: 625. 1891 –
1425 Type: *Forsskaolea tenacissima* L. in Orobalsamum: 18. 1764.

1426

1427 = *Caidbeja* Forssk. in Fl. Aegypt.-Arab.: 82. 1775 – Type: *Caidbeja adhaerens* Forssk. in Fl. Aegypt.-
1428 Arab.: 82 (1775) – **Lectotype (designated here)**: Egypt, *Forsskal* s.n. (C barcode C10001905).

1429

1430 **Notes** □ Afrotropics, Indomalaya; 7 spp. Last revised by Friis & Wilmot-Dear (Friis & Wilmot-Dear,
1431 1988).

1432

1433 **26. *Didymodoxa*** E. Mey. ex Wedd. in Monogr. Fam. Urtic.: 547. 1856 – Type: *Didymodoxa acuminata*
1434 (Wedd.) Wedd. in Monogr. Fam. Urtic.: 549. 1856.

1435

1436 **Notes** □ Afrotropics; 2 spp. Last revised by Friis & Wilmot-Dear (Friis & Wilmot-Dear, 1988).

1437

1438 **27. *Australina*** Gaudich. in Voy. Uranie: 505. 1830. Type: *Australina pusilla* (Poir.) Gaudich. in Voy.
1439 Uranie: 505. 1830.

1440

= *Didymotoca* E. Mey. in Zwei Pflanzengeogr. Docum. (Drège): 178 1843, nom. nud.

1441

= *Anaganthos* Hook.f. in Fl. New Zealand 1: 226. 1854, nom. inval.

1442 **Notes** □ Australasia; 1 sp. Last revised by Friis & Wilmot-Dear (1988). *Australina*, as delimited by
1443 Weddell (Weddell, 1869) and Friis (Friis, 1989), included two species, *A. flaccida* (A. Rich.) Wedd., and *A.*
1444 *pusilla* that occur in east Africa and Australasia respectively. *Australia flaccida* are opposite-leaved and *A.*
1445 *pusilla* alternate-leaved. Our analyses (Fig. xx) recover *A. flaccida* as sister to the Afrotropical *Droguetia*, to
1446 which we have moved it (see *Droguetia* below), and the type, *A. pusilla* as sister to a clade comprising
1447 *Droguetia* and *Metatrophis*.

1448

1449 28. ***Metatrophis*** F.Br. in Bull. Bernice P. Bishop Mus. 130: 34. 1935. Type: *Metatrophis margaretae* F.Br. in
1450 Bull. Bernice P. Bishop Mus. 130: 35. 1935.

1451 **Notes** □ Australasia (Austral islands, Polynesia); 1 sp. First ascribed to Moraceae (Brown, 1935) based on
1452 the catkin-like inflorescences. Florence (1997) correctly moved it to the Urticaceae based on the basal
1453 placentation of the ovary and the position of the stamens in bud. With respect to flower morphology and
1454 arrangement, *Metatrophis* is very similar to *Australina* (as delimited here), the main difference being the
1455 arrangement of the male glomerules into spikes in *Metatrophis*, as opposed to free in *Australina*. The two
1456 genera, however, differ greatly morphologically. Further research may decide that *Metatrophis* and
1457 *Australina* be combined into a single genus.

1458 Whilst both Brown (Brown, 1935) and Florence (Florence, 1997) describe *Metatrophis* as having caducous
1459 stipules we could find neither stipules or stipule scars on the single sheet at K, or images available at
1460 JSTOR Global Plants (BISH10052652022, BISH1005268, BISH1005269, P00636979). We believe,
1461 therefore, that Brown and Florence may have mistaken very immature leaves for stipules. The presence of
1462 stipules should be resolvable from the examination of living material. If confirmed, the absence of
1463 stipules is a trait shared with *Parietaria*.

1464

1465 29. ***Droguetia*** Gaudich. in Voy. Uranie: 505. 1830. Type: *Droguetia leptostachys* Gaudich. in Voy. Uranie:
1466 505. 1830.

1467 = *Didymogyne* Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 207. 1854, nom. illeg., superfl. (Friis &
1468 Wilmot-Dear, 1988) – Type: *Didymogyne abyssinica* Wedd in Ann. Sci. Nat., Bot., sér. 4, 1: 207. 1854.

1469 ***Droguetia flaccida*** (A.Rich.) A.K. Monro, I. Friis & Wilmot-Dear, **comb. nov.** ≡ *Australina flaccida*
1470 (A.Rich.) Wedd. in Prodr. [A.P.de Candolle] 16(1): 235⁶⁰. 1869 ≡ *Pouzolzia flaccida* A.Rich. in Tent. Fl.
1471 Abyss. 2: 259. 1850 – **Lectotype (designated here)**: Abyssinia [Ethiopia], R. *Quartin-Dillon* s.n. ‘Sept.
1472 1839’ (P barcode P00435811; isoelectotypes: P barcode P00435810, P barcode P00435812).

1473 **Notes** □ Afrotropics, Indomalaya; 8 spp. Last revised by Friis & Wilmot-Dear (Friis & Wilmot-Dear,
1474 1988). In the light of changes to the delimitation of *Australina* and *Droguetia* suggested here, *Droguetia* can
1475 now be distinguished from *Australina* based on the presence of punctiform cystoliths versus fusiform or
1476 oblongiform in the latter.

1477

1478 BOEHMERIEAE. Fig. 10.

1479

1480 30. ***Oreocnide*** Miq. in Pl. Jungh. 39. 1851 – **Lectotype (designated here)**: *Oreocnide sylvatica* (Blume)
1481 Miq. in Miq., Pl. Jungh.: 40. 1851. ≡ *Urtica sylvatica* Blume in Bijdr. Fl. Ned. Ind. 506. 1825.

- 1482 = *Villebrunea* Gaudich. in Voy. Bonite, Bot., Atlas: t. 91. 1844 – **Lectotype (designated here):**
 1483 *Villebrunea integrifolia* Gaudich. in Voy. Bonite, Bot., Atlas: t. 91. 1844.
- 1484 **Notes** □ Palearctic, Indomalaya, Australasia; 16 spp.
 1485
- 1486 **31. *Phenax*** Wedd. in Ann. Sci. Nat. Bot. sér. 4. 1: 191. 1854 – Type: *Phenax vulgaris* Wedd., Ann. Sci. Nat.
 1487 Bot., sér. 4. 1: 191. 1854 ≡ *Gesnoulinia boehmerioides* Miq. in Martius, Fl. Bras. 4: 194. 1853.
- 1488 **Notes** □ Neotropics, Afrotropics (Madagascar); 28 spp. *Phenax* remains very poorly studied with no
 1489 comprehensive revision since Weddell (Weddell, 1869). The disjunct distribution of the Neotropics and
 1490 Madagascar, together with very few species having been sampled for DNA suggest that *Phenax* should be
 1491 a high priority for future study.
 1492
- 1493 **32. *Boehmeria*** Jacq. in Enum. Syst. Pl. 9, 31. – Type: *Boehmeria ramiflora* Jacq. in Enum. Syst. Pl. 9: 31.
 1494 1760.
- 1495 = *Cypholophus* Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 198. 1854 – Type: *Cypholophus macrocephalus*
 1496 (Blume) Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 198. 1854.
- 1497 = *Duretia* Gaudich. in Voy. Uranie: 500. 1830, nom. nud.
- 1498 = *Splitgerbera* Miq. in Comm. Phytogr.: 133. t. 14. 1840. Type: *S. japonica* Miq. in Comm. Phytogr.:
 1499 134. 1840.
- 1500
- 1501 ***Boehmeria brunneola*** (Elmer) A.K.Monro & Wilmot-Dear **comb. nov.** ≡ *Cypholophus brunneolus* Elmer
 1502 in Leaf. Philipp. Bot. 3: 896. 1910 — Holotype: Philippines, Mindanao, Davao District, Todaya (Mt.
 1503 Apo), 1200 masl, Sept. 1909, *A.D.E. Elmer 11641* (A barcode A00039518*).
- 1504
- 1505 ***Boehmeria chamaephyton*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** ≡ *Cypholophus*
 1506 *chamaephyton* H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 582. 1922. Type: Papua New Guinea, Madang Province]
 1507 Mount Hellwig summit, 2500 m, Nov. 1909, *L.S.A.M. von Römer 1213* (B†).
- 1508
- 1509 ***Boehmeria decipiens*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** ≡ *Cypholophus decipiens*
 1510 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 573. 1922 – Lectotype (designated by Wilmot-Dear & Friis, 1998:
 1511 922): Papua New Guinea, Kaiser Wilhelmsland, 1889 □ 1891, *K. Weinland 169* (L barcode L0281467*).
- 1512
- 1513 ***Boehmeria engleriana*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** ≡ *Cypholophus englerianus*

1514 in H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 578. 1922 – Syntypes: Indonesia, Papua, Mt. Hellwig summit, 2500
1515 m, 5 Jan. 1913, *A.A.Pulle* 919, 920 (B†, WRS�*).

1516

1517 ***Boehmeria friesiana*** (K.Schum.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Pilea friesiana* K.Schum. in
1518 K.M.Schumann & C.A.G.Lauterbach in Fl. Schutzgeb. Südsee, Nachtr.: 252. 1905 $\equiv$ *Cypholophus friesianus*
1519 (K.Schum.) H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 584. 1922 – Holotype: [Papua New Guinea, Morobe
1520 Province, Huon Peninsula] Kaiser Wilhelmsland, Sattelberg, June 1899, *E.O.A. Nyman* 420 (B†; isotype:
1521 L!, UPS, WRS�*?).

1522 Material corresponding to Nyman 420 was seen at WRS� but it lacks collector labels. Winkler
1523 deposited a set of duplicatesupplcate type collections at WRS� for names that he described from New
1524 Guinea (1922).

1525

1526 ***Boehmeria gjellerupii*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus gjellerupii*
1527 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 580. 1922 — Holotype: Papua New Guinea, upper Tami river
1528 between Eti and Arfom rivers, 80 m, 27 Mar. 1910, *K. Gjellerup* 8 (B†; isotype: WRS�*).

1529

1530 ***Boehmeria harveyi*** Seem. Fl Vitiens. t. 62 (1868). Replaced name: *Cypholophus heterophyllus* (Wedd.)
1531 Wedd. in Prodr. [A. P. de Candolle] 16(1): 235¹⁸ (1869). $\equiv$ *Cypholophus macrophyllus* var. *heterophyllus*
1532 Wedd (1857:435.), non *Boehmeria heterophylla* Wedd. — **Type:** Fl Vitiens. t. 62 (1868).

1533 Seemann’s name has only a colour plate as description and type (1868). A specimen collected by
1534 Harvey in Fiji in 1855 (*s.n.*, BM, K) is annotated ‘Gov.Miss Fiji 1st Append.’ This would suggest that there
1535 may be an earlier place of publication. We have, however, been able to locate this publication

1536

1537 ***Boehmeria hochreutineri*** A.K.Monro & Wilmot-Dear **nom. nov.** Replaced name: *Cypholophus stipulatus*
1538 Hochr. in Candollea 2: 348 (1925) non *Boehmeria stipularis* Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 200.
1539 1854 — Holotype: Samoa, Upola Island, road to Lanuto Lake, 500 m, Mar. 21 1905, *B.P.G. Hochreutiner*
1540 3248 (G barcode 00354082*).

1541

1542 ***Boehmeria integer*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus integer*
1543 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 584. 1922 – Holotype: [Indonesia, Sandaun, East Sepik] Sepik area,
1544 Felsspitzec station, 1400 to 1500 m, Aug. 4 1913, *C.L. Ledermann* 12587 (B†, WRS�*)

1545

1546 ***Boehmeria kerewensis*** (P.Royen) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus kerewensis*
1547 P.Royen in Alp. Fl. New Guinea 3: 2137. 1982 — Holotype: Papua New Guinea, South Highland District,

- 1548 Tari Subdistrict, N slopes of Mt. Kerewa, 6°S 143°E, 2940 m, June 29 1966, *C. Kalkman* 4720 (BISH
1549 barcode BISH1005216; isotype: K!).
- 1550 ***Boehmeria lauterbachiana*** A.K.Monro & Wilmot-Dear **nom. nov.** Replaced name: *Cypholophus velutinus*
1551 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 578. 1922, non *Boehmeria velutina* Decne. in Herb. Timor.: 163 (1834)
1552 — **Lectotype (designated here)**: Northeast New Guinea [Papua New Guinea], Toliba, 300 m, Dec. 15
1553 1908, *F.R.F. Schlechter* 18966, (K barcode K000741427; isoelectotype BR barcode BR0000005623464*).
1554 [Syntypes: NE New Guinea [Papua New Guinea], Shigaun, 400 m, Jun. 9 1896, *C.A.G. Lauterbach* 2298
1555 (B†, BO, K); Toliba, 300 m, Dec. 15 1908, *F.R.F. Schlechter* 18966 (B†, isosyntypes BR barcode
1556 BR0000005623464, K barcode K000741427)].
- 1557
- 1558 ***Boehmeria ledermannii*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus*
1559 *ledermannii* H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 581. 1922 — Holotype: Indonesia, Sandaun, East Sepik]
1560 Sepik area, Felsspitzec station, 1400 to 1500 m, Jul. 30 1913, *C.L. Ledermann* 12383 (B†; isotype: WRS�).
1561
- 1562 ***Boehmeria melanocarpoides*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus*
1563 *melanocarpoides* H.J.P.Winkl. in Nova Guinea 14: 129. 1924 — Holotype: Indonesia, Papua], Mount
1564 Hellwig, 1800 m, Dec. 18 1912, *A.A.Pulle* 755 (B†; isotype: WRS�).
1565
- 1566 ***Boehmeria microphylla*** (Elmer) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus microphyllus*
1567 Elmer in Leaf. Philipp. Bot. 3: 895. 1910 — Holotype: Philippines, Mindanao, Davao District, Mt. Apo,
1568 Todaya, [1800 m], Aug. 1909, *A.D.E. Elmer* 11588 (A barcode A00039519; isotypes: BISH barcode
1569 BISH1005217, E barcode E00504430, G barcode G00354073, G barcode G00354081, HBG barcode
1570 HBG513214, K barcode K000741437!, MO barcode MO204580, NY barcode NY00284304, NY barcode
1571 NY00284305, US barcode US00090906).
1572
- 1573 ***Boehmeria montana*** (Ridl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus montanus* Ridl. in
1574 Trans. Linn. Soc. London, Bot. 9: 157. 1916 — Holotype: Dutch New Guinea [Indonesia, Papua], Camp
1575 10-11, Jan 27 1912, *C. Boden-Kloss* s.n. (BM barcode 000951675; isotype: K! barcode K000741433).
1576
- 1577 ***Boehmeria nummularis*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus*
1578 *nummularis* H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 582. 1922 — **Lectotype (designated here)**: New Guinea
1579 [Papua New Guinea], Madang Province, Kani Mountains, 1000 m, Dec. 5 1907, *F.R.F. Schlechter* 16959
1580 (B†; isoelectotype WRS�) [Note: Two B collections were cited by Winkler, *Schlechter* 16959 and *Warburg*
1581 20780. The Berlin duplicates were destroyed in WWII/ *Warburg* 20780 could not be traced, but a
1582 duplicate of *Schlechter* 16959, annotated as 'original' was located in WRS� and selected as lectotype.]
1583

- 1584 ***Boehmeria pachycarpa*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus*
1585 *pachycarpus* H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 574. 1922 — Syntypes: [Indonesia, Sandaun, East Sepik]
1586 Sepik, Schraderberg, 2070 m, May 29 1913, *C.L. Ledermann 11764* (B†); May 28 1913, *C.L. Ledermann*
1587 *11695* (B†, WRS�).
1588
1589 ***Boehmeria patens*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ — *Cypholophus patens*
1590 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 577. 1922. — Holotype: Indonesia, Irian Jaya, South slope of the
1591 Hellwig Mountains, 1750 m, Dec. 20. 1912, *A.A.Pulle 786* (B†, WRS�).
1592
1593 ***Boehmeria pulleana*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus pulleanus*
1594 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 584. 1922 — Holotype: [Indonesia, Papua] South slope of the Hellwig
1595 Mountains, 1700-1800 m, Dec. 10. 1912, *A.A.Pulle 756*(B†, WRS�).
1596
1597 ***Boehmeria radicans*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus radicans*
1598 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 576. 1922 — Holotype: Indonesia, Papua, South slope of the Orange
1599 Mountains, Parames bivouac, 750 m, Dec. 3. 1912, *A.A.Pulle 541* (B†, WRS�).
1600
1601 ***Boehmeria reticulata*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus reticulatus*
1602 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 577. 1922 — Holotype: [Indonesia, Sandaun, East Sepik] Sepik,
1603 Schraderberg, 2070 m, Jun. 2 1913, *C.L. Ledermann 11946* (B†, WRS�).
1604
1605 ***Boehmeria rudis*** (Ridl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus rudis* Ridl. in Trans.
1606 Linn. Soc. London, Bot. 9: 157. 1916 — **Lectotype (designated here)**: Dutch New Guinea [Indonesia,
1607 Papua], Camp 9-10, 1500-2000 m, Jan 26 1912, *C. Boden-Kloss s.n.* (K barcode 000741430; isolectotype:
1608 BM barcode 000951677).
1609 ***Boehmeria schlehtendahlana*** A.K.Monro & Wilmot-Dear **nom. nov.** Replaced name: non *Boehmeria*
1610 *rotundifolia* D.Don. in Prodr. Fl. Nepal.: 60. 1825 $\equiv$ *Cypholophus rotundifolius* H.J.P.Winkl. Bot. Jahrb. Syst.
1611 57: 571 (1922), — Holotype: New Guinea [Papua New Guinea], Finisterre Mountains, 1300 m, Jan. 10
1612 1909, *F.R.F. Schlechter 19051* (B†; isotypes: K barcode 000741432, BR barcode BR0000005623792*,
1613 WRS�).
1614
1615 ***Boehmeria trapula*** (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus trapula*
1616 H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 579. 1922 — Holotype: [Papua New Guinea] Northeastern New
1617 Guinea, Jul. 14 1907, *F.R.F. Schlechter 16263* (B†; isotypes: A barcode 00035011, BISH barcode 1005218, E
1618 barcode 00301048, G barcode 00354086, K barcode 000741428, K barcode 000741429, S (S07-9824),

SING barcode 0062080, SING barcode 0062081).

Boehmeria treubii (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus treubii*

H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 583. 1922 — Holotype: Southwest New Guinea [Papua New Guinea]

North slope of the Treub Mountains, 2400 m, Feb. 17 1913, *A.A.Pulle 1087* (B†).

Boehmeria vaccinioides (H.J.P.Winkl.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus*

vaccinioides H.J.P.Winkl. in Bot. Jahrb. Syst. 57: 583. 1922 — Holotype: [Indonesia, Papua], between Mount

Hellwig and Alkmaar camp, *L.S.A.M. von Römer 724* (B†); summit of Mount Hellwig, 2600 m, 1700-1800

m, Jan. 2. 1913, *A.A.Pulle 877* (B†). — **Lectotype (selected here):**

Boehmeria vriesiana A.K.Monro & Wilmot-Dear **nom. nov.** Replaced name: *Cypholophus ellipticus* Wedd.

in Prodr. [A.P.de Candolle] 16(1): 235(12) (1869), *Cypholophus ellipticus* Wedd. in Prodr. 16(1): 235(12)

(1869), non *Boehmeria elliptica* Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 200 (1854). Holotype: — [Indonesia,

Sulawesi, Celebes] Java [see note below], *G.H. de Vriese 23* (P barcode 06873943).

There are four specimens collected by *de Vriese* at L, one of which is numbered '23', 'Celebes' and 'type

duplicate' (L barcode 2070508), all of which were collected in the Celebes Islands, Sulawesi. The

presumed holotype in P (P06873943) is labelled *De Vriese '23'* and 'Java', P. The L duplicate has the more

complete label and indicates the collectors as '*G.H. de Vriese & J.E. Teijsmann 23*', the P specimen label

indicates '23', '*de Vriese*' and 'Java'. Given that Weddell described the species in P, the latter is the

holotype. The locality given is, however, likely incorrect, given that all of the De Vries collections of this

taxon in L include the Celebes as the locality.

Boehmeria warburgiana (Lauterb.) A.K.Monro & Wilmot-Dear **comb. nov.** $\equiv$ *Cypholophus warburgianus*

Lauterb. in K.M.Schumann & C.A.G.Lauterbach in Fl. Schutzgeb. Südsee, Nachtr.: 255. 1905 —

Holotype: Kaiser-Wilhelmsland [Papua New Guinea], Bismark Mountains, 1800 m, Jan. 1902, *F.R.F.*

Schlechter 14007 (B†).

Notes □ Nearctic, Neotropics, Palearctic, Afrotropics, Indomalaya, Australasia; ca 85 spp.

Our increased taxon and genome sampling confirmed the findings of previous studies (Wu et al., 2013,

2018) that *Boehmeria* is both poly- and para- phyletic (Fig. 3, 4.1). Translating our results into a

phylogenetic classification required us to choose one of several scenarios: 1) treat all species of *Boehmeria*,

together with those genera with which they form a monophyletic clade (see Figs 3, 4.1), as a single genus.

This would require treating *Archiboehmeria*, *Astrothalamus*, *Chamabainia*, *Cypholophus*, *Debregeasisa*, *Gonostegia*,

Neraudia, *Phenax*, *Pipturus*, and *Pouzolzia* as a single genus and establishing a grouping with no diagnostic

morphological characters; or 2) retain the morphologically distinct genera above but place *Cypholophus* in synonymy with the core of *Boehmeria* and propose a new genus to account for *Boehmeria ourantha* and *B. nivea*, or 3) maintain *Cypholophus* as a distinct genus and propose two new genera, one to accommodate *Boehmeria ourantha* and *B. nivea* (*Boehmeria* II, Fig. 3, 4.1), and another to accommodate *B. depauperata* and *B. pseudotricuspis*. We have chosen scenario 2 as we believe that it represents the best compromise between morphologically diagnosable and monophyletic groupings.

Boehmeria needs much greater taxon sampling, and its morphology requires a critical re-evaluation. Although we sampled ca 25% of the described species and much of the geographical distribution, there is a large number of subspecies and varieties in the list of accepted species in Wilmot-Dear & Friis (Wilmot-Dear & Friis, 1996, 2013) that warrant further investigation. Given the strong geographical signal within the family and genus, and the broad distribution of some of these taxa, we would not be surprised if many of the varieties and subspecies should be raised to the rank of species following a detailed taxon sample including several accessions of each subspecies and variety and close morphological evaluation.

33. *Pouzolziella* A.K.Monro, Friis & Wilmot-Dear, **gen. nov.** Type: *Pouzolziella australis* (Endl.) A.K.Monro, Friis & Wilmot-Dear, **comb. nov.** $\equiv$ *Pouzolzia australis* (Endl.) Friis & Wilmot-Dear in Nordic J. Bot. 24: 15. 2006. $\equiv$ *Ramium australe* Kuntze in Revis. Gen. Pl. 2: 633. 1891. $\equiv$ *Boehmeria australis* Endl. in Prodr. Fl. Norfolk.: 38. 1833 – Holotype: “Crescit in insula Norfolk, mense Octobri florens”, *F.L. Bauer s.n.* (W destroyed; isotype: K). Fig. 13.

Diagnosis: most similar to *Pouzolzia* Gaudich. but lacking uncinat hairs and possessing the combination of serrate leaves with dense white and shiny tomentose pubescence below and fruiting perianths that are distinctly winged.

Densely branched shrub or small tree with spreading crown; young stems with abundant pubescence; stipules soon deciduous. Leaves alternate, slightly or moderately dimorphic, broadly or narrowly ovate to rhombic-ovate; margin serrate; chartaceous; basal veins extending just into upper third of lamina, upper lateral veins 3-6 but often scarcely distinguishable from coarser tertiary venation, lowermost arising near middle, veins slender but at least basal veins visible above, lateral veins and coarser reticulation visible beneath; upper surface glabrous or with scattered hairs, scabrid with extremely dense prominent cystoliths, lower surface with dense shining white or greyish tomentum, this absent from main veins and often from even fine reticulation. Petiole densely pubescent. Inflorescences unisexual or bisexual axillary clusters, bracteate, with few to < 50 flowers, clusters sometimes so large as to be almost continuous along stem. Male flowers 4-merous, sessile, with sparse adpressed or dense fine spreading hairs. Female flowers with perianth not accrescent, fused to form a tube with a pronounced beak, pubescent, compressed-ovoid, narrowly winged; style persistent. Fruiting perianth as in flower but more prominently winged and with 1-2 facial ribs. Seed light brown, shiny, easily detachable from perianth at maturity.

Notes □ Australasia; 1 sp. *Pouzolziella australis*, as delimited by Wilmot-Dear & Friis (Wilmot-Dear & Friis, 1996) had been considered as three distinct island endemics by previous authors (*P. australis* □ Norfolk Island; *Boehmeria calophleba* C. Moore & F. Muell. □ Lord Howe Island; *B. dealbata* Cheesem. □ Kermadec Island). Increased taxon sampling and the resulting morphological and molecular observations may lead to these taxa again being considered as distinct species.

Pouzolziella was recovered as relatively distantly related to *Pouzolzia* within the Boehmeriaceae and sister to the Indomalayan and Australasian genus *Pipturus* (Pouzolzia II Fig. 3, Fig. 4.1) with which it shares a woody habit, densely tomentose lower leaf surfaces and absence of uncinat hairs, alternate serrate leaves, a long stigma and glossy achene surface. Wilmot-Dear & Friis (Wilmot-Dear & Friis, 2004) had already noted that *P. australis* was an atypical member of *Pouzolzia* based on the combination of serrate leaf margins, leaves with densely tomentose lower leaf surfaces and relatively long persistent stigmas and winged fruit. We also observed that it lacks the uncinat (hooked) hairs characteristic of *Pouzolzia*. We considered moving *P. australis* to *Pipturus* but despite the similarities listed above, it can be distinguished by the bracteate inflorescences (*versus* ebracteate), persistent stigma in fruit (*versus* soon caducous) and non-articulated ((*versus* articulated) stigmas that are dorsally glabrous (*versus* pubescent for the full circumference) and winged fruit (*versus* fleshy fruit) (see Table 5 below). For the above reasons we proposed this new genus.

34. *Pipturus* *Pipturus* Wedd. in Ann. Sci. Nat. Bot., sér. 4. 1: 196. 1854 – Type: *Pipturus velutinus* (Decne.) Wedd. in Ann. Sci. Nat. Bot., sér. 4. 1: 196. 1854 – Lectotype designated by Skottsberg in Acta Horti Gothob. 8: 117. 1933); *Boehmeria velutina* Decne. in Nouv. Ann. Mus. Hist. Nat., sér. 3. 3: 491. 1834.
= *Nothocnide* Blume in Mus. Bot. 2: t. 14 – Type: *Nothocnide repanda* Blume in Mus. Bot. 2: t. 14. 1856 ≡ *Urtica repanda* Blume in Bijdr. Fl. Ned. Ind. 10: 501. 1826.

= *Pseudopipturus* Skotts. in Acta Horti Gothob. 8: 117. 1933. ≡ *Urtica repanda* Blume in Bijdr. Fl. Ned. Ind. 10: 501. 7 Dec 1825–24 Jan 1826. Type: *Pseudopipturus repandus* (Blume) Skotts. in Acta Horti Gothob. 8: 117. 1933.

Notes □ Indomalaya, Australasia, Pacific Islands; 34 spp. *Pipturus* was recovered as polyphyletic with respect to *Nothocnide*. The taxa differ in habit, *Pipturus* comprises trees and shrubs, *Nothocnide* vines. They are otherwise identical with respect to the morphological characters sampled here (see Table 2) and share the same geographical distribution (See Fig. S2).

The perianth of *Pipturus* appears completely fused in flower, the caducous stigma leaving a characteristic hole at the flower apex. In fruit, however, once dried it can be observed that the perianth

splits into two, exposing the achene, suggesting that the perianth may not be fully fused. This would benefit from further research.

One of two accessions of *Pouzolzia sanguinea* var. *aspera* (Li) Friis & Wilmot-Dear, extracted from material from Taiwan, was recovered sister to *Pipturus aspera* Wedd., also sampled from Taiwan. Both originated from samples at KUN generated by Wu & al. (Wu et al., 2013). It would be worthwhile revising the identification of this material.

35. *Neraudia* Gaudich. In Voy. Uranie: t. 117. 1826. Type: *Neraudia melastomifolia* Gaudich. In Voy. Uranie: t. 117. 1826.

Praetoria Baill. In Étude Euphorb. 470, t. 11. 1858, nom. Nud.

Notes □ Endemic to Hawaii; 5 spp.

36. *Margarocarpus* Wedd. In Ann. Sci. Nat., Bot., sér. 4, 1: 203. 1854 – **Lectotype (designated here):** *Margarocarpus 56xasperates* Wedd. In Ann. Sci. Nat., Bot., sér. 4, 1: 204. 1854. Fig 14.

Margarocarpus rugulosus (Wedd.) A.K.Monro & Wilmot-Dear **comb. Nov.** ≡ *Pouzolzia rugulosa* (Wedd.) Acharya & Kravtsova in Edinburgh J. Bot. 66: 60. 2009. ≡ *Boehmeria rugulosa* Wedd. In Arch. Mus. Hist. Nat. 9: 378. 1856 – Lectotype (designated by Wilmot-Dear & al. 2009): Nepal, *Wallich 4597* (K-W barcode K001039434; isoelectotypes: BR!, G!, K!, M!).

Margarocarpus sanguineus (Blume) A.K.Monro & Wilmot-Dear **comb. Nov.** ≡ *Pouzolzia sanguinea* (Blume) Merr. In J. Straits Branch Roy. Asiat. Soc. Special Number: 233. 1921 ≡ *Boehmeria sanguinea* (Blume) Hassk. In Cat. Hort. Bot. Bogor. Alt.: 79. 1844 ≡ *Urtica sanguinea* Blume in Bijdr. Fl. Ned. Ind.: 501. 1826 – Holotype?: Indonesia, Java, Salak, *Blume 1550* [L barcode L0397592].

Margarocarpus calophyllus (W.T.Wang & C.J.Chen) A.K.Monro & Wilmot-Dear **comb. Nov.** ≡ *Pouzolzia calophylla* W.T.Wang & C.J.Chen in Acta Phytotax. Sin. 17(1): 108. 1979. Holotype: China, Xizang, Chayu, 1900 □ 2000 m, 8 or 9 July 1973, *Qinghai-Xizang Expedition 647* (PE).

Notes □ Indomalaya; 2 spp. Pfeiffer (1873) selected *M. vimineus* as lectotype of *Margarocarpus*, presumably on mechanical grounds, as it is the first of 11 species assigned to the genus at the time of its description (Weddell, 1854). *Margarocarpus vimineus* is however an invalid name as the basionym cited by Weddell is illegitimate being both a *nomen nudum* and a later name for *Pouzolzia borbonica* Wight (≡ *P. sanguinea* var. *sanguinea* (Blume) Merr.). For this reason, we have selected *Margarocarpus aspera* Wedd. as lectotype, the next available name in the sequence.

Wu & al. (Z. Y. Wu et al., 2018, Supplementary Fig. 1) (2018, Supplementary Figs1) and we recovered *Pouzolzia sanguinea* and *P. rugulosa* sister to a clade comprising *Neraudia*, *Pipturus* and *Pouzolziella*,

rather than with the other species of *Pouzolzia* (Pouzolzia III Fig. 3, 4.1) sampled which were recovered in a clade comprising *Gonostegia* and *Pouzolzia* (Fig. 3, 4.1). *Pouzolzia sanguinea* and *P. rugulosa* are morphologically distinct from *Neraudia*, *Pipturus* and *Pouzolziella* as shown in Table 5 (below).

[Table 5. Diagnostic comparison of *Margarocarpus*, *Neraudia*, *Pouzolziella* and *Pipturus*.]

Wilmot-Dear & al. (Wilmot-Dear & Friis, 2004) identified *P. sanguinea* and *P. rugulosa* as forming part of a distinct grouping within *Pouzolzia* that also included *P. australis*, *P. niveotomentosa*, *P. sanguinea*, *P. rubricaulis*, *P. variifolia*, *P. fadenii* and *P. parasitica*, all of which share toothed leaf margins. We did not, however, recover this group of toothed species as a monophyletic, *Pouzolzia fadenii* and *P. parasitica* being recovered within a clade comprising entire-leaved species of *Pouzolzia*, suggesting that serrate leaf margins are homoplastic across these genera. In light of the above molecular and morphological observations, we decided to resurrect *Margarocarpus* Wedd.

37. *Pouzolzia* Gaudich. in Voy. Uranie: 503. 1830 – Type: *Pouzolzia laevigata* Gaudich. in Voy. Uranie: 503. 1830 – **Lectotype (designated here)**: Mauritius, *Anon. s.n.*, (P barcode P-LAM 05238550; isolectotype: P barcode P06818056).

=*Rousselia* Gaudich. in Voy. Uranie, Bot. pt. 12: 503. 1830 – **Lectotype (designated here)**: *Rousselia humilis* (Sw.) Urb. in Symb. Antill. (Urban) 4: 205. 1905 ≡ *Urtica humilis* Sw. in Kongl. Vetensk. Acad. Nya Handl., ser. 2, 6: 34. 1785. Type: ‘Habitat in Jamaicae petrosis vulgatissima.’ ≡ *Urtica lappulacea* Sw. in Kongl. Vetensk. Acad. Nya Handl., ser. 2, 8: 69. 1787, nom. illeg. & superfl. ≡ *Lithocnide lappulacea* (Sw.) Raf. in Fl. Tellur. 3: 48 (1836)[Nov.-Dec. 1837], comb. illeg. ≡ *R. lappulacea* (Sw.) B. D. Jackson in Index Kewensis 2(2 = fasc. 4): 744. 1895.

Lithocnide Raf. in Fl. Tellur. 3: 48. 1836[Nov.-Dec. 1837], nom. superfl.

=*Hemistylus* Benth. in Pl. Hartw. [Bentham]: 123. [late Dec. 1843-early Jan. 1844] – Holotype: *Hemistylus boehmerioides* Benth. in Pl. Hartw. [Bentham]: 123. [late Dec. 1843-early Jan. 1844] – **Lectotype (selected here)**: Ecuador, near Guyaquil, April, *Hartweg 696* (K barcode K000575855; isotype: K barcode K000575854).

=*Leucococcus* Liebm. in Kongel. Danske Vidensk.-Selsk. Skr. ser. 5. 2: 311. 1851 – Type: *Leucococcus occidentalis* Liebm. in Kongel. Danske Vidensk.-Selsk. Skr. ser. 5. 2: 311. 1851 – **Lectotype (selected here)**: Nicaragua, 1845, *A.S. Orsted 14258* (C; isolectotype, MO).

=*Stachyocnide* Blume in Mus. Bot. 2: 227. 1857 – Type: *Stachyocnide luzonica* Blume in Mus. Bot. 2: 227. 1857.

=*Praetoria* Baill. in Étude Euphorb. 470, t. 11. 1858, nom. nud.

- 1787 =*Elkania* Schlecht. ex Wedd. in Prodr. [A. P. de Candolle] 16(1): 227. 1869 – Type: *Elkania*
1788 *multinervis* Schlecht. ex Wedd. in Prodr. [A. P. de Candolle] 16(1): 227. 1869.
- 1789 =*Goethartia* Herzog, Meded. Rijks-Herb. 27: 77. 1915 – Type: *Goethartia edentata* (Kuntze) Herzog,
1790 Meded. Rijks-Herb. 27: 77. 1915. ≡ *Ramium edentatum* Kuntze, Revis. Gen. Pl. 3: 294. 1898.
- 1791 =*Neodistemon* Babu & A.N.Henry in Taxon 19: 651. 1970 – Type: *Neodistemon indicus* (Wedd.)
1792 Babu & A.N.Henry in Taxon 19: 651. 1970.
- 1793 ***Pouzolzia boehmerioides*** (Benth.) A.K.Monro **comb. nov.** ≡ *Hemistylus boehmerioides* Benth. in Pl.
1794 Hartw.: 123. 1843.
- 1795 ***Pouzolzia macrostachya*** (Wedd.) A.K.Monro **comb. nov.** ≡ *Hemistylus macrostachya* in Ann. Sci. Nat.,
1796 Bot., sér. 4, 1: 208. 1854.
- 1797 ***Pouzolzia zollingeriana*** A.K.Monro **nom. nov.** ≡ *Neodistemon indicus* (Wedd.) Babu & A.N.Henry in
1798 Taxon 19: 651 (1970) ≡ *Distemon indicus* Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 208. 1854. Monogr. Fam.
1799 Urtic.: 551. 1856. **Lectotype (designated here)**: Ins. Javae [Indonesia], *Zollinger 2785* (P barcode
1800 06783132).
- 1801 A replacement name was selected as the combination *Pouzolzia indica* has previously been
1802 published by Wight (1853: 10).
- 1803 ***Pouzolzia humilis*** (Sw.) A.K.Monro, **comb. nov.** ≡ *Rousselia humilis* (Sw.) Urb. in Symb. Antill. (Urban)
1804 4: 205. 1905 ≡ *Urtica humilis* Sw. in Kongl. Vetensk. Acad. Nya Handl., ser. 2, 6: 34. 1785.
- 1805 **Notes** □ Neotropics, Afrotropics, Indomalaya, (Australasia); ca 60 spp. We recovered *Pouzolzia* as poly-
1806 and para-phyletic (see Discussion). Resolving a classification that reflected both phylogenetic relationships
1807 and morphological characters was very challenging. Our solution is to separate out *Pouzolzia australis* (= *Pouzolziella*
1808 *gen. nov.*), *P. sanguinea* & *P. rugulosa* (= *Margarocarpus*) and *P. rubricaulis* (= *Leptocnide*), and to
1809 place *Neodistemon*, *Hyrtanandra*, *Hemistylus* and *Rousselia* within *Pouzolzia*. The justification for the latter is
1810 that, despite their morphological diagnosability, retaining *Neodistemon*, *Hyrtanandra*, *Hemistylus* and *Rousselia*
1811 would require the delimitation of several new genera for which morphological diagnoses are currently
1812 lacking, rendering the recognition of taxa even more complicated than it already is.
- 1813 We decided not to place *Gonostegia* into synonymy with *Pouzolzia* as proposed by Wilmot-Dear &
1814 Friis (Wilmot-Dear & Friis, 2004). This suggestion had also been discussed, and ultimately rejected by
1815 Weddell (Weddell, 1856). *Gonostegia* (cited by Weddell as *Memorialis*) is morphologically very distinct (see
1816 below) and phylogenetically, together with *Pouzolzia rubricaulis* (= *Leptocnide*, below), borne on a relatively
1817 long branch that is estimated to have diverged from the remainder of the taxa included in *Pouzolzia*
1818 (*Pouzolzia* I, Figs 3, 4.1) >30 MYA. Including *Gonostegia* and *Leptocnide* in *Pouzolzia* would result in a

grouping lacking shared diagnostic morphological characters and on this basis we decided to exclude these taxa from *Pouzolzia*.

The combination, *Rousselia lappulacea* (Sw.) Gaudich., was never made by Gaudichaud, – he merely quoted '*Urtica lappulacea*, Swartz (Herb. Mérat) and Jackson made the combination retrospectively in Index Kewensis (Ref.).

Pouzolzia needs much greater taxon sampling and a critical re-evaluation of its morphology. Although we sampled ca 25% of the described species and much of the geographical distribution, there are a large number of subspecies and varieties concealed in the list of accepted species in Wilmot-Dear & al. (Wilmot-Dear & Friis, 2004). Given the strong geographical signal within the family and genus, and the broad distribution of some of these taxa we would not be surprised if many of the varieties and subspecies were to be raised to the rank of species following a detailed taxon sample including several accessions of each subspecies and variety.

The type for *Pouzolzia laevigata* was incorrectly cited in Wilmot-Dear & Friis (Wilmot-Dear & Friis, 2004). Marais (Marais, 1985) cites 'Mauritius, *Anon.* s.n. (P-LA)' as holotype but did not include any identifying information for the specimen (e.g. folder number or loan number).

38. Leptocnide Blume in Mus. Bot. Lugd.-Bat. 2: 193. 1857 ≡ *Pouzolzia rubricaulis* (Blume) Wedd. in A.P.de Candolle, Prodr. 16(1): 229. 1869. – **Lectotype (designated here):** *Leptocnide rubricaulis* Blume in Mus. Bot. Lugd.-Bat. 2: 194. 1857. Fig. 15.

Notes □ Indomalaya, Australasia; 1 sp.

Leptocnide rubricaulis Blume was included in *Pouzolzia* by Weddell and later Wilmot-Dear & al. (2004). The latter considered this toothed-leaved species to form part of an anomalous group of *Pouzolzia* which also included *P. sanguinea*, *P. rugulosa* (≡ *Margarocarpus* above) *P. australis* (≡ *Pouzolziella* above), *P. niveotomentosa*, *P. variifolia*, *P. fadenii* and *P. parasitica*. We recovered this taxon as sister to *Gonostegia* on a long branch within the Boehmeriaceae (*Pouzolzia* IV, Figs 3, 4.1). As above, we feel there is strong support for not incorporating *Gonostegia* into *Pouzolzia* and so by association, neither for *L. rubricaulis*. Wilmot-Dear & Friis (2004) noted that *L. rubricaulis* (as *Pouzolzia rubricaulis*) is unique within *Pouzolzia* in its very broad, caudate and thick stipules. *L. rubricaulis* is morphologically distinct from *Gonostegia* with respect to leaf arrangement, margin, stipule, staminate and pistillate flowers as summarised in Table 6 (below). Combining *Gonostegia* and *Leptocnide* would therefore result in a grouping lacking shared diagnostic morphological characters. We therefore decided to treat the taxa as distinct at generic rank and to resurrect *Leptocnide*.

- 1852 [Table 6. Diagnostic comparison of *Pouzolzia*, *Leptocnide* and *Gonostegia*.]
1853
1854 **39. *Gonostegia*** Turcz. in Bull. Soc. Imp. Naturalistes Moscou 19: 509. 1846. Type: *Gonostegia oppositifolia*
1855 Turcz. in Bull. Soc. Imp. Naturalistes Moscou 19: 510. 1846.
1856 *Hyrtanandra* Miq. in Pl. Jungh.: 25. 1851 – **Lectotype (designated here):** *Hyrtanandra javanica*
1857 Miq. in Pl. Jungh.: 25. 1851.
1858 *Memorialis* Wedd. in Arch. Mus. Hist. Nat. 9: 415. 1857 – **Lectotype (selected here):** *M. ciliaris*
1859 Wedd. in Arch. Mus. Hist. Nat. 9: 417. 1857 – **Lectotype (designated here):** Anon s.n. 4598A [ex Herb.
1860 Roxburgh], (K-W).
1861 ***Gonostegia cymosa*** (Wight) A.K. Monro, Friis & Wilmot-Dear, **comb. nov.** $\equiv$ *Pouzolzia cymosa*
1862 Wight in Icon. Pl. Ind. Orient. 6: 42. 1853 – Holotype: India, Tamil Nadu, Nilgiris, *Wight* s.n. (K barcode
1863 000741370; isotypes: K barcode K000741371, L barcode L0484261, MEL barcode MEL2421129, NY
1864 barcode NY00063608).
1865 **Notes** $\square$ Palearctic, Indomalaya; 3 spp. Miquel (Junghuhn & Miquel, 1853) described two species of
1866 *Hyrtanandra* at the time of describing the genus and we have elected *H. javanica* on the basis that the
1867 description is the more comprehensive of the two. There has been considerable debate as to whether
1868 *Gonostegia* should be included within *Pouzolzia* or not (Weddell, 1856; Wilmot-Dear & Friis, 2004). Based
1869 on its morphological (see Table 6 above) and molecular distinctiveness we have followed Weddell's
1870 proposal to maintain *Gonostegia* as distinct (cited by Weddell as *Memorialis*), not least because combining
1871 the genera would result in a grouping for which there is no morphological diagnosis. *Gonostegia pentandra*
1872 (Roxb.) Bennett & Brown is geographically widespread and morphologically variable (Wilmot-Dear &
1873 Friis, 2004) and it may be that future research determines it to comprise several species.
1874
1875 **40. *Chamabainia*** Wight in Icon. Pl. Ind. Orient. [Wight] vi. 11. t. 1981. 1853. Type: *Chamabainia cuspidata*
1876 Wight in Pl. Ind. Orient. [Wight] vi. 11. t. 19.
1877 **Notes** $\square$ Indomalaya; 1 sp.
1878
1879 **41. *Muimar*** A.K.Monro, Friis & Wilmot-Dear, **gen. nov.** $\square$ Type *Muimar nivea* (L.) A.K.Monro, Friis &
1880 Wilmot-Dear. Fig. 16.
1881 Differs from *Boehmeria* by the combination of intrapetiolar stipules and shiny pubescence on the
1882 lower leaf surface.
1883 Shrub or subshrub, monoecious or dioecious. Stems pubescent. Stipules interpetiolar, prominent, a pair at
1884 each leaf base, partially fused or free. Leaves alternate or opposite; margin serrate; basal pair of lateral

1885 veins more prominent than subsequent pairs; adaxial surface sparsely pubescent or glabrous, abaxial
 1886 surface densely pubescent, the hairs shiny, cystoliths punctiform. Inflorescences paniculate or few-
 1887 branched raceme-like cymes, unisexual or bisexual, bracts ≤ 3 mm, visible. Flowers borne in sessile
 1888 unisexual or bisexual clusters, bracteoles ≤ 1 mm inconspicuous, entirely male clusters small, 2–4 mm diam,
 1889 bearing 5–15 flowers, entirely female clusters (2–)5–6(–8) mm diam, bearing 10–100 flowers. Male
 1890 flowers 4-merous, sessile or pedicellate, mature buds globose or depressed-globose, sepals fused for basal
 1891 1/3 of their length, with or without dorsal appendages, pubescent. Female flowers ovoid, subcompressed,
 1892 perianth fused, tubular, rim entire, pubescent; stigma elongated, exerted, curved, hairs borne only on side.
 1893 Fruiting perianth ovoid, ellipsoid or obovoid, without beak, $\pm$ flattened; surface conspicuously pubescent.

1894

1895 Key to the species

1896 1. Leaves alternate, inflorescences branched, flower clusters discrete, never contiguous *M. nivea*

1897 1. Leaves opposite, inflorescences unbranched, flower clusters $\pm$ contiguous *M. ourantha*

1898

1899 ***Muimar nivea*** (L.) A.K. Monro, Friis & Wilmot-Dea. **comb. nov.** *Urtica nivea* L. in Sp. Pl.: 985. 1753 $\equiv$
 1900 *Boehmeria nivea* (L.) Gaudich. in Voy. Uranie: 499. 1830 $\equiv$ *Ramium niveum* (L.) Kuntze in Revis. Gen. Pl. 2:
 1901 632. 1891, *nom. illegit. superfl.* — Lectotype (designated by Ghaffoor, 1977: 18): Anon., Herb. Linn. 1111.19
 1902 (LINN 1111.19). Fig. 16.

1903 *Boehmeria candicans* Hassk. in Cat. Pl. Hort. Bot. Bogor.: 79. 1844 $\equiv$ *Urtica candicans* Blume (1825) 503, *nom.*
 1904 *illeg.*, *non Urtica candicans* Burm. f. (1768: 197) $\equiv$ *Boehmeria nivea* (L.) Gaudich. var. *candicans* (Hassk.) Wedd.
 1905 in Prodr. [A. P. de Candolle]: 207. 1869 — **Neotype (designated here)**: [Indonesia] Java, Zollinger 750
 1906 (G barcode G00354563*).

1907 We were unable to trace the Blume type material at L or BO and so selected material collected
 1908 from the type area, Java (Indonesia).

1909 *Urtica tenacissima* Roxb., in [Wissett], Suppl. Observ. Sunn Hemp Bengal: 41. 1811 $\equiv$ *Boehmeria tenacissima*
 1910 (Roxb.) Blume in Mus. Bot. 2: 211. 1857 $\equiv$ *Boehmeria nivea* var. *tenacissima* (Roxb.) Miq. in Fl. Ned. Ind. 1:
 1911 253. 1859 — Lectotype (designated by Turner, 2013: 166): [icon] Roxburgh drawing 1670, K) — Epitype
 1912 (designated by Turner, 2013: 166): [cultivated in Calcutta Botanic Gardens] *W. Roxburgh s.n.* (BR
 1913 barcode0000005203147*; ?isoepitypes: BM barcode 000835422*, G barcode G00354054*).

1914 *Boehmeria mollicoma* Miq. in H. Zollinger, Syst. Verz. Ind. Archip. 2: 100. 1854. $\equiv$ *Ramium mollicoma* (Miq.)
 1915 Kuntze in Revis. Gen. Pl. 2: 633. 1891 — Holotype: [Indonesia] Java, H. Zollinger 1454 (BO not traced;
 1916 isotype: U barcode 1749531*).

- 1917 *Boehmeria compacta* Blume in Mus. Bot. 2: 210. 1857 — Holotype: [Indonesia] Java, *Anon.* (?Blume) *s.n.* (L
1918 barcode L0836071*).
- 1919 *Boehmeria nivea* (L.) Gaudich. var. *reticulata* Blume in Mus. Bot. 2: 211. 1857 — **Lectotype (designated**
1920 **here)**: Japan, *P.F. von Siebold s.n.* (L barcode L0836072*).
- 1921 *Boehmeria nivea* (L.) Gaudich. var. *concolor* Makino in Bot. Mag. (Tokyo) 23: 251. 1909 $\equiv$ *Boehmeria frutescens*
1922 (Thunb.) Thunb. var. *concolor* (Makino) Nakai in Bot. Mag. (Tokyo) 41: 514. 1927 $\equiv$ *Boehmeria nipononivea*
1923 Koidz. var. *concolor* (Makino) Ohwi in Fl. Japan: 441. 1953 $\equiv$ *Boehmeria nivea* (L.) Gaudich. forma *concolor*
1924 (Makino) Kitam. in Acta Phytotax. Geobot. 20: 208. 1962 — **Lectotype (designated here)**: Japan, near
1925 Kyoto, Nov. 7 1893, *Makino s.n.* (MAK(124723*).
- 1926 *Boehmeria nivea* (L.) Gaudich. var. *viridula* Yamam in J. Soc. Trop. Agric., Taihoku [Taipei] 4: 50. 1932 —
1927 Replacement name for *Boehmeria frutescens* (Thunb.) Thunb. var. *viridula* (Yamam.) T.Suzuki in Short Fl.
1928 Formos. (ed. Masamune G): 47. 1936 $\equiv$ *Boehmeria nivea* (L.) Gaudich. forma *viridula* (Yamam.) Hatus. in Fl.
1929 Ryukyus: 234. 1971 — Types: *Yamamoto 542* (not traced), Taiwan, Kwaremko Pr., Beisan; *Suzuki 1168* (not
1930 traced), Taiwan, between Doba and Taiheizan, 28 July 1928.
- 1931 *Boehmeria nipononivea* Koidz. in Acta Phytotax. Geobot. 10: 223. 1941.
- 1932 $\equiv$ *Boehmeria nivea* (L.) Gaudich. subsp. *nipononivea* (Koidz.) Kitam. in Acta Phytotax. Geobot. 20: 208. 1962
1933 $\equiv$ *Boehmeria nivea* (L.) Gaudich. forma *nipononivea* (Koidz.) Hatus. in Fl. Ryukyus (S. Hatusima ed): 234.
1934 1971 $\equiv$ *Boehmeria nivea* (L.) Gaudich. var. *nipononivea* (Koidz.) W.T.Wang in Acta Bot. Yunnan. 3: 320. 1981
1935 — Type: No material cited or traced.
- 1936 *Boehmeria thailandica* Yahara Acta Phytotax. Geobot. 32: 4. 1981 — Holotype: Thailand, Phitsanulok,
1937 Thung Salang Luang, *Tagawa et al. 11233* (KYO barcode KYO00020601*).
- 1938
- 1939 ***Muimar ourantha*** (Miq.) A.K.Monro, Friis & Wilmot-Dear. **comb. nov.** $\equiv$ *Boehmeria ourantha* Miq. in Pl.
1940 Jungh.: 33. 1851 $\equiv$ *Boehmeria caudata* (Burm.f.) J.J.Sm. var. *ourantha* (Miq.) J.J.Sm. in Meded. uitgaande Dep.
1941 Landbouw. Bd.12: 714. 1910 $\equiv$ *Boehmeria platyphylla* D.Don var. *ourantha* (Miq.) Hochr. in Candollea 2:
1942 344. 1925 — Holotype: *Junghuhn s.n.*, Indonesia, Jawa [Java], Bantam Dist. (U (U barcode 0256222*).
- 1943 *Boehmeria pseudotomentosa* Yahara in Acta Phytotax. Geobot. 32: 16. 1981 — Holotype: Thailand, Loei, top
1944 area of Phu Kradung, Phu Kradung District, 1220 — 1280 m, Nov. 17 1979, T. *Shimizu & al. 22957*
1945 (KYO barcode 00020600*).
- 1946 *B. tomentosa* sensu auct., incl. Wedd. (p.p.), non *B. tomentosa* Wedd. s.str.;
- 1947 *B. macrophylla* Hornem. var. *tomentosa* (Wedd.) D.G.Long, sensu D.G.Long, non var. *tomentosa* (Wedd.)
1948 D.G.Long, s.str.

- 1949 **Etymology** □ The name *Muimar* is an anagram of *Ramium* an illegitimate name proposed by Kuntze
1950 based on the local name, ‘Ramie’.
- 1951 **Discussion** □ Within the Boehmerieae, we recover *Muimar* as distantly related to *Boehmeria* and sister or
1952 congeneric to *Archiboehmeria* (Fig. 1). Whilst the type, *M. nivea* was recognised as atypical within the genus
1953 by Friis & Wilmot-Dear (Wilmot-Dear & Friis, 2013) and the species had been recovered as part of a
1954 large paraphyletic and polyphyletic *Boehmeria* (Wu et al., 2013, 2018) identifying synapomorphies has been
1955 challenging. In part because of the great morphological variation in *Boehmeria* as currently delimited, which
1956 comprises species with alternate or opposite leaves, partially or fully fused stipules, indefinite or definite
1957 inflorescences and the presence or absence of hooked hairs. An extensive review of herbarium collections
1958 enabled a unique combination of characters to be identified which enable *Muimar* to be distinguished
1959 from *Boehmeria* and *Archiboehmeria*
- 1960 **Notes** □ Indomalaya, 2 spp. The misapplication of the epithet “tomentosa” to material of *B. ourantha* is
1961 common in the literature (Chen et al., 2005). The combination, *B. macrophylla* Hornem. var. *tomentosa*
1962 (Wedd.) Long, based on the Afro-Malagasy species *B. tomentosa* Wedd., was first misapplied to Asian
1963 material in the Flora of Bhutan (Grierson & Long, 1983: 126). Friis & Wilmot-Dear (Wilmot-Dear &
1964 Friis, 2013: 181) distinguish *Boehmeria virgata* subsp. *macrophylla* var. *tomentosa* from *B. ourantha* in the
1965 arrangement of male flowers, colour, margin and shape of the leaves, and the spacing of the flowers along
1966 the inflorescence.
- 1967
- 1968 [Table 7. Morphological characters which distinguish *Muimar* from *Boehmeria* and *Archiboehmeria*]
- 1969
- 1970 **42. *Archiboehmeria*** C.J.Chen in Acta Phytotax. Sin. 18: 479. 1980 – Type: *Archiboehmeria atrata*
1971 (Gagnep.) C.J.Chen in Acta Phytotax. Sin. 18: 479. 1980 ≡ *Debregeasia atrata* Gagnep. in Bull. Soc. Bot.
1972 France 75: 556. 1928.
- 1973 **Notes** □ Indomalaya (China, Vietnam); 1 sp.
- 1974
- 1975 **43. *Astrothalamus*** C.B.Rob. in Philipp. J. Sci., Bot. 6: 19. 1911 – Type: *Astrothalamus reticulatus* (Wedd.)
1976 C.B.Rob. in Philipp. J. Sci., Bot. 6: 19. 1911 – **Lectotype (designated here)**: Guam, *Gaudichaud* 167 (P
1977 barcode 00698510).
- 1978 **Notes** □ Indomalaya; 1 sp.
- 1979

- 1980 **44. *Debregeasia*** Gaudich. in Voy. Bonite, Bot., Atlas: t. 90. (1844) – Lectotype (selected by Wilmot-
1981 Dear 1988): *Debregeasia velutina* Gaudich. in Bot., Voy. Bonite: t. 90. 1844.
- 1982 *Leucocnide* Miq. in Pl. Jungh.: 36. 1851 – Type: *Leucocnide dichotoma* (Blume) Miq. in Pl. Jungh.: 38.
1983 1851 ≡ *Urtica dichotoma* Blume in Bijdr. Fl. Ned. Ind. 10: 499. 1825-6 – Type: Indonesia, *Blume s.n.* (L
1984 barcode L0039694).
- 1985 *Morocarpus* Siebold & Zucc. in Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4(3): 218. 1846,
1986 nom. illegit., non *Morocarpus* Boehm (1760: 385).
- 1987 **Notes** □ AfroTropics, Palearctic, Indomalaya; 9 spp.
- 1988
- 1989 LEUKOSYKEAE. Fig. 11.
- 1990 **45. *Leukosyke*** Zoll. & Moritzi in Syst. Verz.: 100. 1845. Type: *Leukosyke javanica* Zoll. & Moritzi in Syst.
1991 Verz.: 100. 1845 – **Lectotype (designated here)**: Indonesia, *Zollinger, H. 629*, (G barcode G00354275).
1992 = *Missiessya* Gaudich. ex Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 194. 1854 – Type: *Missiessya*
1993 *wallichiana* Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 195. 1854.
- 1994 **Notes** □ Indomalaya, Australasia; 33 spp.
- 1995
- 1996 **46. *Sarcochlamys*** Gaudich. in Voy. Bonite, Bot. t. 89. 1844 – Type: *Sarcochlamys pulcherrima* Gaudich. in
1997 Voy. Bonite, Bot. t. 89. 1844.
1998 = *Sphaerotylos* C.J.Chen in Acta Phytotax. Sin. 23: 452. 1985 – Type: *Sphaerotylos medogensis* C.
1999 J.Chen in Acta Phytotax. Sin. 23: 453. 1985.
- 2000 **Notes** □ Palearctic, Indomalaya; 1 sp.
- 2001
- 2002 **47. *Maoutia*** Wedd. in Ann. Sci. Nat., Bot., sér. 4, 1: 193. 1854 – Type: *Maoutia platystigma* Wedd. in Ann.
2003 Sci. Nat., Bot., sér. 4, 1: 194. 1854 – **Lectotype (designated here)**: Phillipines, *Cumming 1441*, (P barcode
2004 P00698294; isolectotypes: G barcode G00354217, G barcode G00354220, P barcode P00698295).
2005 = *Lecanocnide* Blume in Mus. Bot. 2: t12. 1857 – Type: *Lecanocnide diversifolia* Blume in Mus. Bot. 2:
2006 t12. 1857.
2007 = *Robinsoniodendron* Merr. in Interpr. Herb. Amboin.: 204. 1917 – Type: *Robinsoniodendron ambiguum*
2008 (Wedd.) Merr. in Interpr. Herb. Amboin.: 204. 1917.
- 2009 **Notes** □ Australasia (New Guinea), Indomalaya; 10 spp. Wilmot-Dear & Friis (Wilmot-Dear & Friis,
2010 2013) suggest that *Maoutia* be included within *Leukosyke*. Our results suggest (Fig. 3 & 4.1) that *Maoutia* is
2011 instead sister to the New Guinean endemic, *Gibbsia*, which itself is morphologically distinct from both
2012 *Maoutia* and *Leukosyke* in its inflorescence and pistillate flower morphology, and the in disposition of the

- 2013 achene relative to the perianth in fruit. We therefore decided to maintain all three as distinct genera.
- 2014
- 2015 **48. *Gibbsia*** Rendle in Fl. Arfak Mts.: 129. 1917 – Type: *Gibbsia insignis* Rendle in Fl. Arfak Mts.: 130.
- 2016 1917 – **Lectotype (designated here)**: Indonesia, *L.S. Gibbs 5961* (BM barcode BM000571389; isotype:
- 2017 K barcode K000741628 (2 leaves and an inflorescence fragment only)).
- 2018 **Notes** □ Australasia (New Guinea); 2 spp.
- 2019
- 2020 CECROPIEAE. Fig. 12.
- 2021 **49. *Cecropia*** Loefl. in Iter Hispan.: 272. 1758 – Type: *Cecropia peltata* L. in Syst. Nat. (ed. 10): 1286. 1759.
- 2022 = *Ambaiba* Adans. in Fam Pl. 2: 377. 1763 – Type: *Ambaiba peltata* (L.) Kuntze in Revis. Gen. Pl.
- 2023 2: 623. 1891.
- 2024 = *Coilotapalus* P. Browne in Civ. Nat. Hist. Jamaica: 111. 1756. nom. nud.
- 2025 **Notes** □ Indomalaya, Neotropics; ca 65 spp.
- 2026
- 2027 **50. *Pourouma*** Aubl. in Hist. Pl. Guiane 2: 891–892, t. 341. 1775 – Type: *Pourouma guianensis* Aubl. in
- 2028 Hist. Pl. Guiane 2: 892, t. 341. 1775.
- 2029 **Notes** □ Neotropics; 31 spp.
- 2030
- 2031 **51. *Coussapoa*** Aubl. in Hist. Pl. Guiane: 2: 955, t. 362. 1775 – Type: *Coussapoa latifolia* Aubl. in Hist. Pl.
- 2032 Guiane 2: 955. 1775 – **Lectotype (designated here)**: French Guiana, *Aublet s.n.*: (BM barcode
- 2033 BM000993414).
- 2034 **Notes** □ Nearctic, Neotropics; 50 spp.
- 2035
- 2036 **52. *Musanga*** R.Br. in Pl. Jav. Rar. (Bennett): 49, 1838 – Type: *Musanga smithii* R.Br. in Pl. Jav. Rar.
- 2037 (Bennett): 49, 1838 – **Lectotype (designated here)**: Congo, *Smith s.n.*, (BM barcode BM000911480).
- 2038 **Notes** □ Afrotropics; 2 spp.
- 2039
- 2040 **53. *Myrianthus*** P.Beauv. in Fl. Oware 1: 16. 1805. Type: *Myrianthus arboreus* P. Beauv. in Fl. Oware 1: 17,
- 2041 t. 11. 1805. Type: Benin, *Palisot de Beauvois s.n.* (lectotype designated here), G barcode G00008686.
- 2042 **Notes** □ Afrotropics; 8 spp.
- 2043

2044

2045 **Unplaced names**

2046

2047 *Metapilea* W.T.Wang in Bull. Bot. Res., Harbin 36: 166. 2016. – Type: *Metapilea jingxiensis* W.T.Wang in

2048 Bull. Bot. Res., Harbin 36: 166. 2016. Please see notes under *Pilea*.

2049 *Parsana* Parsa & Maleki Fl. Iran, Suppl. Gen.: 548. 1952. The genus *Parsana* Parsa & Maleki likely belongs

2050 within this genus. The description and illustration do not correspond to any known specimens, the type

2051 collections having not been deposited where stated in the description (Mahmoud Bidarlord (FAR), Pers.

2052 Comm.) could not be located or sampled and no other collections match the description. Based on the

2053 locality information and aspects of the illustrations, however, we believe that the description may have

2054 been based on material of *Laportea*.

2055 *Pellionia* Gaudich. in Voy. Uranie: 494. 1830 – Type: *Pellionia elatostemoides* Gaudich. in Voy. Uranie: 494.

2056 1830 (typ. cons.). See notes under *Elatostema*.

2057

2058

2059

2060

2061 Acknowledgements

2062 We would like to thank curators at B, BM, F, GH, K, MO, P, TEX, US for the loan of herbarium
 2063 collections over the years; Sven Buerki for earlier iterations of the analyses of a subset of the Sanger
 2064 sequence data; Stephen Russell (Natural History Museum, London) for support generating Sanger
 2065 sequence data. We would also like to thank the Plant and Fungal Trees of Life Project and the Calleva
 2066 Foundation for the generation of the Angiosperms353 data.

2067

2068

2069 References

- 2070 Bansal, P., Paul, P., Mudgal, J., G. Nayak, P., Thomas Pannakal, S., Priyadarsini, K. I., & Unnikrishnan,
2071 M. K. (2012). Antidiabetic, antihyperlipidemic and antioxidant effects of the flavonoid rich fraction
2072 of *Pilea microphylla* (L.) in high fat diet/streptozotocin-induced diabetes in mice. *Experimental and*
2073 *Toxicologic Pathology*, 64(6), 651–658. <https://doi.org/10.1016/j.etp.2010.12.009>
- 2074 Bechtel, A. R. (1921). The floral anatomy of the Urticales. *American Journal of Botany*, 8, 386–410.
- 2075 Bentham, G., & Hooker, J. D. (1883). *Genera Plantarum III* (G. Bentham & J. D. Hooker, Eds.). Reeve and
2076 Co.
- 2077 Berg, C. C. (1973). Some remarks on the classification and differentiation of Moraceae. *Mededelingen van*
2078 *Het Botanisch Museum En ...*, 386, 1–10.
- 2079 Berg, C. C. (1978a). Cecropiaceae a New Family of the Urticales. *Taxon*, 27(1), 39–44.
2080 <https://doi.org/10.2307/1220477>
- 2081 Berg, C. C. (1978b). Cecropiaceae a New Family of the Urticales. In *Source: Taxon* (Vol. 27, Issue 1).
- 2082 Berg, C. C., Franco Rosselli, P., & Davidson, D. W. (2005). Cecropia. *Flora Neotropica*, 94, 1–230.
- 2083 Bertin, R. I., & Kerwin, M. A. (1998). Floral sex ratios and gynomonoeccy in *Aster* (Asteraceae). *American*
2084 *Journal of Botany*, 85(2), 235–244. <https://doi.org/10.2307/2446311>
- 2085 Blume, C. L. (1857). Museum botanicum Lugduno-Batavum, sive, Stirpium exoticarum novarum vel
2086 minus cognitarum ex vivis aut siccis brevis expositio et descriptio / auctore C.L. Blume. *Museum*
2087 *Botanicum Lugduno-Batavum, Sive, Stirpium Exoticarum Novarum Vel Minus Cognitarum Ex Vivis Aut Siccis*
2088 *Brevis Expositio et Descriptio / Auctore C.L. Blume., t2*, 137–256.
- 2089 Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: a flexible trimmer for Illumina sequence
2090 data. *Bioinformatics*, 30(15), 2114–2120. <https://doi.org/10.1093/bioinformatics/btu170>
- 2091 Bolmgren, K., & Eriksson, O. (2005). Fleshy fruits - origins, niche shifts, and diversification. *Oikos*,
2092 109(2), 255–272. <https://doi.org/10.1111/j.0030-1299.2005.12663.x>
- 2093 Brown, F. (1935). Flora of Southwestern Polynesia III: Metatrophis. *Bull. Bernice P. Bishop Mus.*, 130, 34–
2094 35.
- 2095 Candolle, A. D. (1813). *Théorie élémentaire de la botanique etc.* . Déterville.

- 2096 Capella-Gutiérrez, S., Silla-Martínez, J. M., & Gabaldón, T. (2009). trimAl: a tool for automated alignment
2097 trimming in large-scale phylogenetic analyses. *Bioinformatics*, 25(15), 1972–1973.
2098 <https://doi.org/10.1093/bioinformatics/btp348>
- 2099 Carvalho, M. R., Jaramillo, C., de la Parra, F., Caballero-Rodríguez, D., Herrera, F., Wing, S., Turner, B.
2100 L., D’Apolito, C., Romero-Báez, M., Narváez, P., Martínez, C., Gutierrez, M., Labandeira, C.,
2101 Bayona, G., Rueda, M., Paez-Reyes, M., Cárdenas, D., Duque, Á., Crowley, J. L., ... Silvestro, D.
2102 (2021). Extinction at the end-Cretaceous and the origin of modern Neotropical rainforests. *Science*,
2103 372(6537), 63–68. <https://doi.org/10.1126/science.abf1969>
- 2104 Chandler, M. E. J. (1961). Flora of the Lower Headon beds of Hampshire and the Isle of Wight. *Bulletin of*
2105 *the British Museum (Natural History), Geology*, 5, 91–151.
- 2106 Chandler, M. E. J. (1963). *The Lower Tertiary floras of Southern England. III. Flora of the Bournemouth Beds; the*
2107 *Boscombe, and the Highcliff Sands* (M. E. J. Chandler, Ed.). Order of the Trustees of the British
2108 Museum.
- 2109 Charles-Dominique, P. (1986). *Inter-relations between frugivorous vertebrates and pioneer plants: Cecropia, birds and*
2110 *bats in French Guyana* (pp. 119–135). https://doi.org/10.1007/978-94-009-4812-9_12
- 2111 Chen, C. J. (1982). A monograph of Pilea (Urticaceae) in China. *Bull. Bot. Res., Harbin*, 2, 1–132.
- 2112 Chen, C. J., Wilmot-Dear, C. M., & Friis, I. (2005). Notes on Chinese and Indochinese Boehmeria
2113 (Urticaceae). *Kew Bulletin*, 60, 449–453.
- 2114 Chew, W.-L. (1963). A revision of the genus Poikilospermum (Urticaceae). *Gard. Bull. Singapore*, 20, 1–103.
- 2115 Chew, W.-L. (1965). Laportea and allied genera (Urticaceae). *Gard. Bull. Singapore*, 21, 195–208.
- 2116 Christenhusz, M. J. M., & Byng, J. W. (2016). The number of known plants species in the world and its
2117 annual increase. In *Phytotaxa* (Vol. 261, Issue 3, pp. 201–217). Magnolia Press.
2118 <https://doi.org/10.11646/phytotaxa.261.3.1>
- 2119 Christenhusz, M. J. M., Reveal, J. L., Farjon, A., Gardner, M. F., Mill, R. R., & Chase, M. W. (2011). A
2120 new classification and linear sequence of extant gymnosperms. *Phytotaxa*, 19(1), 55.
2121 <https://doi.org/10.11646/phytotaxa.19.1.3>
- 2122 Collinson, M. E. (1989). The fossil history of the Moraceae, Urticaceae (including Cecropiaceae), and
2123 Cannabaceae. In P. R. Crane & S. Blackmore (Eds.), *Evolution, Systematics, and Fossil History of the*
2124 *Hamamelidae* (Vol. 2, pp. 319–339). Clarendon Press.

- 2125 Conn, B. J., & Hadiah, J. T. (2009). Nomenclature of tribes within the Urticaceae. *Kew Bulletin*, 64(2), 349–
2126 352. <https://doi.org/10.1007/s12225-009-9108-4>
- 2127 Corner, E. J. H. (1962). The classification of Moraceae Gard. *Bull. Singapore*, 19, 187–252.
- 2128 Datwyler, S. L., & Weiblen, G. D. (2004). On the origin of the fig: phylogenetic relationships of Moraceae
2129 from *ndb* F sequences. *American Journal of Botany*, 91(5), 767–777.
2130 <https://doi.org/10.3732/ajb.91.5.767>
- 2131 Dávalos, L. M., Velazco, P. M., Warsi, O. M., Smits, P. D., & Simmons, N. B. (2014). Integrating
2132 Incomplete Fossils by Isolating Conflicting Signal in Saturated and Non-Independent
2133 Morphological Characters. *Systematic Biology*, 63(4), 582–600. <https://doi.org/10.1093/sysbio/syu022>
- 2134 Dejean, A., Petitclerc, F., Roux, O., Orivel, J., & Leroy, C. (2012). Does exogenic food benefit both
2135 partners in an ant-plant mutualism? The case of *Cecropia obtusa* and its guest Azteca plant-ants.
2136 *Comptes Rendus Biologies*, 335(3), 214–219. <https://doi.org/10.1016/j.crv.2012.01.002>
- 2137 Deng, T., Kim, C., Zhang, D. G., Zhang, J. W., Li, Z. M., Nie, Z. L., & Sun, H. (2013). *Zhengyia*
2138 *shennongensis*: A new bulbiferous genus and species of the nettle family (Urticaceae) from central
2139 China exhibiting parallel evolution of the bulbil trait. *Taxon*, 62(1), 89–99.
2140 <https://doi.org/10.1002/tax.621008>
- 2141 DeVore, M. L., Nyandwi, A., Eckardt, W., Bizuru, E., Mujawamariya, M., & Pigg, K. B. (2020). Urticaceae
2142 leaves with stinging trichomes were already present in latest early Eocene Okanogan Highlands,
2143 British Columbia, Canada. *American Journal of Botany*, 107(10), 1449–1456.
2144 <https://doi.org/10.1002/ajb2.1548>
- 2145 Diazgranados, M., *et al.* (2020). *World Checklist of Useful Plant Species*. Royal Botanic Gardens Kew.
- 2146 Doyle, J. J., D. J. L. (1987). A rapid DNA isolation procedure for small quantities of fresh leaf tissue.
2147 *Phytochem. Bull.*, 19, 11–15.
- 2148 Edlund, A. F. (2004). Pollen and Stigma Structure and Function: The Role of Diversity in Pollination.
2149 *THE PLANT CELL ONLINE*, 16(suppl_1), S84–S97. <https://doi.org/10.1105/tpc.015800>
- 2150 Engler, A. (1894). Urticaceae. In *Die natürlichen Pflanzenfamilien* (Vol. 3, pp. 98–118). Engelmann.
- 2151 Farr, E. R., & Zijlstra, G. (1996). *Index Nominum Genericorum (Plantarum)*. [Http://Botany.Si.Edu/Ing/](http://Botany.Si.Edu/Ing/)
2152 (Accessed May 3 2019).
- 2153 Florence, J. (1997). Metatrophis. In J. Florence (Ed.), *Flore de la Polynésie Française* (Vol. 1, pp. 229–232).
2154 IRD.

- 2155 Friis, I. (1989). The Urticaceae: a systematic review. In P. Crane (Ed.), *Evolution, Systematics, and Fossil*
2156 *History of the Hamamelidae* (Vol. 2, pp. 285–308). Clarendon Press.
- 2157 Friis, I., & Wilmot-Dear, C. M. (1988). A revision of the tribe Forsskaoleae (Urticaceae). *Nordic Journal of*
2158 *Botany*, 8(1), 25–59. <https://doi.org/10.1111/j.1756-1051.1988.tb01705.x>
- 2159 Friis, I., Wilmot-dear, C. M., & Monro, A. K. (2003). *Flora of China* 5: 76-189. 2003. 76–189.
- 2160 Fu, L. (2021). *Systematic studies of tribe Elatostemateae (Urticaceae) from China* [PhD]. Beijing Forestry
2161 University.
- 2162 Fu, L., Wen, F., Maurin, O., Rodda, M., Gardner, E. M., Xin, Z., Wei, Y., & Monro, A. K. (2022). A
2163 revised delimitation of the species-rich genus *Pilea* (Urticaceae) supports the resurrection of
2164 *Achudemia* and a new infrageneric classification. *TAXON*, 71(4), 796–813.
2165 <https://doi.org/10.1002/tax.12711>
- 2166 Fu, L.-F., Su, L.-Y., Mallik, A., Wen, F., & Wei, Y.-G. (2017). Cytology and sexuality of 11 species of
2167 *Elatostema* (Urticaceae) in limestone karsts suggests that apomixis is a recurring phenomenon. *Nordic*
2168 *Journal of Botany*, 35(2), 251–256. <https://doi.org/10.1111/njb.01281>
- 2169 Funk, V. A. (2003). An opinion: down with alphabetically arranged herbaria (and alphabetically arranged
2170 floras too for that matter). *Pl. Sci. Bull.*, 49, 131–132.
- 2171 Gaudichaud, C. (1830). Botanique. In H. L. C. de Freycinet (Ed.), *Voyage autour du monde...exécuté sur les*
2172 *corvettes de S.M. l'Uranie et la Physicienne* (Vol. 12, pp. 465–522). Pilet-Ainé.
- 2173 Gonçalves, D. J. P., Simpson, B. B., Ortiz, E. M., Shimizu, G. H., & Jansen, R. K. (2019). Incongruence
2174 between gene trees and species trees and phylogenetic signal variation in plastid genes. *Molecular*
2175 *Phylogenetics and Evolution*, 138(October 2018), 219–232.
2176 <https://doi.org/10.1016/j.ympev.2019.05.022>
- 2177 Govaerts, R., Nic Lughadha, E., Black, N., Tumer, R., & Paton, A. (2021). The World Checklist of
2178 Vascular Plants, a continuously updated resource for exploring global plant diversity. *Scientific Data*,
2179 8(1), 215. <https://doi.org/10.1038/s41597-021-00997-6>
- 2180 Gregg, K. B. (1975). The effect of light intensity on sex expression in species of *Cynoches* and
2181 *Catasetum* (Orchidaceae). *Selbyana*, 1, 101–113.
- 2182 Grierson, A. J. C., & Long, D. G. (1983). *Flora of Bhutan, including a record of plants from Sikkim* (A. J. C.
2183 Grierson & D. G. Long, Eds.; Vol. 1). Royal Botanic Garden.

- 2184 Hadijah, J. T., Conn, B. J., & Quinn, C. J. (2008). Infra-familial phylogeny of Urticaceae, using chloroplast
2185 sequence data. *Australian Systematic Botany*, 21(5), 375–385. <https://doi.org/10.1071/SB08041>
- 2186 Hall, T. (2011). *Bioedit* (7.2). North Carolina State University.
- 2187 Haston, E., Richardson, J. E., Stevens, P. F., Chase, M. W., & Harris, D. J. (2007). *A Linear Sequence of*
2188 *Angiosperm Phylogeny Group II Families* (Vol. 56, Issue 1). <https://www.jstor.org/stable/25065731>
- 2189 Hawkins, J. A., Hughes, C. E., & Scotland, R. W. (1997). Primary Homology Assessment, Characters and
2190 Character States. *Cladistics*, 13(3), 275–283. <https://doi.org/10.1111/j.1096-0031.1997.tb00320.x>
- 2191 Hodcroft, E. (2013). *TreeCollapserCL4*. <http://emmahodcroft.com/TreeCollapseCL.html>.
- 2192 Hörandl, E. (2010). The evolution of self-fertility in apomictic plants. In *Sexual Plant Reproduction* (Vol. 23,
2193 Issue 1, pp. 73–86). <https://doi.org/10.1007/s00497-009-0122-3>
- 2194 Huang, X., Deng, T., Moore, M. J., Wang, H., Li, Z., Lin, N., Yusupov, Z., Tojibaev, K. S., Wang, Y., &
2195 Sun, H. (2019). Tropical Asian Origin, boreotropical migration and long-distance dispersal in
2196 Nettles (Urticaceae, Urticaceae). *Molecular Phylogenetics and Evolution*, 137(May), 190–199.
2197 <https://doi.org/10.1016/j.ympev.2019.05.007>
- 2198 Humphries, C. J., & Blackmore, S. (1989). A review of the classification of the Moraceae. In P. Crane &
2199 S. Blackmore (Eds.), *Evolution, systematics, and fossil history of the Hamamelidae*. (Vol. 2, pp. 267–277).
2200 Clarendon Press.
- 2201 Johnson, M. G., Gardner, E. M., Liu, Y., Medina, R., Goffinet, B., Shaw, A. J., Zerega, N. J. C., &
2202 Wickett, N. J. (2016). HybPiper: Extracting coding sequence and introns for phylogenetics from
2203 high-throughput sequencing reads using target enrichment. *Applications in Plant Sciences*, 4(7),
2204 1600016. <https://doi.org/10.3732/apps.1600016>
- 2205 Johnson, M. G., Pokorny, L., Dodsworth, S., Botigué, L. R., Cowan, R. S., Devault, A., Eiserhardt, W. L.,
2206 Epitawalage, N., Forest, F., Kim, J. T., Leebens-Mack, J. H., Leitch, I. J., Maurin, O., Soltis, D. E.,
2207 Soltis, P. S., Wong, G. K. S., Baker, W. J., & Wickett, N. J. (2019a). A Universal Probe Set for
2208 Targeted Sequencing of 353 Nuclear Genes from Any Flowering Plant Designed Using k-Medoids
2209 Clustering. *Systematic Biology*, 68(4), 594–606. <https://doi.org/10.1093/sysbio/syy086>
- 2210 Johnson, M. G., Pokorny, L., Dodsworth, S., Botigué, L. R., Cowan, R. S., Devault, A., Eiserhardt, W. L.,
2211 Epitawalage, N., Forest, F., Kim, J. T., Leebens-Mack, J. H., Leitch, I. J., Maurin, O., Soltis, D. E.,
2212 Soltis, P. S., Wong, G. K. S., Baker, W. J., & Wickett, N. J. (2019b). A Universal Probe Set for
2213 Targeted Sequencing of 353 Nuclear Genes from Any Flowering Plant Designed Using k-Medoids
2214 Clustering. *Systematic Biology*, 68(4), 594–606. <https://doi.org/10.1093/sysbio/syy086>

- 2215 Junghuhn, F. W., & Miquel, F. A. W. (1853). *Plantae junghubnianae*: enumeratio plantarum, quas, in insulis Java
2216 et Sumatra. H.R. de Breuk. <https://doi.org/10.5962/bhl.title.388>
- 2217 Jussieu, A. L. (1789). *Genera plantarum secundum ordines naturales disposita*... Herissant & Barrois.
- 2218 Katoh, K., & Standley, D. M. (2013). MAFFT Multiple Sequence Alignment Software Version 7:
2219 Improvements in Performance and Usability. *Molecular Biology and Evolution*, 30(4), 772–780.
2220 <https://doi.org/10.1093/molbev/mst010>
- 2221 Kim, C., Deng, T., Chase, M., Zhang, D. G., Nie, Z. L., & Sun, H. (2015a). Generic phylogeny and
2222 character evolution in Urticeae (Urticaceae) inferred from nuclear and plastid DNA regions. *Taxon*,
2223 64(1), 65–78. <https://doi.org/10.12705/641.20>
- 2224 Kim, C., Deng, T., Chase, M., Zhang, D. G., Nie, Z. L., & Sun, H. (2015b). Generic phylogeny and
2225 character evolution in Urticeae (Urticaceae) inferred from nuclear and plastid DNA regions. *Taxon*,
2226 64(1), 65–78. <https://doi.org/10.12705/641.20>
- 2227 Kim, C., Deng, T., Chase, M., Zhang, D. G., Nie, Z. L., & Sun, H. (2015c). Generic phylogeny and
2228 character evolution in Urticeae (Urticaceae) inferred from nuclear and plastid DNA regions. *Taxon*,
2229 64(1), 65–78. <https://doi.org/10.12705/641.20>
- 2230 Kravtsova, T. I., Friis, I., & Wilmot-Dear, C. M. (2003). Morphology and Anatomy of Fruits in Pouzolzia
2231 (Urticaceae) in Relation to Taxonomy. *Kew Bulletin*, 58(2), 297. <https://doi.org/10.2307/4120618>
- 2232 Lee, M. S. Y., & Palci, A. (2021). Evolution: Morphological saturation and release in mammals. *Current*
2233 *Biology*, 31(13), R838–R840. <https://doi.org/10.1016/j.cub.2021.05.003>
- 2234 Lin, C.-C., Yen, M.-H., Lo, T., & Lin, J.-M. (1998). Evaluation of the hepatoprotective and antioxidant
2235 activity of Boehmeria nivea var. nivea and B. nivea var. tenacissima. *Journal of Ethnopharmacology*,
2236 60(1), 9–17. [https://doi.org/10.1016/S0378-8741\(97\)00122-0](https://doi.org/10.1016/S0378-8741(97)00122-0)
- 2237 Lobova, T. A., Mori, S. A., Blanchard, F., Peckham, H., & Charles-Dominique, P. (2003). Cecropia as a
2238 food resource for bats in French Guiana and the significance of fruit structure in seed dispersal and
2239 longevity. *American Journal of Botany*, 90(3), 388–403. <https://doi.org/10.3732/ajb.90.3.388>
- 2240 Marais, W. (1985). Urticacées (excl. Procris). In J. Bosser, T. Cadet, J. Guého, & W. Marais (Eds.), *Flore*
2241 *des Mascareignes*. ORSTOM.
- 2242 Matzke, N. J. (2013). *BioGeoBEARS: BioGeography with Bayesian (and Likelihood) Evolutionary Analysis in R*
2243 *Scripts*. R Package, Version 0.2.

- 2244 Maurin, K. J. L. (2020). *An empirical guide for producing a dated phylogeny with treePL in a maximum likelihood*
2245 *framework*. arXiv preprint, arXiv:2008.07054.
- 2246 Monro, A. K. (2004). Three New Species, and Three New Names in Pilea (Urticaceae) from New Guinea.
2247 Contributions to the Flora of Mt Jaya XV. *Kew Bulletin*, 59(4), 573.
2248 <https://doi.org/10.2307/4110914>
- 2249 Monro, A. K. (2006). The revision of species-rich genera: a phylogenetic framework for the strategic
2250 revision of Pilea (Urticaceae) based on cpDNA, nrDNA, and morphology. *American Journal of Botany*,
2251 93(3), 426–441. <https://doi.org/10.3732/ajb.93.3.426>
- 2252 Monro, A. K., Bystriakova, N., Fu, L., Wen, F., & Wei, Y. (2018). Discovery of a diverse cave flora in
2253 China. *PLoS ONE*, 13(2), 1–16. <https://doi.org/10.1371/journal.pone.0190801>
- 2254 Monro, A. K., Dodsworth, S., Fu, L.-F., Friis, I., Wilmot-Dear, C. M., & Maurin, O. (2021). Paraphyly of
2255 the genus Boehmeria (Urticaceae): a response to Liang et al. ‘Relationships among Chinese
2256 Boehmeria species and the evolution of various clade.’ *Plant Systematics and Evolution*, 307(1), 1.
2257 <https://doi.org/10.1007/s00606-020-01732-1>
- 2258 Monro, A. K., Wilmot-Dear, C. M., & Friis, I. (2015). Urticaceae. In G. Davidse, M. Sousa, S. Knapp, &
2259 F. Chiang (Eds.), *Flora Mesoamericana* (Vol. 2, pp. 116–174). Universidad Autónoma de México /
2260 Missouri Botanical Garden / The Natural History Museum (London).
- 2261 Ohwi, J. (1936). *Laportea macrostachya*. *Journal of Japanese Botany*, 12, 331–331.
- 2262 Olson, D. M., & Dinerstein, E. (2002). The Global 200: Priority Ecoregions for Global Conservation.
2263 *Annals of the Missouri Botanical Garden*, 89(2), 199–224. <https://doi.org/10.2307/3298564>
- 2264 Ramírez-Barahona, S., Sauquet, H., & Magallón, S. (2020). The delayed and geographically heterogeneous
2265 diversification of flowering plant families. *Nature Ecology & Evolution*, 4(9), 1232–1238.
2266 <https://doi.org/10.1038/s41559-020-1241-3>
- 2267 Rokas, A., Williams, B. L., King, N., & Carroll, S. B. (2003). *Genome-scale approaches to resolving incongruence in*
2268 *molecular phylogenies*. www.nature.com/nature
- 2269 Schüßler, C., Bräuchler, C., Reyes-Betancort, J. A., Koch, M. A., & Thiv, M. (2019). Island biogeography
2270 of the Macaronesian *Gesnouinia* and Mediterranean *Soleirolia* (Parietariaceae, Urticaceae) with
2271 implications for the evolution of insular woodiness. *TAXON*, 68(3), 537–556.
2272 <https://doi.org/10.1002/tax.12061>

- 2273 Scotland, R. W. (1992). Systematics, similarity and Acanthaceae pollen morphology. *Botanical Journal of the*
2274 *Linnean Society*, 109, 529–541.
- 2275 Scotland, R. W., Olmstead, R. G., & Bennett, J. R. (2003). Phylogeny Reconstruction: The Role of
2276 Morphology. *Systematic Biology*, 52, 539–548.
- 2277 Sfiligoj Smole, M., Hribernik, S., Kurečič, M., Urbanek Krajnc, A., Kreže, T., & Stana Kleinschek, K.
2278 (2019). *Non-conventional Plant Fibres* (pp. 17–48). https://doi.org/10.1007/978-3-030-10407-8_3
- 2279 Smith, S. A., & O'Meara, B. C. (2012). treePL: divergence time estimation using penalized likelihood for
2280 large phylogenies. *Bioinformatics*, 28(20), 2689–2690. <https://doi.org/10.1093/bioinformatics/bts492>
- 2281 Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large
2282 phylogenies. *Bioinformatics*, 30(9), 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- 2283 Stevens, P. F. (2017). *Angiosperm Phylogeny Website. Version 14, July 2017*.
2284 [Http://www.mobot.org/MOBOT/Research/APweb/](http://www.mobot.org/MOBOT/Research/APweb/).
- 2285 Stevenson, P. R., Link, A., González-Caro, S., & Torres-Jiménez, M. F. (2015). Frugivory in Canopy
2286 Plants in a Western Amazonian Forest: Dispersal Systems, Phylogenetic Ensembles and Keystone
2287 Plants. *PLOS ONE*, 10(10), e0140751. <https://doi.org/10.1371/journal.pone.0140751>
- 2288 Sytsma, K. J., Morawetz, J., Pires, J. C., Nepokroeff, M., Conti, E., Zjhra, M., Hall, J. C., & Chase, M. W.
2289 (2002). Urticalean rosids: circumscription, rosid ancestry, and phylogenetics based on rbcL, trnL-F,
2290 and ndhF sequences. *American Journal of Botany*, 89(9), 1531–1546.
2291 <https://doi.org/10.3732/ajb.89.9.1531>
- 2292 Takhtajan, A. (1982). Ulmaceae-Betulaceae. In A. Takhtajan (Ed.), *Magnoliophyta Fossilia URSS* (Vol. 2, pp.
2293 1–216). NAUKA.
- 2294 Tange, O. (2018). *GNU parallel 2018*. Lulu.com.
- 2295 The Angiosperm Phylogeny Group. (2016). An update of the Angiosperm Phylogeny Group classification
2296 for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181(1),
2297 1–20. <https://doi.org/10.1111/boj.12385>
- 2298 Treiber, E. L., Gaglioti, A. L., Romaniuc-Neto, S., Madriñán, S., & Weiblen, G. D. (2016). Phylogeny of
2299 the Cecropieae (Urticaceae) and the evolution of an ant-plant mutualism. *Systematic Botany*, 41(1), 56–
2300 66. <https://doi.org/10.1600/036364416X690633>

- 2301 Tseng, Y.-H., Monro, A. K., Wei, Y.-G., & Hu, J.-M. (2019). Molecular phylogeny and morphology of
2302 *Elatostema* s.l. (Urticaceae): Implications for inter- and infrageneric classifications. *Molecular*
2303 *Phylogenetics and Evolution*, 132, 251–264. <https://doi.org/10.1016/j.ympev.2018.11.016>
- 2304 Turczaninow, N. S. (1846). Decas secunda generum adhuc non descriptorum. *Bulletin de La Société Impériale*
2305 *Des Naturalistes de Moscou*, 19, 497–510.
- 2306 Turland, N., Wiersema, J., Barrie, F., Greuter, W., Hawksworth, D., Herendeen, P., Knapp, S., Kusber,
2307 W.-H., Li, D.-Z., Marhold, K., May, T., McNeill, J., Monro, A., Prado, J., Price, M., & Smith, G.
2308 (Eds.). (2018). *International Code of Nomenclature for algae, fungi, and plants* (Vol. 159). Koeltz Botanical
2309 Books. <https://doi.org/10.12705/Code.2018>
- 2310 Wang, W. T. (2014). *Elatostema (Urticaceae) in China* (W. T. Wang, Ed.). Qingdao Publishing House.
- 2311 Wang, W.-T. (2016). Nova classification specierum sinensium Pellioniae (Urticaceae). *Guihaia*, 36(1), 1–
2312 29. <https://doi.org/https://10.11931/guihaia.gxzw201509011>
- 2313 Weddell, H. A. (1854). Revue de la famille des Urticées. *Ann. Arch. Mus. Hist. Nat. Ser. 4, 1*, 173–212.
- 2314 Weddell, H. A. (1856). Monographie de la famille des Urticées. *Nouv. Arch. Mus. Hist. Nat.*, 9, 1–400.
- 2315 Weddell, H. A. (1869). Urticaceae. In *Prodromus systematis naturalis regni vegetabilis* (Vol. 6, pp. 32–35).
- 2316 Wells, T., Maurin, O., Dodsworth, S., Friis, I., Cowan, R., Epitawalage, N., Brewer, G., Forest, F., Baker,
2317 W. J., & Monro, A. K. (2021). Combination of Sanger and target-enrichment markers supports
2318 revised generic delimitation in the problematic ‘Urena clade’ of the nettle family (Urticaceae).
2319 *Molecular Phylogenetics and Evolution*, 158, 107008. <https://doi.org/10.1016/j.ympev.2020.107008>
- 2320 Willis, K. J. (2017). *State of the World's Plants 2017*.
- 2321 Wilmot-Dear, C. M., Acharya, N., Kravtsova, T. I., & Friis, I. (2009). POUZOLZIA RUGULOSA
2322 TRANSFERRED FROM BOEHMERIA, AND THE DISTINCTION BETWEEN
2323 BOEHMERIA AND POUZOLZIA (URTICACEAE). *Edinburgh Journal of Botany*, 66(1), 51–64.
2324 <https://doi.org/10.1017/S096042860900523X>
- 2325 Wilmot-Dear, C. M., & Friis, I. (1996). The New World species of Boehmeria and Pouzolzia (Urticaceae,
2326 tribus Boehmerieae): a taxonomic revision. *Nordic Journal of Botany*, 129, 1–103.
- 2327 Wilmot-Dear, C. M., & Friis, I. (2004). The Old World species of Pouzolzia (Urticaceae, tribus
2328 Boehmerieae). A taxonomic revision. *Nordic Journal of Botany*, 24(1), 5–111.
2329 <https://doi.org/10.1111/j.1756-1051.2004.tb00825.x>

- 2330 Wilmot-Dear, C. M., & Friis, I. (2013). The old World species of *Boehmeria* (*Urticaceae* , tribus *Boehmerieae*).
2331 A taxonomic revision. *Blumea - Biodiversity, Evolution and Biogeography of Plants*, 58(2), 85–216.
2332 <https://doi.org/10.3767/000651913X674116>
- 2333 Winkler, H.J.P.Winkl. (1922). *Die Urticaceen Papuasians*. In *Bot. Jahrb. Syst.* 57: 584
- 2334 Wu, Z. Y., Liu, J., Provan, J., Wang, H., Chen, C. J., Cadotte, M. W., Luo, Y. H., Amorim, B. S., Li, D. Z.,
2335 & Milne, R. I. (2018). Testing Darwin’s transoceanic dispersal hypothesis for the inland nettle family
2336 (*Urticaceae*). *Ecology Letters*, 21(10), 1515–1529. <https://doi.org/10.1111/ele.13132>
- 2337 Wu, Z. Y., Milne, R. I., Chen, C. J., Liu, J., Wang, H., & Li, D. Z. (2015). Ancestral state reconstruction
2338 reveals rampant homoplasy of diagnostic morphological characters in urticaceae, conflicting with
2339 current classification schemes. *PLoS ONE*, 10(11), 1–20.
2340 <https://doi.org/10.1371/journal.pone.0141821>
- 2341 Wu, Z. Y., Monro, A. K., Milne, R. I., Wang, H., Yi, T. S., Liu, J., & Li, D. Z. (2013). Molecular
2342 phylogeny of the nettle family (*Urticaceae*) inferred from multiple loci of three genomes and
2343 extensive generic sampling. *Molecular Phylogenetics and Evolution*, 69(3), 814–827.
2344 <https://doi.org/10.1016/j.ympev.2013.06.022>
- 2345 Zhang, L. B., & He, H. (2011). *Polystichum fengshanense*, sp. nov. (sect. *Haplopolystichum*,
2346 *Dryopteridaceae*) from karst caves in Guangxi, China based on morphological, palynological, and
2347 molecular evidence. *Systematic Botany*, 36(4), 854–861. <https://doi.org/10.1600/036364411X604877>
- 2348 Zhang, Q., Onstein, R. E., Little, S. A., & Sauquet, H. (2019). Estimating divergence times and ancestral
2349 breeding systems in *Ficus* and *Moraceae*. *Annals of Botany*, 123(1), 191–204.
2350 <https://doi.org/10.1093/aob/mcy159>
- 2351
- 2352

Figures

Figure 1. Variation in stigma morphology across the Urticaceae, A) *Fleurya aestuans*, Urticeae; B) *Pilea grandis*, Elatostemateae; C) *Myriocarpa stipitate*, Myriocrapeae; D) *Forskaolea tenacissima*, Parietareae; E) *Pouzolzia zeylanica*, Boehmeriaceae; F) *Cecropia obtusifolia*, Cecropiaceae. Images made by Jia Dong and Louis Ronse De Craene

Figure 2. Bayesian analysis of Sanger sequence dataset constrained by the topology of an Astral analysis of the Angiosperms353 HybSeq low copy nuclear gene dataset. Clades 1 and 2 represent the first order subdivision of the family. Clades A to G represent lower order subdivisions corresponding to tribes. Values above branches are bootstrap percentage above 75. Red asterisks indicated branches with high support where genera were not recovered as monophyletic.

Figure 3. Time-calibrated ASTRAL analysis of Angiosperms353 HybSeq low copy nuclear gene dataset. Clades 1 and 2 represent the first order subdivision of the family. Clades A to G represent lower order subdivisions corresponding to tribes. Estimated average age is provided on the right of each node, with age range in bracket and represented with blue bars. Above branches are local posterior probability values followed by normalised quartet support or percentage gene trees that agree with a branch. Red asterisks below branches indicate the null hypothesis of a polytomy could not be rejected with the polytomy test ($p > 0.05$).

Figure 4. Time-calibrated supertree of Sanger sequence and Angiosperms353 HybSeq low copy nuclear gene datasets. Clades 1 and 2 represent the first order subdivision of the family. Clades A to G represent lower order subdivisions corresponding to tribes.

Figure 5. Ancestral area estimates projected onto a time-calibrated supertree of Sanger sequence and Angiosperms353 HybSeq low copy nuclear gene datasets. Clades A to G represent lower order subdivisions corresponding to tribes.

Fig. 6. Urticeae Tribe. *Dendrocnide meyerianum*. **A** leaf lower surface based on xxx 5008 (scale bar = 3 cm); **B** stipule based on xxx 26044 (scale bar = 1 cm); **C** female flower cluster based on xxx 5008 (scale bar = 1 cm); **D** female flower based on xxx 5008 (scale bar = 2 mm); **E** male flowers based on xxx 5008 (scale bar = 2 mm); **F** fruit based on image xxx (scale bar = 2 mm); **G** achene based on xxx 6892 (scale bar = 2 mm). *Girardinia diversifolia*. **H** leaf lower surface based on Biye 124 (scale bar = 3 cm); **I** section of stems with bulbed hairs based on Reekmans 6129 (scale bar = 1 cm); **J** female flower based on Biye 124 (scale bar = 1 mm); **K** male flower based on Reekmans 6129 (scale bar = 2 mm); **L** achene based on Biye 124 (scale bar = 2 mm). *Nanocnide japonica*. **M** leaf lower surface based on Yao 8878 (scale bar = 3 cm); **N**

- 2386 female inflorescence based on Togashi 7840 (scale bar = 2 mm); **O** female flower based Togashi 7840
 2387 (scale bar = 1 mm); **P** stipule based on Yao 8878 (scale bar = 2 mm); **Q** achene based on Furusa 5632
 2388 (scale bar = 1 mm). Illustration by Juliet Beentje.
- 2389 Fig 7 Myriocarpeae Tribe. *Myriocarpa* 79tipitate: **A** leaf lower surface based on *Hualparimachi* 3052 (scale
 2390 bar = 3 cm); **B** stipule () based on *Hualparimachi* 3052 (scale bar = 1 cm); **C** female inflorescence based
 2391 on *Hualparimachi* 3052 (scale bar = 3 cm); **D** female flower cluster based on *Hualparimachi* 3052 (scale bar
 2392 = 1 cm); **E** female flower based on based on *Hualparimachi* 3052 (scale bar = 1 mm); **F** male flowers in
 2393 bud, and open, based on *Ule* 6507 (scale bar = 1 mm); **G** fruit and achene based on *Hualparimachi* 3052
 2394 (scale bar = 1 mm). *Gyrotaenia macrocarpa*. **H** leaf lower surface based on *Monro et al.* 7479 (scale bar = 3
 2395 cm); **I** stipules based on *Breedlove* 68859 (scale bar = 1 cm); **J** female inflorescence based on *Hinton* 757
 2396 (scale bar = 1 cm); **K** female flower cluster based on *Hinton* 757 (scale bar = 1 mm); **L** female flower
 2397 based on *Hinton* 757 (scale bar = 0.5 mm); **M** male flowers based on *Monro et al.* 7479 (scale bar = 1 mm);
 2398 **N** achene based on *Breedlove* 68859 (scale bar = 1 mm). Illustration by Juliet Beentje.
- 2399 Fig 8 Elatostemateae Tribe. *Pilea microphylla*. **A** upper leaf surface based on *Ekman* 695 (scale bar = 2 mm);
 2400 **B** stipule based on photograph by P. York (BM) (scale bar = 0.5 mm); **C** female inflorescences based on
 2401 *Ekman* 695 (scale bar = 0.5 mm); **D** female flower based on *Ekman* 695 (scale bar = 0.5 mm); **E** male
 2402 flower based on based on *Ekman* 695 (scale bar = 0.5 mm); **F** achene based on *Britton & Shafer* 300 (scale
 2403 bar = 0.5 mm). *Elatostema* XX: **G** leaf outline based on *Du* HNK2960 (scale bar = 3 cm); **H** stipules
 2404 based on *Du* HNK2960 (scale bar = 5 mm); **I** female inflorescence based on *Du* HNK2960 (scale bar = 5
 2405 mm); **J** female flower based on Weddell (1856: plate X, 10 (XX)); **K** male flower based on *Parnell* 95-661
 2406 (scale bar = 2 mm); **L** achene based on *Du* HNK2960 (). *Achudemia boniana*. **M** leaf outline based on *Henry*
 2407 9771 (scale bar = 3 cm); **N** stipules based on *Henry* 9771 (scale bar = 2 mm); **O** female inflorescence
 2408 based on *Monro* 6704 (scale bar = 5 mm); **P** female flower based on *Monro* 6704 (); **Q** male flower and bud
 2409 based on *Monro* 6704 and *Morse* 495 (scale bar = 2 mm); **R** achene based on *Henry* 9771 (scale bar = 2
 2410 mm). Illustration by Juliet Beentje.
- 2411 Fig 9 Parietariaceae Tribe. *Australina pusilla*. **A.** stipule based on *Constable* 5468 (scale bar = 2 mm); **B** male
 2412 inflorescence based on *Constable* 5468 (scale bar = 4 mm); **C** male flower based on *Adams* 766 (scale bar =
 2413 2 mm); **D** female inflorescence showing bracts based on *Adams* 766 (scale bar = 2 mm); **E** female flower
 2414 based on *Adams* 766 (scale bar = 1 mm); **F** achene based on *Adams* 766 (scale bar = 2 mm). *Parietaria*
 2415 *Judaica*. **G** leaf outline and lower surface based on *Carter* 893 (scale bar = 3 cm); **H** flower clusters
 2416 comprising female and bisexual flowers based on *Carter* 893 (scale bar = 4 mm); **I** female flower based on
 2417 *Carter* 893 (scale bar = 2 mm); **J** bisexual flowers (side-view) based on *Carter* 893 (scale bar = 2 mm); **K**
 2418 bisexual flowers (top-view) based on *Carter* 893 (scale bar = 2 mm); **L** bisexual fruiting perianth bisexual
 2419 flowers (side-view) based on *Carter* 893 (scale bar = 2 mm); **M** achene bisexual flowers (side-view) based
 2420 on *Carter* 893 (scale bar = 1 mm). *Metatrophis margaretae*. **N** leaf with inflorescence in the axil based on

2421 *Fosberg* 11422 (scale bar = 3 cm); **O** inflorescence detail (female flowers towards the base, male flowers
2422 towards the apex) based on *Stokes* 123 (scale bar = XX); **P** cluster of female flowers and fruits based on
2423 *Stokes* 123 (scale bar = 4 mm); **Q** female flower based on *Fosberg* 11422 (scale bar = 4 mm); **R** male
2424 inflorescence based on *Fosberg* 11422 (scale bar = 3 cm); **S** male flower based on *Fosberg* 11422 (scale bar
2425 = 4 mm). Illustration by Juliet Beentje.

2426 Fig. 10 Boehmeriaceae Tribe. *Astrothalamus reticulatus*. **A** leaf outline based on *Argent* 981987 (scale bar = 2
2427 mm); **B** stipules based on *Argent* 981987 (scale bar = 4 mm); **C** female inflorescence based on SAN 78665
2428 (scale bar = 2 mm); **D** female flowers based on SAN 78665 (scale bar = 2 mm); **E** male flower based on
2429 *Argent* 981987 (scale bar = 1 mm); **F** fruit based on *Argent* 981987 (scale bar = 2 mm). *Neraudia*
2430 *melastomifolia*. **G** leaf outline based on *Cowan* 836 (scale bar = 3 cm); **H** stipules based on *N. angulata* and
2431 *Greenwell* 20832 (scale bar = 4 mm); **I** female inflorescence based on *Cowan* 836 (scale bar = 2 mm); **J**
2432 female flower based on *Cowan* 836 (scale bar = 2 mm); **K** male flower based on field image (scale bar = 2
2433 mm); **L** fruit based on field image of *N. angulata* (scale bar = 2 mm); **M** fruit based on *Cowan* 836 (scale
2434 bar = 2 mm). *Oreocnide* xxx. **N** leaf outline based on *Gardette* 957 (scale bar = 3 cm); **O** stipules based on
2435 *Gardette* 957 (); **P** female inflorescence based on *Gardette* 957 (scale bar = 4 mm); **Q** female flower based
2436 on *Gardette* 957 (scale bar = 4 mm); **R** male flower based on *Lörzing* 13751 (scale bar = 3 cm); **S** fruits
2437 based on field image (scale bar = 4 mm). Illustration by Juliet Beentje.

2438 Fig. 11 Leukosykeae Tribe. *Gibbsia insignis*. **A** leaf lower surface based on *Brass* 12279 (scale bar = 3 cm); **B**
2439 stipule based on *Lae* 59516 (scale bar = 2 mm); **C** female infructescence based on *Brass* 12279 (scale bar =
2440 1 cm); **D** female flower lateral view based on *Brass* 12279 (scale bar = 1 mm); **E** female flower based on
2441 *Lae* 59516 (scale bar = 1 mm); **F** fruit and achene based on *Brass* 12279 (scale bar = 1 mm); **G** male
2442 flower lateral view based on *Brass* 11075 (scale bar = 2 mm); **H** male flower apical view based on *Brass*
2443 12279 (scale bar = 2 mm). *Sarcochlamys pulcherrima*. **I** leaf lower surface based on *Hossain* 1911 (scale bar =
2444 3 cm); **J** stipule based on *Grierson* 1427 (scale bar = 2 mm); **K** female inflorescence based on *Grierson*
2445 1525a (scale bar = 3 cm); **L** female flower based on *Hossain* 1911 (scale bar = 0.5 mm); **M** achene based
2446 on *Grierson* 1525a (scale bar = 0.5 mm); **N** male flower lateral view based on *Grierson* 1427 (scale bar = 1
2447 mm). *Leucosyke corymbulosa*. **O** leaf lower surface based on *Greenwood* 43 (scale bar = 3 cm); **P** stipule based
2448 on *Parham* 47 (scale bar = 1 cm); **Q** female flower based on *Smith* 184 (scale bar = 1 mm); **R**
2449 infructescence based on *Smith* 184 (scale bar = 3 cm); **S** infructescence detail based on *Smith* 184 (scale
2450 bar = 1 cm); **T** achene based on *Greenwood* 43 (scale bar = 1 mm); **U** male flower based on *Meebold* 16699
2451 (scale bar = 2 mm). Illustration by Juliet Beentje.

2452 Fig. 12 Cecropiaceae Tribe. *Coussapoa latifolia*. **A** leaf based on *Lindeman* 249(?) (scale bar = 3 cm); **B** stipule
2453 based on *Lindeman* 249(?) (scale bar = 3 cm); **C** infructescence based on *Lindeman* 249(?) (scale bar = 1
2454 cm); **D** female flower cluster based on *Lindeman* 249(?) (scale bar = 3 mm); **E** female flower lateral based
2455 on *Lindeman* 249(?) (scale bar = 1 mm); **F** female flower apical view based on *Lindeman* 249(?) (); **G** small

2456 section of male inflorescence based on *Cid* 8852 (scale bar = 1 cm); **H** male flower based on *Cid* 8852
 2457 (scale bar = 0.5 mm). *Myrianthus* xx: **I** leaf based on *Osborne* 326 (scale bar = 3 cm); **J** stipule based on
 2458 *Etuge* 5161 (scale bar = 3 cm); **K** fruiting inflorescence based on *Leunwenberg* 5190 (scale bar = 3 cm); **L**
 2459 female flower based on *Osborne* 326 (scale bar = 3 mm); **M** male flower based on *Etuge* 5161 (scale bar = 1
 2460 mm); **N** single unit of fruit based on *Leunwenberg* 5190 (scale bar = 1 cm). *Cecropia* XX: **O** leaf outline
 2461 based on *Benson* 10345 (scale bar = 3 cm); **P** stipule based on *Benson* 10345 (scale bar = 3 cm); **Q**
 2462 infructescence based on *Nee* 42895 (scale bar = 3 cm); **R** cross-section of female inflorescence based on
 2463 *Nee* 42895 (scale bar = 1 cm); **S** surface detail of female inflorescence based on *Nee* 42895 (scale bar = 3
 2464 mm); **T** female flower lateral view based on *Nee* 42895 (scale bar = 1 mm); **U** female flower apical view
 2465 based on *Nee* 42895 (scale bar = 1 mm); **V** male flower based on *Flora Neotropica*: (scale bar = 1 mm);
 2466 **W** fruit based on *Flora Neotropica*: (scale bar = 1 mm). Illustration by Juliet Beentje.

2467 Fig. 13 *Pouzolziella* Plate. *Pouzolziella australis*. Norfolk Islands population: **A** habit with female
 2468 inflorescence based on *Cunningham s.n.* (scale bar = 3 cm); **B** stem pubescence based on *Cunningham s.n.*
 2469 (scale bar = 5 mm); **C** stipule based on *Cunningham s.n.* (scale bar = 5 mm); **D** male flower based on *Green*
 2470 1404 (scale bar = 2 mm); **E** female flower cluster based on *Cunningham s.n.* (scale bar = 5 mm); **F** female
 2471 flower based on *Cunningham s.n.* (scale bar = 2 mm); **G** fruit based on *Cunningham s.n.* (scale bar = 2 mm).
 2472 Kermadec Islands population: **H** leaf outline and margin based on XXX (scale bar = 3 cm); **I** stipule
 2473 based on XXX (scale bar = 5 mm); **J** male flower based on XXX (scale bar = 2 mm); **K** female flower
 2474 based on XXX (scale bar = 2 mm); **L** fruit based on XXX (scale bar = 2 mm). Lord Howe Island
 2475 population: **M** male flower based on *Von Mueller s.n.* (scale bar = 2 mm). Sunday Islands population: **N**
 2476 female flower based on *Oliver s.n.* '10/10/1908' (scale bar = 2 mm). Illustration by Juliet Beentje.

2477 Fig. 14 *Margarocarpus* Plate. *Margarocarpus rugulosus*. **A.** habit with male inflorescences based on *Williams &*
 2478 *Stainton* 8289 (scale bar = 3 cm); **B** stipules based on *Williams & Stainton* 8289 (scale bar = 1 cm); **C**
 2479 uncinat hairs on petiole based on *Williams & Stainton* 8289 (); **D** male flower clusters based on *Williams*
 2480 *& Stainton* 8289 (scale bar = 3 mm); **E** female inflorescences based on *Wall* 4597 (scale bar = 1 cm); **F**
 2481 female flowers based on *Wall* 4597 (scale bar = 1 mm); **G** achene based on *Wall* 4597 (scale bar = 1 mm).
 2482 *Margarocarpus sanguineus*. **H** stipule based on *Hiep* 3867 (scale bar = 3 mm); **I** leaf outline based on *Hiep*
 2483 3867 (scale bar = 3 cm); **J** female inflorescence based on *Hiep* 3867 (scale bar = 3 mm); **K** female flower
 2484 based on *Hiep* 3867 (scale bar = 1 mm). Illustration by Juliet Beentje.

2485 Fig. 15 *Leptocnide* Plate. *Leptocnide rubricaulis*. **A.** habit based on *Koorders* 27600B (scale bar = 3 cm); **B** detail
 2486 of leaf lower surface based on *Koorders* 27600B (scale bar = 3 cm); **C** bract enclosing inflorescence based
 2487 on *Koorders* 27600B (scale bar = 3 mm); **D** female inflorescence detail based on *Koorders* 27600B (scale bar
 2488 = 3 mm); **E** male flowers in bud based on *Koorders* 27600B (scale bar = 1 mm); **F** male flowers based on
 2489 *Koorders* 27600B (scale bar = 1 mm); **G** female flower based on *Koorders* 27600B (scale bar = 1 mm); **H**
 2490 achene based on *Koorders* 27600B (scale bar = 1 mm). Illustration by Juliet Beentje.

2491 Fig. 16 *Muimar* Plate. *Muimar nivea*. **A** habit based on *Guick* 10 (scale bar = 3 cm); **B** stipule position based
 2492 on *Guick* 10 (scale bar = 5 mm); **C** stipule based on *Guick* 10 (scale bar = 5 mm); **D** male flower
 2493 positioned within cluster of female flowers based on *Anon* 193 (scale bar = 3 mm); **E** male flower based
 2494 on *Anon* 193 (scale bar = 3 mm); **F** female flower cluster based on *Hu* 8113 (scale bar = 3 mm); **G** female
 2495 flower based on *Hu* 8113 (scale bar = 1 mm); **H** fruit based on *Hu* 8113 (scale bar = 1 mm).

2496

2497

2498 [Tables](#)

2499 Table 1. Synopsis of genera and their classification within the Urticaceae

2500 Table 2. Morphological characters and their states

2501 Table 3. Estimated stem lineage ages, current distribution, species number, life form and biomes for

2502 Urticaceae genera

2503 Table 4. Diagnostic characters for *Sceptrocnide*, *Laportea*, *Fleurya* and Madagascan *Obetia* previously ascribed

2504 to *Laportea*.

2505 Table 5. Diagnostic comparison of *Margarocarpus*, *Neraudia*, *Pouzolziella* and *Piptrurus*.

2506 Table 6. Diagnostic comparison of *Pouzolzia*, *Leptocnide* and *Gonostegia*.

2507 Table 7. Morphological characters which distinguish *Muimar* from *Boehmeria* and *Archiboehmeria*

2508

2509

2510 [Supplementary materials](#)

2511

2512 Table S1 Molecular accessions

2513 Table S2 PROTEUS Fossil calibrations output, 2023-07-19

2514 Fig. S1 Plot of loci sampled by accession

2515 Fig. S2 Comparison of phylograms generated by RAXML and Bayesian analyses of the Sanger sequence
2516 data

2517 Fig. S3 Ancestral state reconstructions for 21 morphological characters / traits

2518

2519

Table 1.

Genus	Jussieu 1798	Guadichaud 1830	Blume 1857	Weddell 1869	Bentham & Hooker 1880	Engler 1889	Friis	Friis subfamily grouping	Monro et al subfamily grouping
<i>Aboriella</i>							<i>Pilea</i> =	<i>Elatostemateae</i>	<i>Elatostemateae</i> <i>Achudemia</i> =
<i>Achudemia</i>				<i>Urticaceae</i> : Procridae	<i>Urticaceae</i> : Procridae	<i>Urticaceae</i> : Procridae	<i>Pilea</i> =	<i>Elatostemateae</i>	<i>Elatostemateae</i>
<i>Archiboehmeria</i>							<i>Urticaceae</i>	Boehmerieae	Boehmerieae
<i>Astrothalamus</i>							<i>Urticaceae</i>	Boehmerieae	Boehmerieae
<i>Australina</i>		<i>Urticaceae</i> : Forskaleae		<i>Urticaceae</i> : Forskohleae	<i>Urticaceae</i> : Forskohleae	<i>Urticaceae</i> : Forskohleae	<i>Urticaceae</i>	<i>Forsskaoleae</i>	Parietarieae
<i>Boehmeria</i>	<i>Urticaceae</i> : 2	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i>	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i>	Boehmerieae	Boehmerieae
<i>Caidbeja</i>						Forskohlea=			Parietarieae <i>Forsskaolea</i> =
<i>Cecropia</i>	<i>Urticaceae</i> : 2	<i>Urticaceae</i> : Cecropieae			<i>Urticaceae</i> : Conocephalae		Cecropiaceae		Cecropieae
<i>Chamabainia</i>			Boehmeria=	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i>	Boehmerieae	Boehmerieae
<i>Coussapoa</i>		<i>Urticaceae</i> : Cecropieae			<i>Urticaceae</i> : Conocephalae		Cecropiaceae		Cecropieae
<i>Cypholophus</i>			Boehmeria=	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i>	Boehmerieae	Boehmeria=
<i>Debregeasia</i>			Morocarpus=	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae		<i>Urticaceae</i>	Boehmerieae	Boehmerieae
<i>Dendrocide</i>				<i>Laportea</i> =			<i>Urticaceae</i>	Urticeae	Urticeae
<i>Didymodoxa</i>				<i>Urticaceae</i> : Forskohleae		<i>Australina</i> =	<i>Urticaceae</i>	<i>Forsskaoleae</i>	Parietarieae
<i>Didymogyne</i>			Boehmeria=	<i>Droguetia</i> =	<i>Droguetia</i> =	<i>Droguetia</i> =			Parietarieae <i>Droguetia</i> =
<i>Discocarpus</i>				<i>Laportea</i> =	<i>Laportea</i> =	<i>Laportea</i> =			Urticeae <i>Discocnide</i> =
<i>Discocnide</i>				<i>Laportea</i> =			<i>Urticaceae</i>	Urticeae	Urticeae
<i>Distemon</i>				<i>Urticaceae</i> : Forskohleae					nom. illeg. hom.
<i>Droguetia</i>		<i>Urticaceae</i> : Forskaleae		<i>Urticaceae</i> : Forskohleae	<i>Urticaceae</i> : Forskohleae	<i>Urticaceae</i> : Forskohleae	<i>Urticaceae</i>	<i>Forsskaoleae</i>	Parietarieae
<i>Dubrueilia</i>		<i>Urticaceae</i> : <i>Elatostemateae</i>		<i>Pilea</i> =		<i>Pilea</i> =			<i>Pilea</i> =
<i>Dunniella</i>							<i>Urticaceae</i>	<i>Elatostemateae</i>	<i>Elatostemateae</i> <i>Achudemia</i> =
<i>Duretia</i>					Boehmeria=		Boehmeria=		Boehmerieae <i>Boehmeria</i> =
<i>Elatostema</i>	<i>Urticaceae</i> : 2	<i>Urticaceae</i> : <i>Elatostemateae</i>		<i>Urticaceae</i> : Procridae	<i>Urticaceae</i> : Procridae	<i>Urticaceae</i> : Procridae	<i>Urticaceae</i>	<i>Elatostemateae</i>	<i>Elatostemateae</i>

Genus	Jussieu 1798	Guadichaud 1830	Blume 1857	Weddell 1869	Bentham & Hooker 1880	Engler 1889	Friis	Friis subfamily grouping	Monro et al subfamily grouping
<i>Elatostematoides</i>							<i>Elatostema</i> =		Elatostemateae
<i>Elkania</i>			<i>Pouzolzia</i> =		<i>Pouzolzia</i> =	<i>Pouzolzia</i> =			Boehmerieae <i>Pouzolzia</i> =
<i>Fleurya</i>		<i>Urticeae</i>		<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Laportea</i> =		Urticeae
<i>Forsskaolea</i>	<i>Urticeae</i> : 2	<i>Urticeae</i> : Forskaleiae		<i>Urticeae</i> : Forskohleae	<i>Urticeae</i> : Forskohleae	<i>Urticeae</i> : Forskohleae	<i>Urticeae</i>	<i>Forsskaoleae</i>	Parietarieae
<i>Freirea</i>			Parietaria=	Parietaria=	Parietaria=	Parietaria=			Parietarieae <i>Parietaria</i> =
<i>Gesnouinia</i>				<i>Urticeae</i> : Parietarieae	<i>Urticeae</i> : Parietarieae	<i>Urticeae</i> : Parietarieae	<i>Urticeae</i>	Parietarieae	Parietarieae <i>Parietaria</i> =
<i>Gibbsia</i>							<i>Gibbsia</i>	Boehmerieae	Leukosykeae
<i>Girardinia</i>		<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	Urticeae	Urticeae
<i>Goethartia</i>							<i>Pouzolzia</i> =		<i>Pouzolzia</i> =
<i>Gonostegia</i>				Memorialis=		Memorialis=	<i>Hyrtandra</i> =		Boehmerieae
<i>Gyrotaenia</i>				<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	Urticeae	Myriocarpeae
<i>Helxine</i>				<i>Urticeae</i> : Parietarieae	<i>Urticeae</i> : Parietarieae			Parietarieae	Parietarieae <i>Parietaria</i> =
<i>Hemistylus</i>				<i>Urticeae</i> : Parietarieae	<i>Urticeae</i> : Parietarieae	<i>Urticeae</i> : Parietarieae	<i>Urticeae</i>	Parietarieae	Boehmerieae <i>Rousselia</i> =
<i>Hesperocnide</i>				<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	Urticeae	Urticeae <i>Urtica</i> =
<i>Hyrtandra</i>			<i>Pouzolzia</i> =	Memorialis=		Memorialis=	<i>Urticeae</i>	Boehmerieae	Boehmerieae <i>Pouzolzia</i> =
<i>Langeveldia</i>		<i>Urticeae</i> : <i>Elatostemateae</i>		<i>Elatostema</i> =	<i>Elatostema</i> =	<i>Elatostema</i> =		Elatostemateae <i>Elatostema</i> =	Elatostemateae <i>Elatostema</i> =
<i>Laportea</i>		<i>Urticeae</i>		<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	Urticeae	Urticeae
<i>Lecanocnide</i>				<i>Maoutia</i> =	<i>Maoutia</i> =	<i>Maoutia</i> =		Boehmerieae	Leukosykeae <i>Maoutia</i> =
<i>Lecanthus</i>				<i>Urticeae</i> : Procridae	<i>Urticeae</i> : Procridae	<i>Urticeae</i> : Procridae	<i>Urticeae</i>	<i>Elatostemateae</i>	<i>Elatostemateae</i>
<i>Leptocnide</i>			<i>Urticeae</i>	<i>Pouzolzia</i> =	<i>Pouzolzia</i> =	<i>Pouzolzia</i> =		Boehmerieae <i>Pouzolzia</i> =	Boehmerieae
<i>Leucocnide</i>					<i>Debregeasia</i> =	<i>Debregeasia</i> =		Boehmerieae <i>Debregeasia</i> =	Boehmerieae <i>Debregeasia</i> =
<i>Leukosyke</i>				<i>Urticeae</i> : Boehmerieae	<i>Urticeae</i> : Boehmerieae	<i>Urticeae</i> : Boehmerieae	<i>Urticeae</i>	Boehmerieae	Leukosykeae
<i>Maoutia</i>				<i>Urticeae</i> : Boehmerieae	<i>Urticeae</i> : Boehmerieae	<i>Urticeae</i> : Boehmerieae	<i>Urticeae</i>	Boehmerieae	Leukosykeae
<i>Margarocarpus</i>			Boehmeria=	<i>Pouzolzia</i> =	<i>Pouzolzia</i> =	<i>Pouzolzia</i> =		Boehmerieae <i>Pouzolzia</i> =	Boehmerieae
<i>Memorialis</i>				<i>Urticeae</i> : Boehmerieae		<i>Urticeae</i> : Boehmerieae	<i>Hyrtandra</i> =	Boehmerieae <i>Pouzolzia</i> =	Boehmerieae <i>Gonostegia</i> =

Genus	Jussieu 1798	Guadichaud 1830	Blume 1857	Weddell 1869	Bentham & Hooker 1880	Engler 1889	Friis	Friis subfamily grouping	Monro et al subfamily grouping
<i>Meniscogyne</i>							<i>Urticaceae</i>	<i>Elatostemateae</i>	<i>Elatostemateae</i> <i>Lecanthus</i> =
<i>Metatrophis</i>									<i>Parietarieae</i>
<i>Missiessya</i>			<i>Urticaceae</i>	<i>Leukosyke</i> =	<i>Leukosyke</i> =	<i>Leukosyke</i> =	<i>Leukosyke</i> =	<i>Boehmerieae</i> <i>Leukosyke</i> =	<i>Leukosykeae</i> <i>Leukosyke</i> =
<i>Morocarpus</i>			<i>Urticaceae</i>	<i>Debregeasia</i> =	<i>Debregeasia</i> =	<i>Debregeasia</i> =		<i>Boehmerieae</i> <i>Debregeasia</i> =	<i>Boehmerieae</i> <i>Debregeasia</i> =
<i>Muimar</i>								<i>Boehmerieae</i> <i>Boehmerieae</i> =	<i>Boehmerieae</i>
<i>Musanga</i>					<i>Urticaceae</i> : <i>Conocephalae</i>		<i>Cecropiaceae</i>	<i>Cecropiaceae</i>	<i>Cecropieae</i>
<i>Myrianthus</i>					<i>Urticaceae</i> : <i>Conocephalae</i>		<i>Cecropiaceae</i>	<i>Cecropiaceae</i>	<i>Cecropieae</i>
<i>Myriocarpa</i>				<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i>	<i>Boehmerieae</i>	<i>Myriocarpeae</i>
<i>Nanocnide</i>			<i>Urticaceae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticaceae</i>	<i>Urticeae</i>	<i>Urticeae</i>
<i>Neodistemon</i>				<i>Distemon</i> =	<i>Urticaceae</i> as <i>Distemon</i> : <i>Boehmerieae</i>	<i>Distemon</i> =	<i>Urticaceae</i>	<i>Boehmerieae</i>	<i>Boehmerieae</i> <i>Pouzolzia</i> =
<i>NeoPilea</i>							<i>Pilea</i> =	<i>Elatostemateae</i>	<i>Elatostemateae</i> <i>Pilea</i> =
<i>Neraudia</i>		<i>Urticaceae</i> : <i>Boehmerieae</i>		<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i>	<i>Boehmerieae</i>	<i>Boehmerieae</i>
<i>Nothocnide</i>			<i>Boehmeria</i> =	<i>Pipturus</i> =	<i>Pipturus</i> =	<i>Pipturus</i> =	<i>Urticaceae</i>	<i>Boehmerieae</i>	<i>Boehmerieae</i> <i>Pipturus</i> =
<i>Obetia</i>				<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticaceae</i>	<i>Urticeae</i>	<i>Urticeae</i>
<i>Oreocnide</i>				<i>Villebrunea</i> =	<i>Villebrunea</i> =		<i>Urticaceae</i>	<i>Boehmerieae</i>	<i>Boehmerieae</i>
<i>Parietaria</i>	<i>Urticaceae</i> : 2	<i>Urticaceae</i> : <i>Parietarieae</i>	<i>Urticaceae</i>	<i>Urticaceae</i> : <i>Parietarieae</i>	<i>Urticaceae</i> : <i>Parietarieae</i>	<i>Urticaceae</i> : <i>Parietarieae</i>	<i>Urticaceae</i>	<i>Parietarieae</i>	<i>Parietarieae</i>
<i>Parsana</i>							<i>Laportea</i> =		<i>Fleurya</i> =
<i>Pellionia</i>		<i>Urticaceae</i> : <i>Elatostemateae</i>		<i>Urticaceae</i> : <i>Procridae</i>	<i>Urticaceae</i> : <i>Procridae</i>	<i>Urticaceae</i> : <i>Procridae</i>	<i>Urticaceae</i>	<i>Elatostemateae</i>	<i>Elatostema</i> =: <i>Elatostemateae</i>
<i>Petelotiella</i>							<i>Urticaceae</i>	<i>Elatostemateae</i>	<i>Elatostemateae</i> <i>Pilea</i> =
<i>Phenax</i>			<i>Urticaceae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i>	<i>Boehmerieae</i>	<i>Boehmerieae</i>
<i>Pilea</i>				<i>Urticaceae</i> : <i>Procridae</i>	<i>Urticaceae</i> : <i>Procridae</i>	<i>Urticaceae</i> : <i>Procridae</i>	<i>Urticaceae</i>	<i>Elatostemateae</i>	<i>Elatostemateae</i>
<i>Pipturus</i>			<i>Boehmeria</i> =	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>		<i>Urticaceae</i>	<i>Boehmerieae</i>	<i>Boehmerieae</i>
<i>Poikilospermum</i>				<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Urticaceae</i> : <i>Boehmerieae</i>	<i>Cecropiaceae</i>		<i>Urticeae</i>
<i>Polychroa</i>					<i>Pellionia</i> =	<i>Pellionia</i> ?		<i>Elatostemateae</i> <i>Pellionia</i> =	<i>Elatostemateae</i>

Genus	Jussieu 1798	Guadichaud 1830	Blume 1857	Weddell 1869	Bentham & Hooker 1880	Engler 1889	Friis	Friis subfamily grouping	Monro et al subfamily grouping
<i>Pourouma</i>		<i>Urticaceae</i> : Pouroumeae			<i>Urticaceae</i> : Conocephalae		Cecropiaceae	Cecropiaceae	Cecropieae
<i>Pouzolzia</i>			<i>Urticaceae</i>	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i>	Boehmerieae	Boehmerieae
<i>Pouzolziella</i>								<i>Pouzolzia</i> =	Boehmerieae
<i>Margarocarpus</i>								<i>Pouzolzia</i> =	Boehmerieae
<i>Praetoria</i>					<i>Pipturus</i> =	<i>Pipturus</i> =		Boehmerieae <i>Pipturus</i> =	Boehmerieae <i>Pipturus</i> =
<i>Procris</i>	<i>Urticaceae</i> : 2			<i>Urticaceae</i> : Procridae	<i>Urticaceae</i> : Procridae	<i>Urticaceae</i> : Procridae	<i>Urticaceae</i>	<i>Elatostemateae</i>	<i>Elatostemateae</i>
<i>Pseudopipturus</i>							Nothocnide=		Boehmerieae <i>Pipturus</i> =
<i>Robinsoniodendron</i>							<i>Maoutia</i> =		<i>Leukosykeae</i> <i>Maoutia</i> =
<i>Rousselia</i>				<i>Urticaceae</i> : Parietarieae	<i>Urticaceae</i> : Parietarieae	<i>Urticaceae</i> : Parietarieae	<i>Urticaceae</i>	Parietarieae	Boehmerieae
<i>Sarcochlamys</i>				<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i>	Boehmerieae	Boehmerieae
<i>Sarcopilea</i>							<i>Urticaceae</i>	<i>Elatostemateae</i>	<i>Elatostemateae</i> <i>Pilea</i> =
<i>Scepocarpus</i>				<i>Urticeae</i>			<i>Urera</i> =		<i>Urticeae</i>
<i>Sceptrocnide</i>					<i>Urticeae</i>	<i>Urticeae</i>	<i>Laportea</i> =	<i>Urticeae</i>	<i>Urticeae</i>
<i>Schychowskyia</i>				<i>Fleurya</i> =		<i>Laportea</i> =			<i>Urticeae</i> <i>Fleurya</i> =
<i>Sciobia</i>						<i>Procris</i> =			<i>nomen nudum</i>
<i>Sciophila</i>		<i>Urticaceae</i> : <i>Elatostemateae</i>		<i>Procris</i> =	<i>Procris</i> =	<i>Procris</i> =			<i>Elatostemateae</i> <i>Procris</i> =
<i>Sclepsion</i>					<i>Laportea</i> =	<i>Laportea</i> =			<i>nomen ined</i>
<i>Soleirolia</i>		<i>Urticaceae</i> : Parietarieae		<i>Helxine</i> =	<i>Helxine</i> =	<i>Helxine</i> =	<i>Urticaceae</i>	Parietarieae	Parietarieae <i>Parietaria</i> =
<i>Sphaerotylos</i>							<i>Sarcochlamys</i> =		<i>Leukosykeae</i> <i>Sarcochlamys</i> =
<i>Splitgerbera</i>			Boehmeria=		Boehmeria=	Boehmeria=			Boehmerieae <i>Boehmeria</i> =
<i>Stachyocnide</i>			<i>Urticaceae</i> `	<i>Pouzolzia</i> =	<i>Pouzolzia</i> =	<i>Pouzolzia</i> =			Boehmerieae <i>Pouzolzia</i> =
<i>Thaumuria</i>			Parietaria=	Parietaria=	Parietaria=	Parietaria=			Parietarieae <i>Parietaria</i> =
<i>Touchardia</i>				<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i> : Boehmerieae	<i>Urticaceae</i>	Boehmerieae	<i>Urticeae</i>
<i>Urera</i>		<i>Urticeae</i>		<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticaceae</i>	<i>Urticeae</i>	<i>Urticeae</i>
<i>Urtica</i>	<i>Urticaceae</i> : 2	<i>Urticeae</i>	<i>Urticaceae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticeae</i>	<i>Urticaceae</i>	<i>Urticeae</i>	<i>Urticeae</i>

[illegible]

Table 2

Character	States
Habit	herb, shrub, tree, vine, hemi-epiphyte, parasite
Succulence	succulent, not succulent
Habitat	disturbed (open), undisturbed (shaded)
Exudate	present, absent
Stem tubercles (fleshy protuberances)	present, absent
Stem armament	with spines, without
Cystoliths	present, absent
Cystolith form	spindle or fusiform, oblong-elliptic, punctate, na
Leaf arrangement	opposite, alternate
Stipule presence	present, absent
Stipule adnation	not amplexicaulous, amplexicaulous, na
Stipule insertion	interpetiolar, intrapetiolar, na
Stipule scars	inconspicuous, conspicuous, na
Stipule enclose another stipule-leaf iteration	yes, no, na
Stipule division	Free, fused at least in part, na
Leaf lamina division	simple, lobed, palmatilobed, compound-palmatifid
Lamina venation	3 or 5 basal nerves, a single basal nerve (pinnately nerved)
Lamina margin	entire, toothed
Lamina isometry at each / alternating nodes	Equal or subequal, unequal by ration > 1:1.5
Nanophylls (minor leaf < 1/5 length of major leaf)	present, absent, na
Stem or leaf hair assembly	single cell, multicelled, na
Presence of hairs with broad or bulbous base	present, absent, na
Presence of leaf hairs with hooked tip	present, absent, na
Presence of lanate hairs	present, absent, na
Petiole scars	conspicuous, inconspicuous
Inflorescences sexuality	unisexual, bisexual
Staminate inflorescences cymes	paniculate, fused (racemose, receptaculate), flowers solitary
Staminate inflorescence bilaterally symmetrical	bilaterally symmetrical, asymmetrical
Staminate inflorescences branching	branched > 1, unbranched
Staminate flowers borne in compacted cyme branches	no, yes
Staminate flower presentation	pedicellate, sessile
Staminate perianth	free, partially fused, completely fused
Staminate tepal envelopes filament	yes, no
Staminate perianth subapical appendages	present, absent
Pistillode	present, absent
Pistillode pubescence	pubescent, glabrous
Filaments inflexed in bud	Inflexed, not inflexed
Pistillate inflorescence cymes	paniculate, fused (racemose, receptaculate), flowers solitary
Pistillate inflorescence bilaterally symmetry	bilaterally symmetrical, asymmetrical
Pistillate inflorescences branching	branched > 1, unbranched
Pistillate flower presentation	pedicellate, sessile
Pistillate pedicel bracts	Yes, no
Pistillate inflorescence cymes	paniculate, fused (racemose, receptaculate), flowers solitary
Pistillate inflorescence bilaterally symmetry	bilaterally symmetrical, asymmetrical
Pistillate pedicel bracts insertion	inserted at pedicel base, apex
Pistillate involucre formed from bracts	present, absent
Pistillate inflorescence involucre receptaculate	yes, no
Pistillate flower no per inflorescence	<2, >2, >100, >1000
Pistillate flowers borne in compacted cyme	yes, no

branches	
Pistillate perianth parts	equal, unequal
Pistillate perianth accrescent	yes, no
Pistil angle of insertion (fruit)	erect, <45°, >45°
Pistil-stigma insertion	sessile, stalked
Stigma bilateral (vertical axis)	symmetrical, asymmetrical
Stigma branching	branched, unbranched
Stigma articulated	Yes, no
Stigma hair distribution	apical, laterally asymmetrical, laterally symmetrical
Placentation	basal, lateral
Perianth fleshy in fruit	yes, no
Pedicele fleshy in fruit	yes, no
Receptacle fleshy in fruit	yes, no
Peduncle fleshy in fruit	yes, no
Achene longer than broad	yes, no
Achene compressed	yes, no (including subcompressed)
Achene broadest at / below midpoint	yes, no
Achene bilateral symmetry	Symmetrical (including subsymmetrical), asymmetrical
Fruit surface ornamented (including hairs)	yes, no
Stigma persistent	yes, no
Mucilaginous layer in pericarp	yes, no
Filaments fused	yes, no
Pistillate tepal length	parts equal or exceeding the achene, shorter than
Pericarp fleshy	yes, no
Achene transverse symmetry	symmetrical, asymmetrical

Table 3

Genus	Stem age¹	Current area	Species number	Life form	Current biome⁴
<i>Urtica</i>	Eocene 46–50 MYA	Global	70	herb	Temperate broadleaf forest
<i>Zhengyia</i>	Eocene 46–50 MYA	Indomalaya	1	herb	Temperate broadleaf forest
Sceptrocnide (<i>L. cuspidata</i>)	Eocene 37–46 MYA	Indomalaya	1*	herb	Temperate broadleaf forest
<i>Nanocnide</i>	Eocene 37–46 MYA	Indomalaya	3	herb	Temperate broadleaf forest
<i>Laportea</i> (<i>L. canadensis</i>)	Upper Paleocene / Lower Eocene 52–58 MYA	Indomalaya, Afrotropics, Nearctic	20**	herb	Temperate broadleaf forest
Girardinia	Upper Paleocene / Lower Eocene 52–58 MYA	Indomalaya, Afrotropics, Palearctic	2	Herb. shrub	Temperate broadleaf forest, Tropical and subtropical dry broadleaf forest, Tropical and subtropical moist broadleaf forest
Discocnide	Upper Eocene / Oligocene 30–41 MYA	Neotropics	1	Shrub	Tropical and subtropical moist broadleaf forest
Dendrocnide	Upper Eocene / Oligocene 30–41 MYA	Indomalaya, Australasia, Pacific	42	Tree, shrub	Tropical and subtropical moist broadleaf forest
<i>Obetia</i>	Upper Eocene / Oligocene 29–39 MYA	Afrotropics	12**	Tree, shrub	Tropical and subtropical dry broadleaf forest, Tropical and subtropical grasslands, savannas and shrublands
Scepcarpus	Upper Eocene / Oligocene 29–39 MYA	Afrotropics	15**	Lianas, trees	Tropical and subtropical moist broadleaf forest
<i>Urera</i>	Eocene 41–47 MYA	Neotropics	22**	Tree, shrub, liana	Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest,
<i>Poikilospermum</i>	Upper Eocene / Lower Oligocene	Indomalaya	27	Hemi- epiphyte , tree	Tropical and subtropical moist broadleaf forest

	39–45 MYA				
<i>Touchardia</i>	Lower Miocene 17–22 MYA	Pacific	3**	Tree, shrub	Tropical and subtropical moist broadleaf forest,
<i>Fleurya</i> (<i>Laportea</i> II)	Lower Miocene 17–22 MYA	Afrotropics, Neotropics, Pacific	4*	Herb	Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest,
<i>Myriocarpa</i>	Miocene 14–19 MYA	Neotropics	14	Tree	Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest
<i>Gyrotaenia</i>	Miocene 14–19 MYA	Neotropics	5	Tree	Tropical and subtropical moist broadleaf forest
<i>Elatostema</i>	Lower Oligocene 50–56 MYA	Australasia, Afrotropics, Indomalaya, Pacific, Palearctic	700**	Herb	Tropical and subtropical moist broadleaf forest, Temperate broadleaf forest
<i>Elatostemoides</i>	Lower Oligocene 50–56 MYA	Indomalaya	22	Shrub	Tropical and subtropical moist broadleaf forest
<i>Procris</i>	Upper Oligocene 28–34 MYA	Afrotropics, Australasia, Indomalaya	24	Herb	Tropical and subtropical moist broadleaf forest,
<i>Polychroa</i>	Upper Oligocene 28–34 MYA	Indomalaya	1	Herb	Tropical and subtropical moist broadleaf forest,
<i>Lecanthus</i>	Lower Eocene 58–63 MYA	Afrotropics, Indomalaya, Palearctic	3	Herb	Tropical and subtropical moist broadleaf forest,
<i>Achudemia</i>	Lower Eocene 58–63 MYA*	Indomalaya, Palearctic	5	Herb	Tropical and subtropical moist broadleaf forest, Temperate broadleaf forest
<i>Pilea</i>	Paleocene 58–63 MYA*	Afrotropics, Indomalaya, Pacific, Palearctic, Nearctic, Neotropics	715**	Herb	Tropical and subtropical moist broadleaf forest, Temperate broadleaf forest, Tropical and subtropical dry broadleaf forest
<i>Parietaria</i>	Lower Paleocene 65–70 MYA	Afrotropics, Australasia, Indomalaya, Palearctic, Nearctic, Neotropics	26	Herb	Mediterranean vegetation, Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest, Temperate broadleaf forest, Deserts and xeric shrublands
<i>Forsskaolea</i>	Paleocene	Afrotropics,	7	Shrub	Mediterranean vegetation, Deserts and

	59–63 MYA	Palaearctic, Indomalaya			xeric shrublands
<i>Didymodoxa</i>	Lower Eocene 50–55 MYA	Afrotropics	2	Herb	Mediterranean vegetation, Tropical and subtropical grasslands, savannas and shrubland, Subtropical and tropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest,
<i>Australina</i>	Eocene 45–49 MYA	Australasia	1	Herb	Temperate broadleaf forest, Tropical and subtropical moist broadleaf forest
<i>Metatrophis</i>	Eocene 38–44 MYA	Pacific	1	Shrub	Tropical and subtropical moist broadleaf forest
<i>Droguetia</i>	Eocene 38–44 MYA	Afrotropics, Indomalaya, Palaearctic	7	Herb	Tropical and subtropical moist broadleaf forest
<i>Oreocnide</i>	Upper Cretaceous / Lower Paleocene 65–70 MYA	Indomalaya	16	Trees, shrubs	Tropical and subtropical moist broadleaf forest, Temperate broadleaf forest
<i>Phenax</i>	Upper Cretaceous / Lower Paleocene 64–68 MYA	Afrotropics, Indomalaya, Nearctic, Neotropics	28	Trees, shrubs, herbs	Tropical and subtropical moist broadleaf forest
<i>Boehmeria</i>	Paleocene 56–60 MYA	Afrotropics, Australasia, Indomalaya, Nearctic, Neotropics, Palaearctic	85**	Trees, shrubs, herbs	Tropical and subtropical moist broadleaf forest, Temperate broadleaf forest, Tropical and subtropical dry broadleaf forest,
<i>Pouzolziella</i>	Lower Miocene 16–22 MYA	Australasia	1 or 3**	Shrubs	Tropical and subtropical moist broadleaf forest
<i>Pipturus</i>	Lower Miocene 16–22 MYA	Australasia, Indomalaya, Pacific	34**	Trees, lianas, shrubs	Tropical and subtropical moist broadleaf forest,
<i>Neraudia</i>	Lower Miocene / Upper Oligocene 18–24 MYA	Pacific	5	Trees, shrubs	Tropical and subtropical moist broadleaf forest,
<i>Margarocarpus</i>	Lower Oligocene / Upper Eocene 28–35 MYA	Indomalaya, Palaearctic	4**	Shrubs, herbs	Tropical and subtropical moist broadleaf forest
<i>Pouzolzia</i>	Upper Eocene /	Afrotropics, Indomalaya,	57**	Shrubs,	Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry

	Lower Oligocene 26–28 MYA	Neotropics, Palearctic, Australasia		herbs	broadleaf forest,
<i>Leptocnide</i>	Lower Oligocene 30–33 MYA	Australasia	1	Shrubs, herbs	Tropical and subtropical moist broadleaf forest
<i>Gonostegia</i>	Lower Oligocene 30–33 MYA	Australasia, Indomalaya, Palearctic	3	Shrubs, herbs	Tropical and subtropical moist broadleaf forest, Temperate broadleaf forest
<i>Chamabainia</i>	Lower Eocene 48–55 MYA	Indomalaya	1	Herbs	Tropical and subtropical moist broadleaf forest, Temperate broadleaf forest
<i>Muimar</i>	Miocene 11–17 MYA	Indomalaya, Palearctic	2	Shrubs, Trees	Tropical and subtropical moist broadleaf forest, Temperate broadleaf forest
<i>Archiboehmeria</i>	Miocene 11–17 MYA	Indomalaya, Palearctic	1	Shrubs	Tropical and subtropical moist broadleaf forest
<i>Astrothalamus</i>	Miocene 14–17 MYA	Indomalaya	1	Shrubs	Tropical and subtropical moist broadleaf forest
<i>Debregeasia</i>	Miocene 14–17 MYA	Afrotropics, Australasia, Palearctic, Indomalaya	9	Trees, shrubs	Tropical and subtropical moist broadleaf forest, Deserts and xeric shrublands, Tropical and subtropical dry broadleaf forest,
<i>Leucosyke</i>	Upper Eocene 36–39 MYA	Indomalaya	33	Trees, shrubs	Tropical and subtropical moist broadleaf forest
<i>Sarcochlamys</i>	Upper Eocene 9–10 MYA	Indomalaya, Palearctic	1	Trees, shrubs	Tropical and subtropical moist broadleaf forest
<i>Maoutia</i>	Upper Miocene 9–10 MYA	Indomalaya	10	Trees, shrubs	Tropical and subtropical moist broadleaf forest
<i>Gibbsia</i>	Upper Miocene 36–39 MYA	Indomalaya	2	Shrubs	Tropical and subtropical moist broadleaf forest
<i>Cecropia</i>	Lower Miocene 20–22 MYA	Nearctic, Neotropics	63	Trees	Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest,
<i>Pourouma</i>	Upper Oligocene / Lower Miocene 22–25 MYA	Neotropics	31	Trees	Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest,
<i>Coussapoa</i>	Lower Miocene 20–22 MYA	Nearctic, Neotropics	50	Hemiepiphytes, trees	Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest,

Musanga	Upper Oligocene / Lower Miocene 21–25 MYA	Afrotropics	2	Trees	Tropical and subtropical moist broadleaf forest
Myrianthus	Upper Oligocene / Lower Miocene 21–25 MYA	Afrotropics	8	Trees	Tropical and subtropical moist broadleaf forest, Tropical and subtropical dry broadleaf forest,

Table 4

Character	Sceptrocnide	Laportea	Fleurya	Obetia (ex Laportea)
Geography	Indomalaya	Nearctic, Palearctic, Afrotropics, Indomalaya	Afrotropics, Indomalaya, Australasia	Madagascar
Stipule insertion	Intrapetiolar	Intrapetiolar	Intrapetiolar	Interpetiolar
Stipule scar	Conspicuous	Conspicuous	Inconspicuous	Inconspicuous
Staminate perianth	Free	Free	Partially fused	Partially fused
Filament partially adnate to sepal?	Yes	No	No	No
Pistillate inflorescence	Racemose spike	Paniculate	Paniculate	Paniculate
Stigma shape	Subcaudiform	Caudiform	Capitate	Ligulate
Stigma branched?	No	No	No	Yes
Stigma hair distribution	Laterally asymmetrical	Laterally symmetrical	Apical only	Apical only
Achene longer than broad	Yes	No	Yes	No
Sepal length in fruit	Equal or exceeding achene	Shorter than achene	Shorter than achene	Equal or exceeding achene

Table 5

Character state	<i>Margarocarpus</i>	<i>Neraudia</i>	<i>Pouzolzia</i>	<i>Pouzolziella</i>	<i>Pipturus</i>
Uncinate hairs	present	present	present	absent	absent
Stigma articulation	articulated	articulated	Not articulated	not articulated	articulated
Distribution of papillae on stigma	asymmetrical, portion of circumference glabrous	radially symmetrical, whole circumference pubescent	asymmetrical, portion of circumference glabrous	asymmetrical, portion of circumference glabrous	whole circumference pubescent
Stigma persistence in fruit	Not persistent	persistent	Persistent	Persistent	Not persistent
Female inflorescence	compact cymose	cymose / fasciculate	compact cymose	compact cymose	fused capitate
Fruit winged?	not winged	winged	Winged or not	winged	not winged
Achene colour	Cream to white	brown	Pale brown, white	Pale brown	Brown-grey
Geography	Indomalaya	Hawaii	Afrotropics, Australasia, Indomalaya, Nearctic, Neotropics, Pacific Islands, Palearctic	Australasia	Australasia, Indomalaya, Pacific Islands

Table 6

Character state	<i>Pouzolzia</i>	<i>Leptocnide</i>	<i>Gonostegia</i>
Stipule	Longer than broad, lacking an abrupt apex	Broader than long, with abrupt apex	Longer than broad, lacking an abrupt apex
Leaf arrangement	alternate	alternate	opposite
Leaf margin	Entire or toothed	toothed	entire
Leaf venation	Lateral 'primary' veins extending $\frac{1}{2}$ to $\frac{3}{4}$ the lamina length	Lateral 'primary' veins extending ca $\frac{2}{3}$ the lamina length	Lateral 'primary' veins extending the full length of the lamina, including the apex
Staminate flowers in bud	Sepals fused or not, where fused, for $<1/2$ their length, the free portions not subtended by a crest	Sepals fused or not, where fused, for $<1/2$ their length, the free portions not subtended by a crest	Sepals fused for $>1/2$ their length, free portions subtended by a crest forming a sub-apical circumferential ring

Table 7

	<i>Boehmeria</i>	<i>Archiboehmeria</i>	<i>Muimar</i>
Stem pubescence	hairs hooked or not	hairs hooked	hairs not hooked
Degree of stipule fusion	fully fused to fused for < 1/3 of their length	Stipules fused for > 1/2 of their length	Stipules fused for < 1/3 of their length
Point of stipule insertion	interpetiolar	interpetiolar	intrapetiolar
Leaf pubescence	hairs not shiny / glistening	hairs not shiny / glistening	hairs shiny / glistening
Bisexual flowers	absent	present	absent
Male flowers	Sepals fused for < 1/3 of their length	Sepals fused for ca 1/2 of their length	Sepals fused for < 1/3 of their length
Female inflorescences	sessile, pedunculate or on modified stems	pedunculate	pedunculate

Figure 1

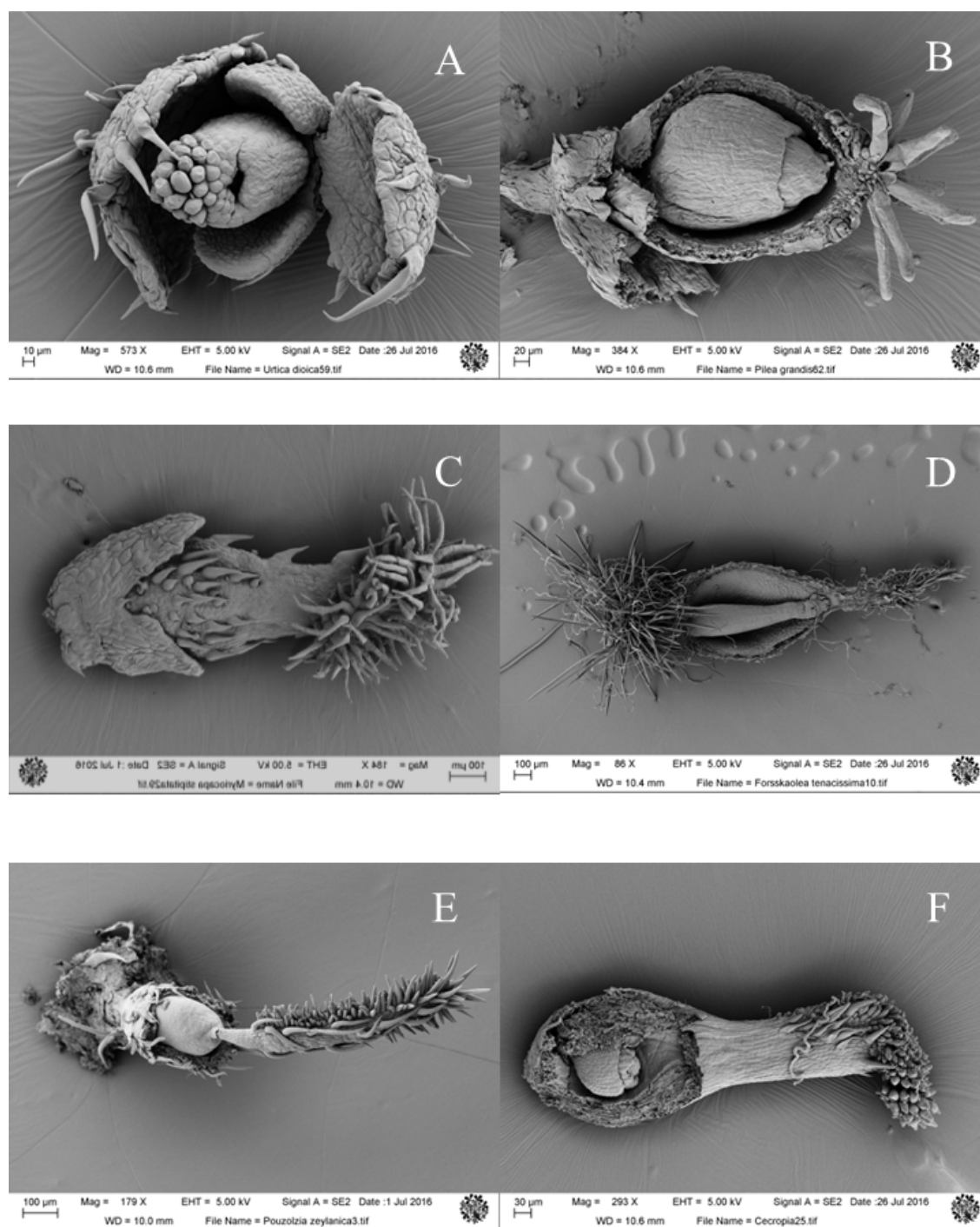






Figure 3

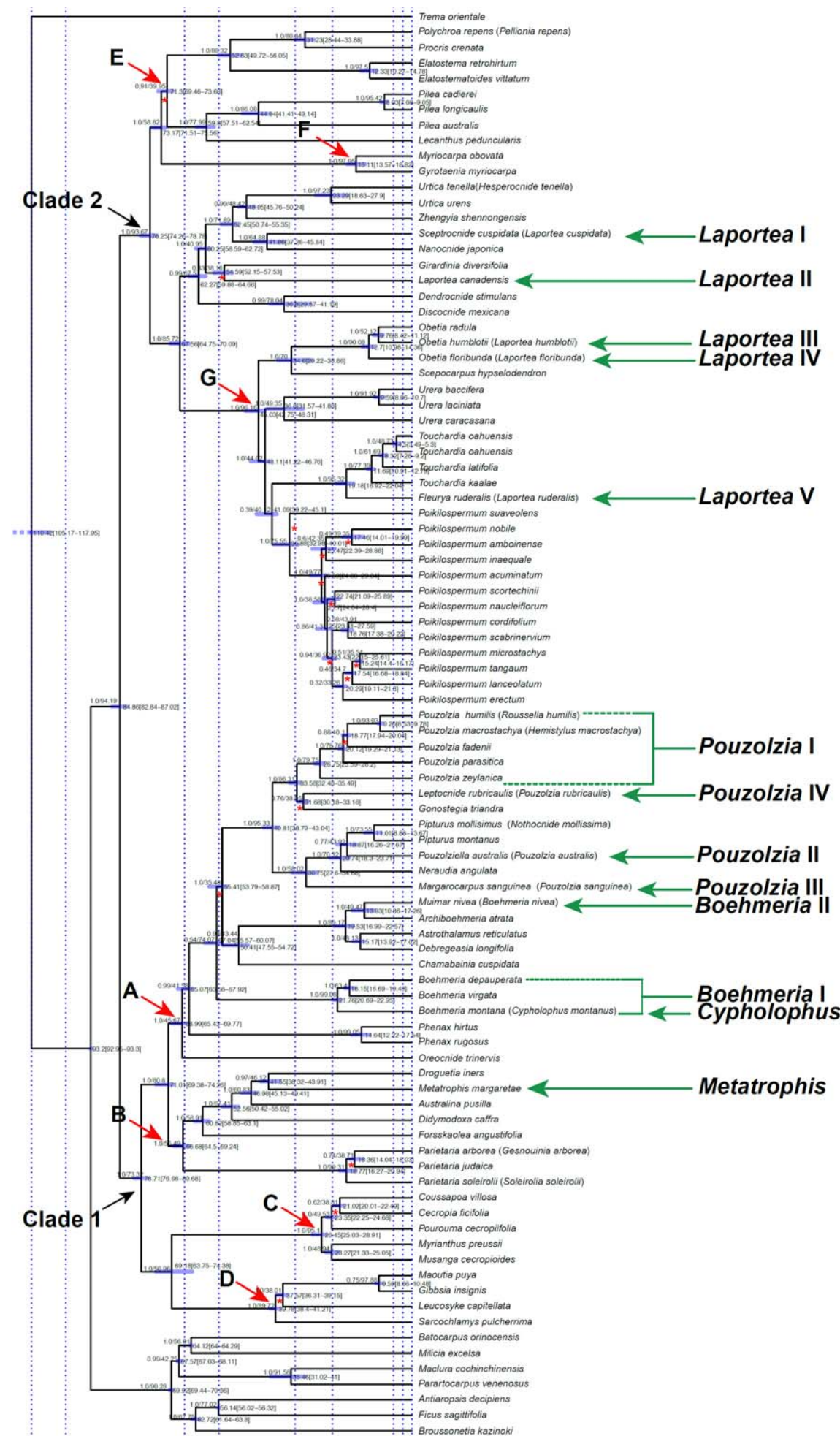


Figure 4.1

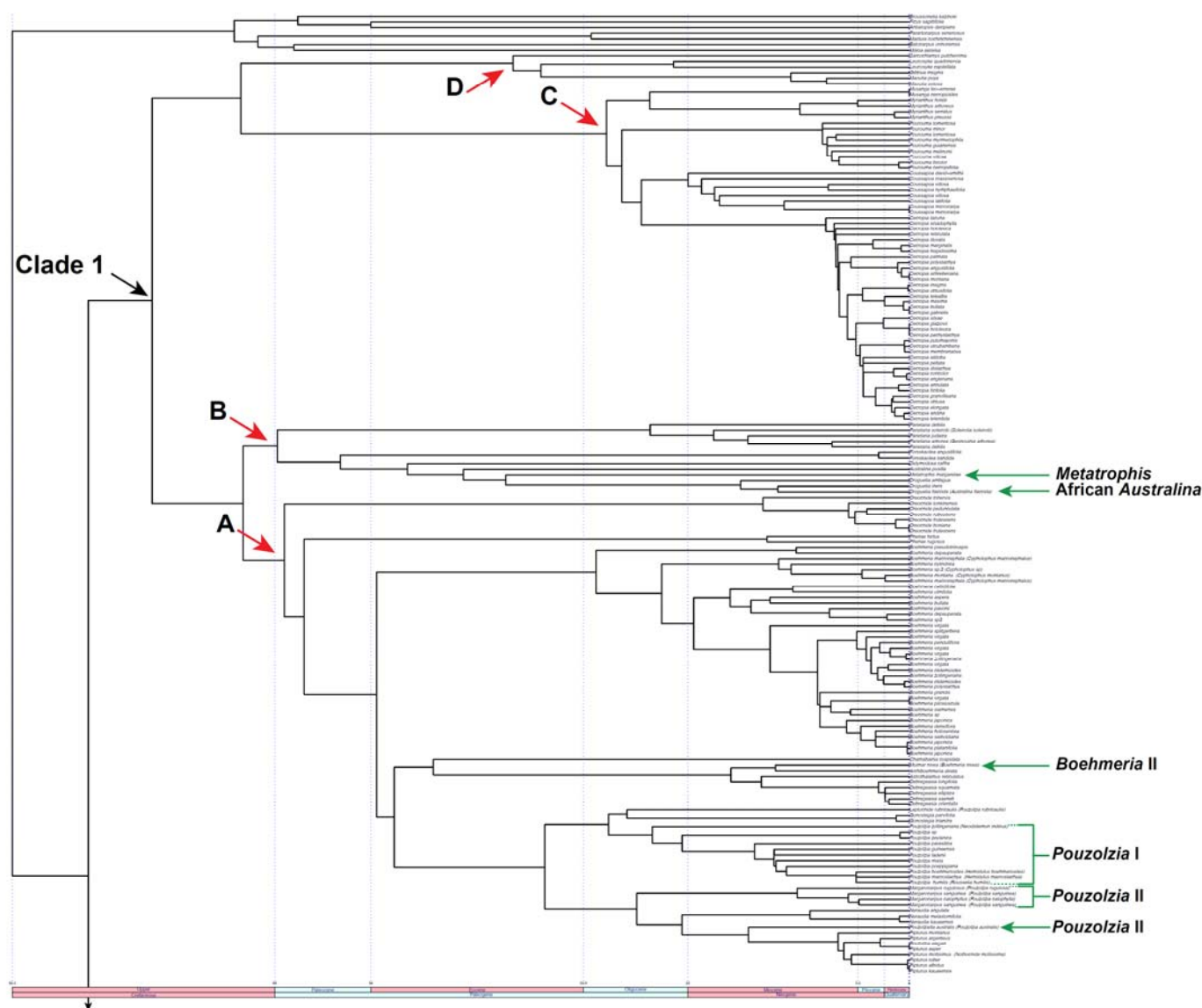


Figure 4.2

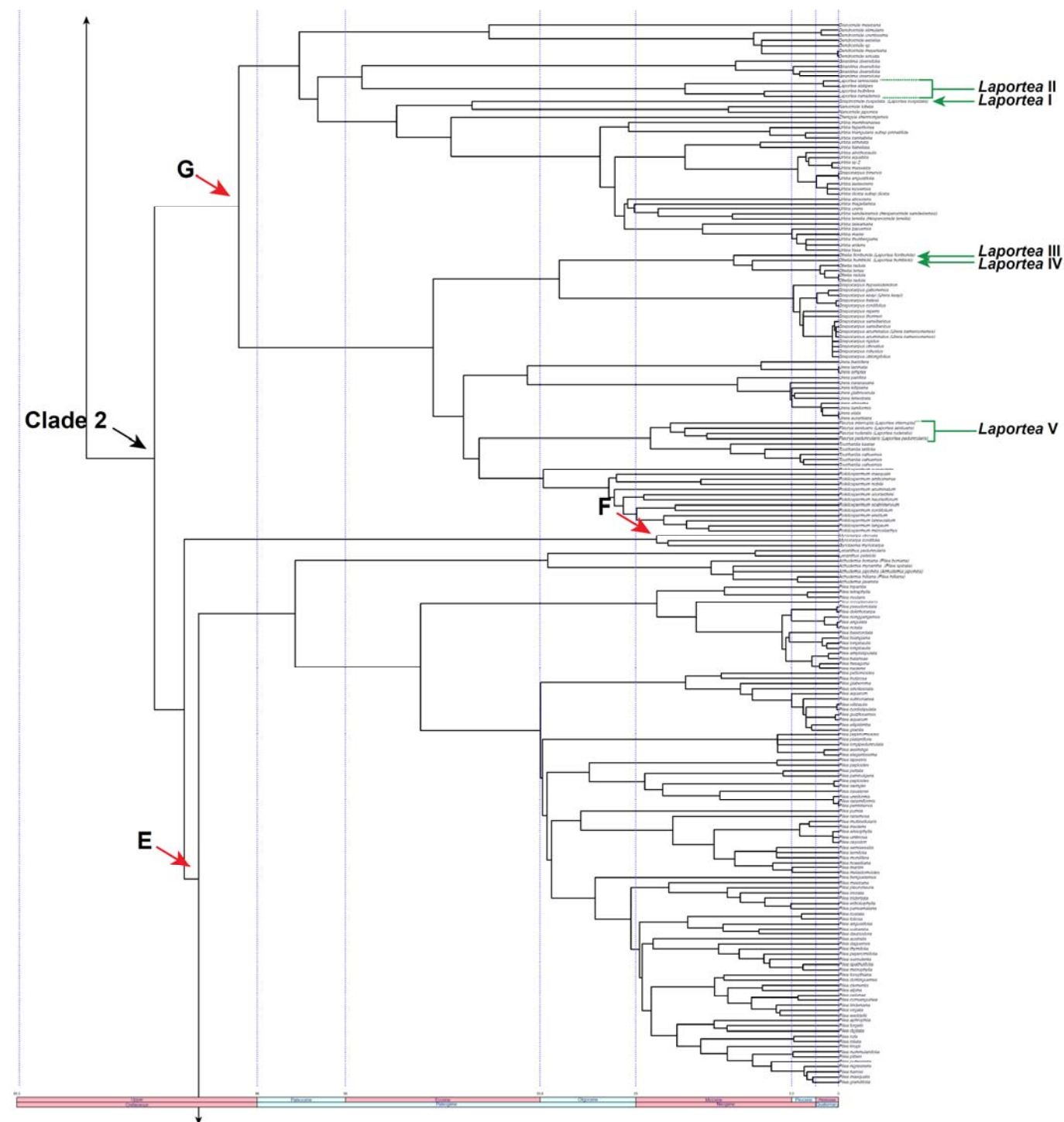


Figure 4.3

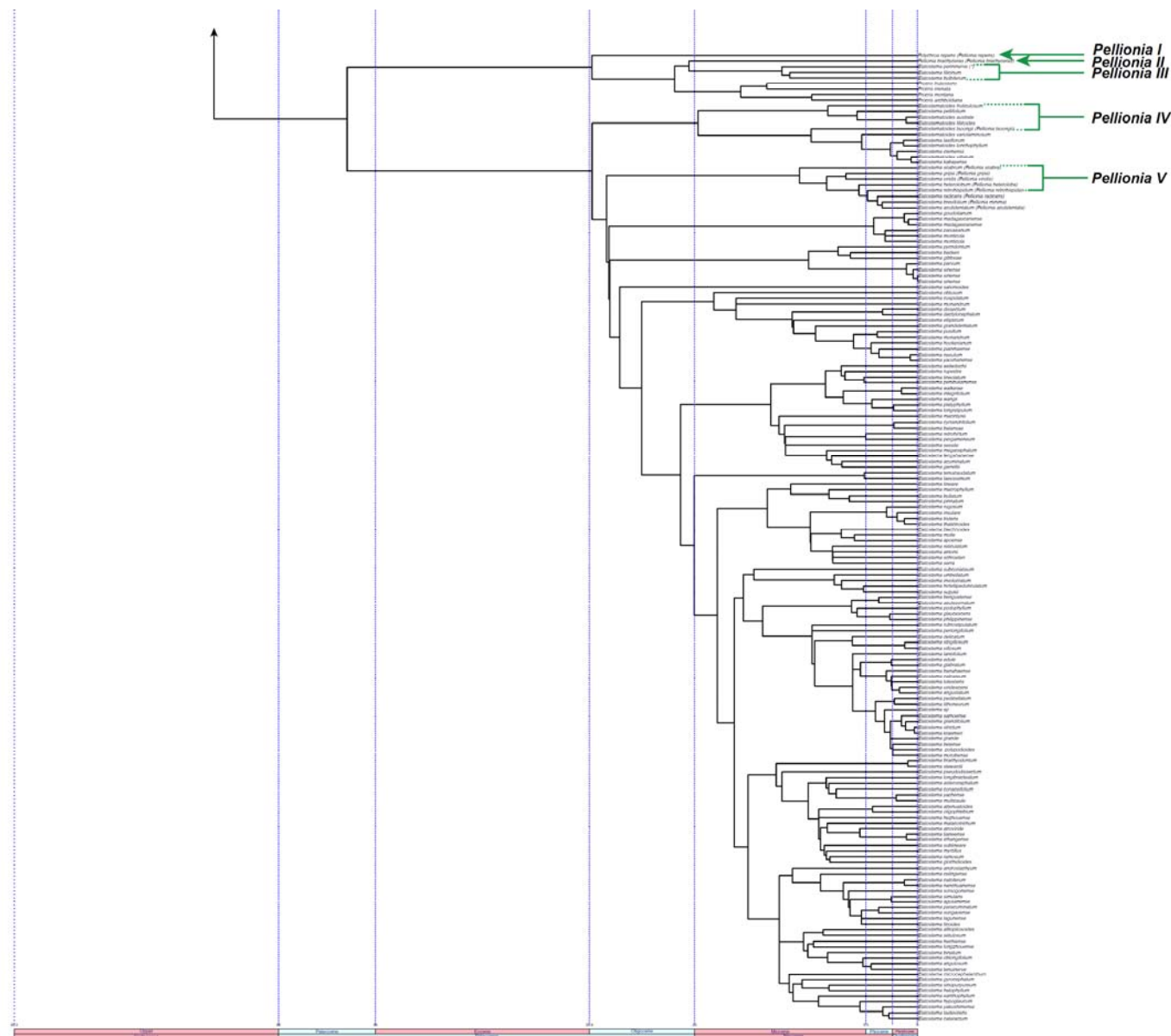


Figure 3 part 1: Cecropiaceae, Leukosykeae, Parietarieae, Boehmerieae)

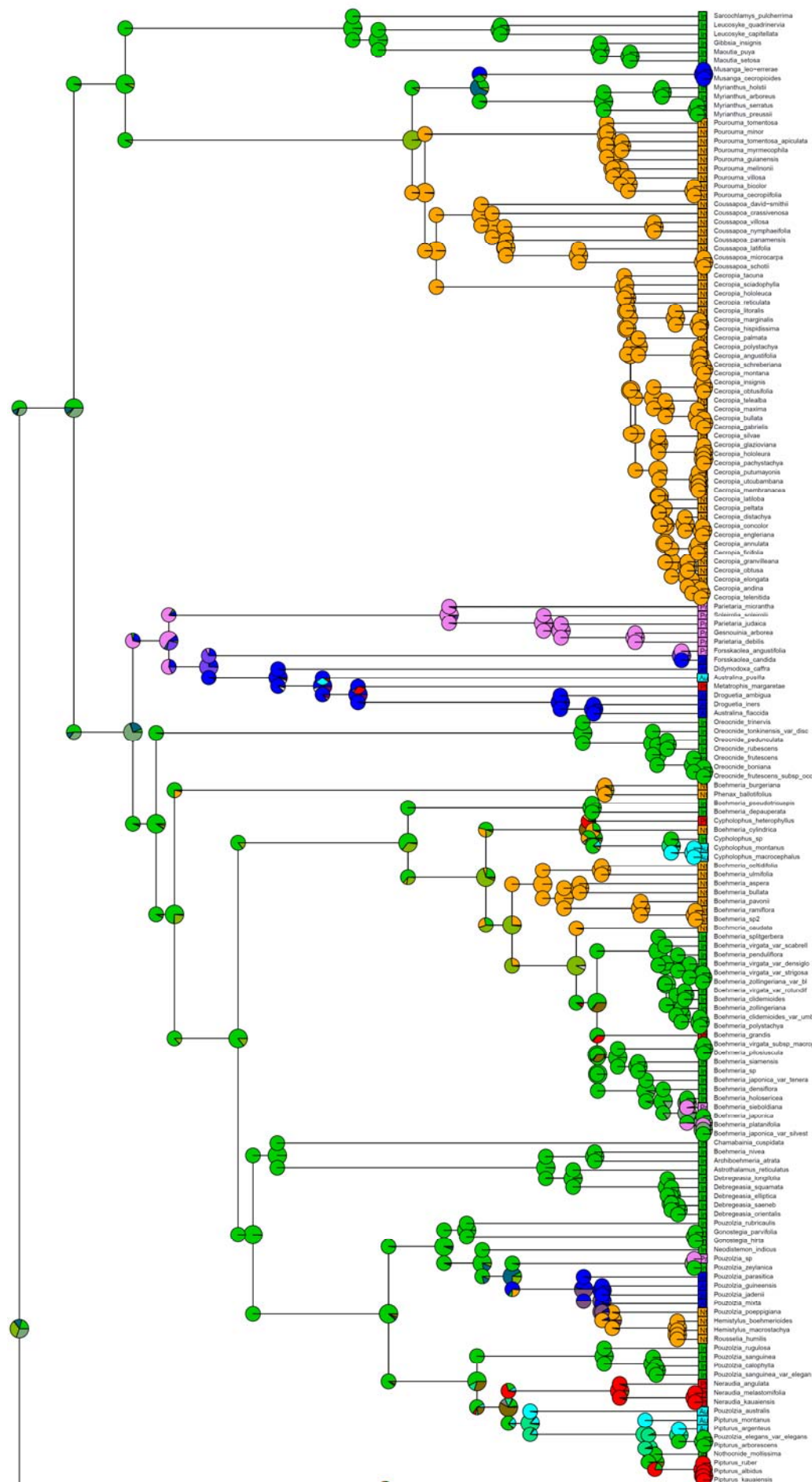
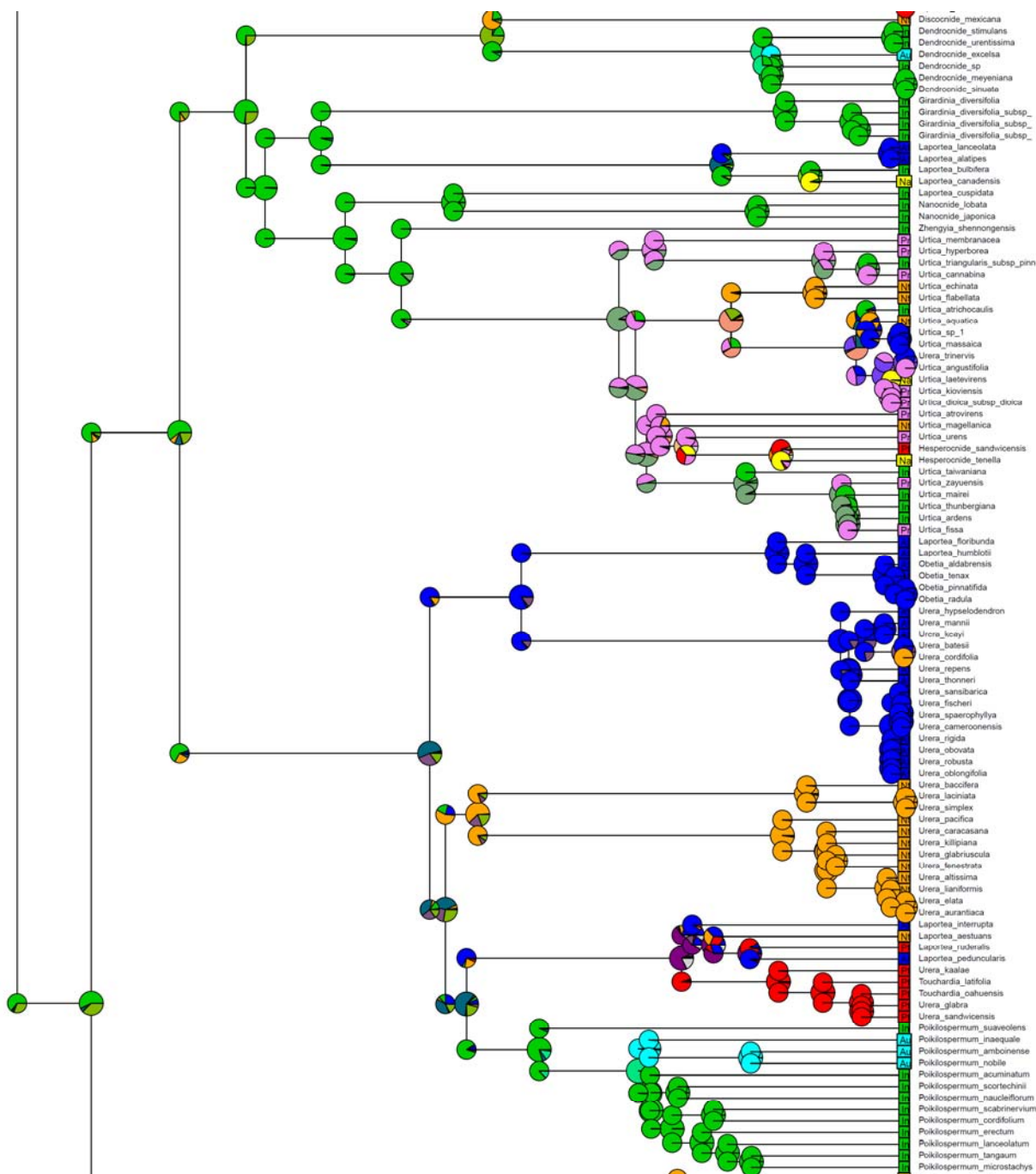


Figure 3 part 2 (Urticeae)



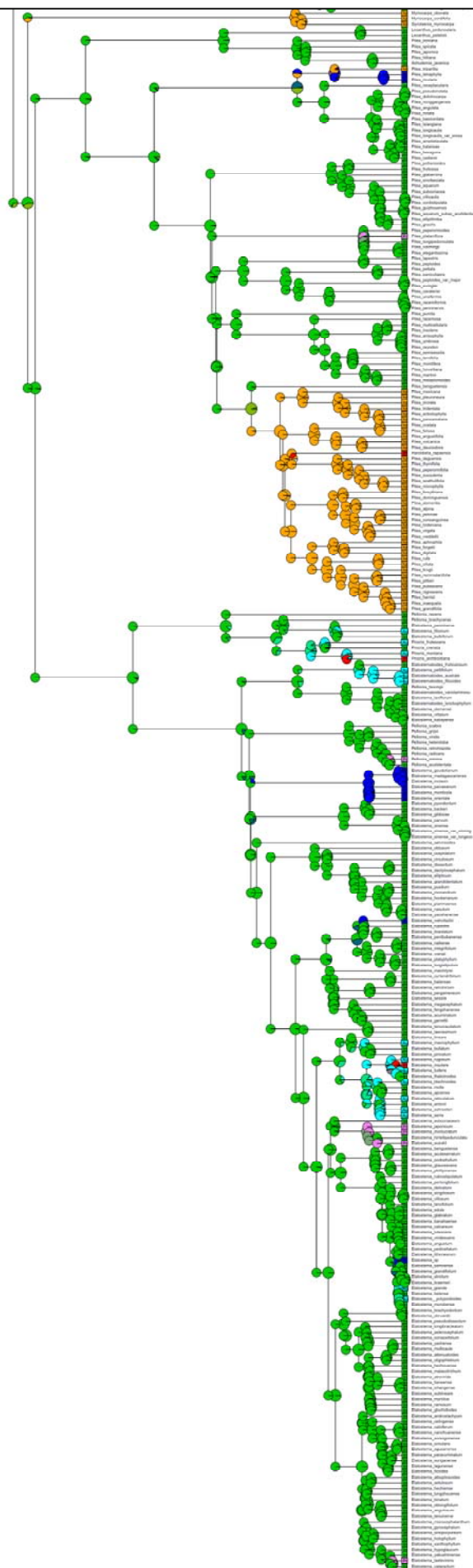


Figure 6. Urticeae.

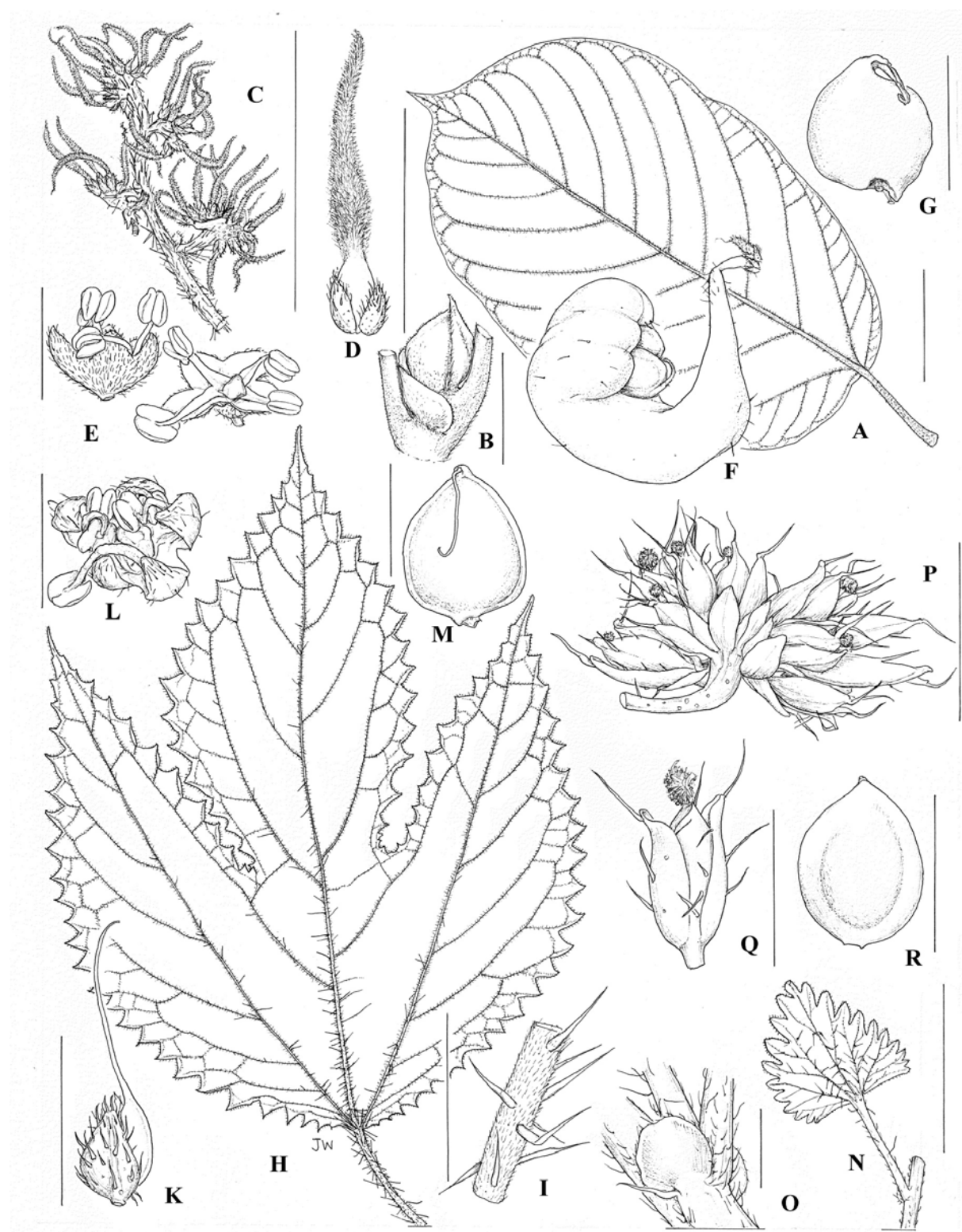


Figure 7. Myriocarpeae.

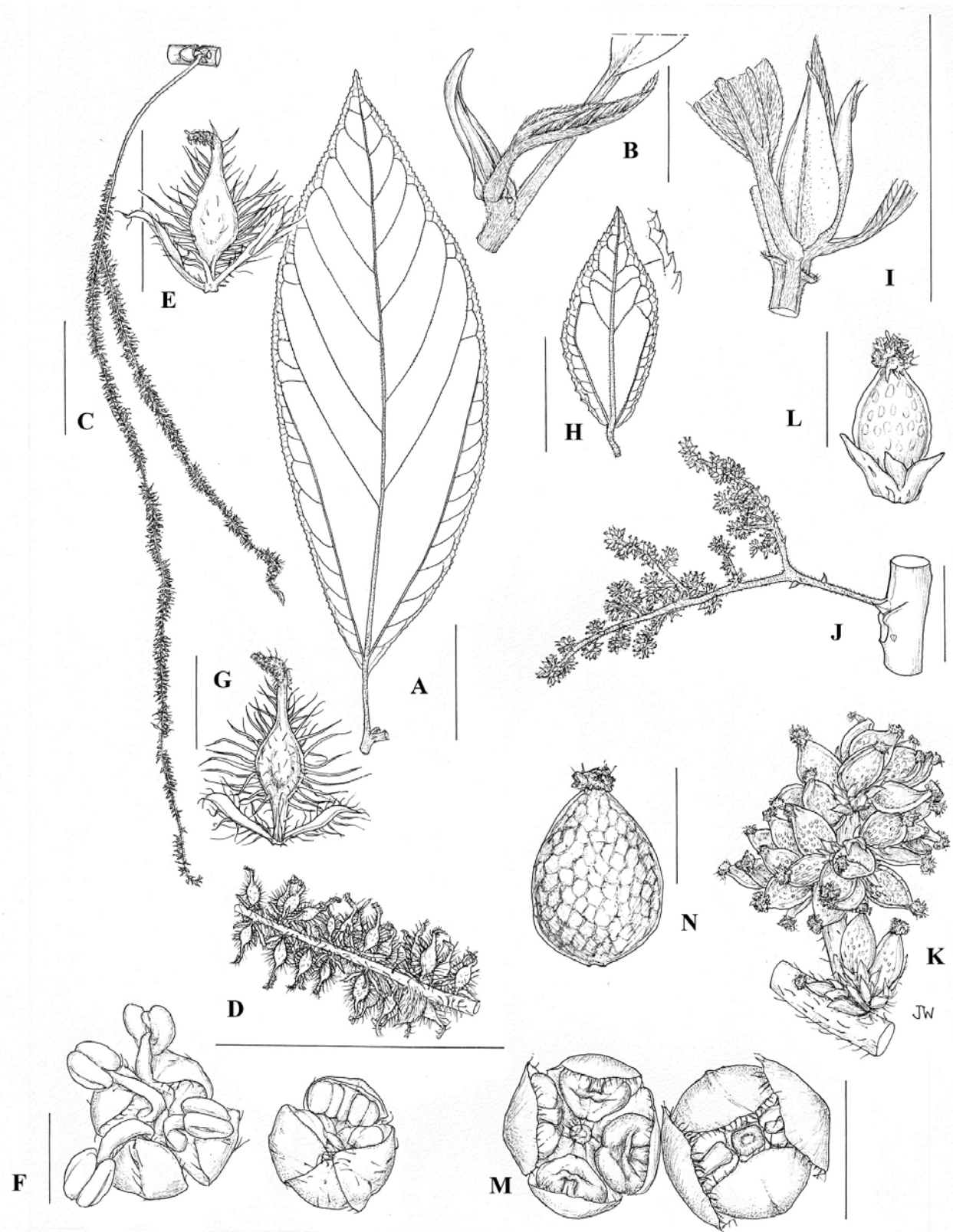


Figure 8. Elatostemateae.

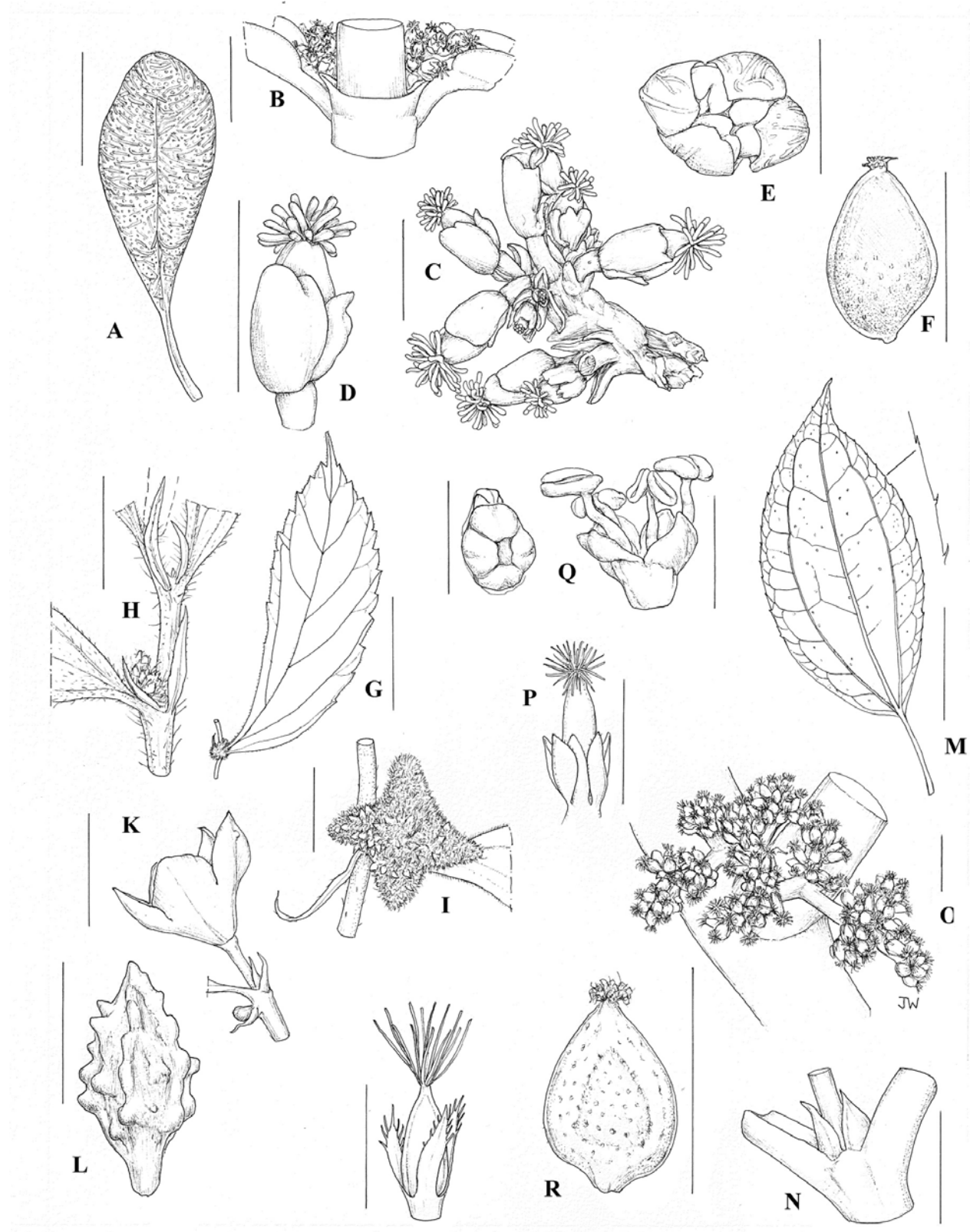


Figure 9. Parietarieae

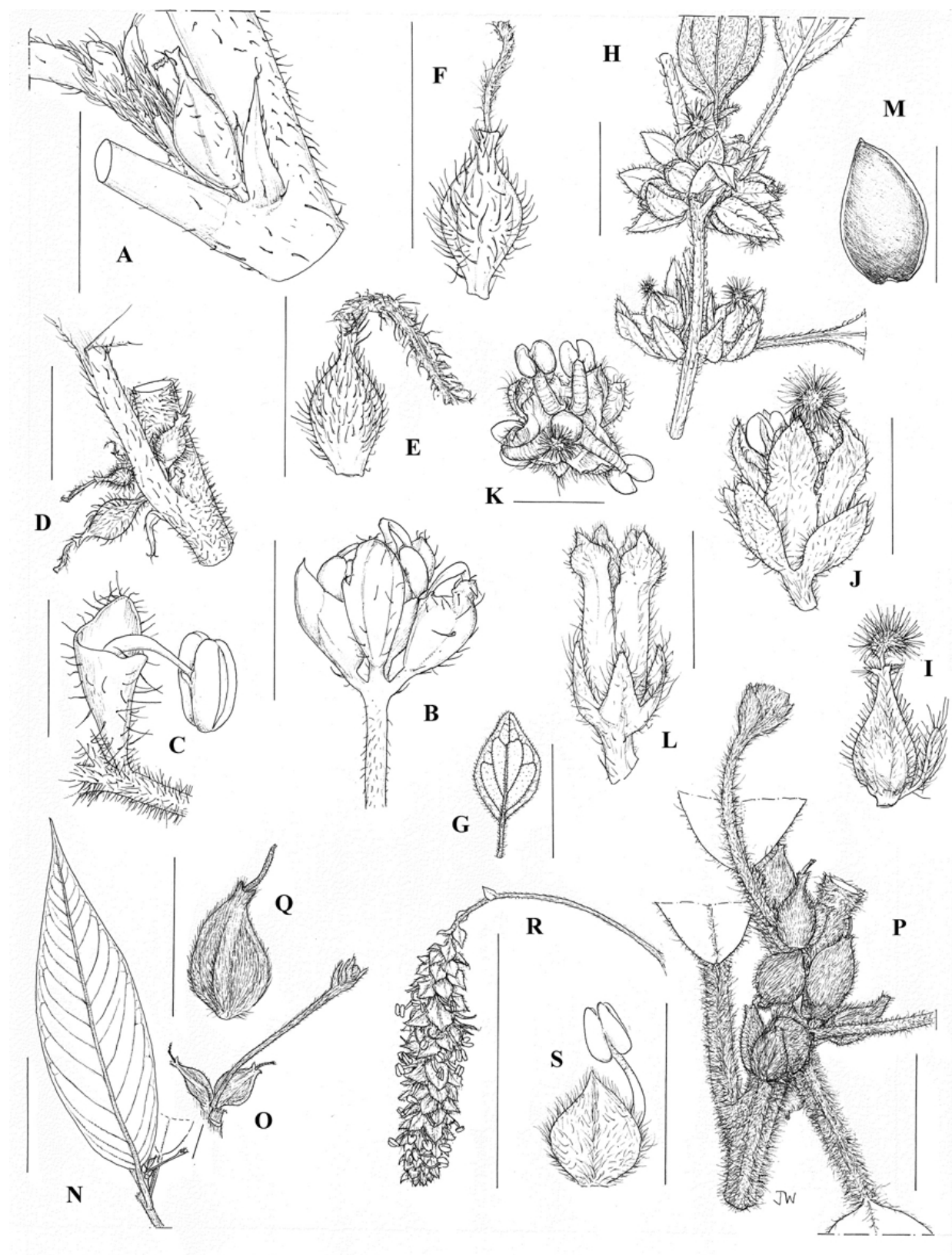


Figure 10. Boehmerieae

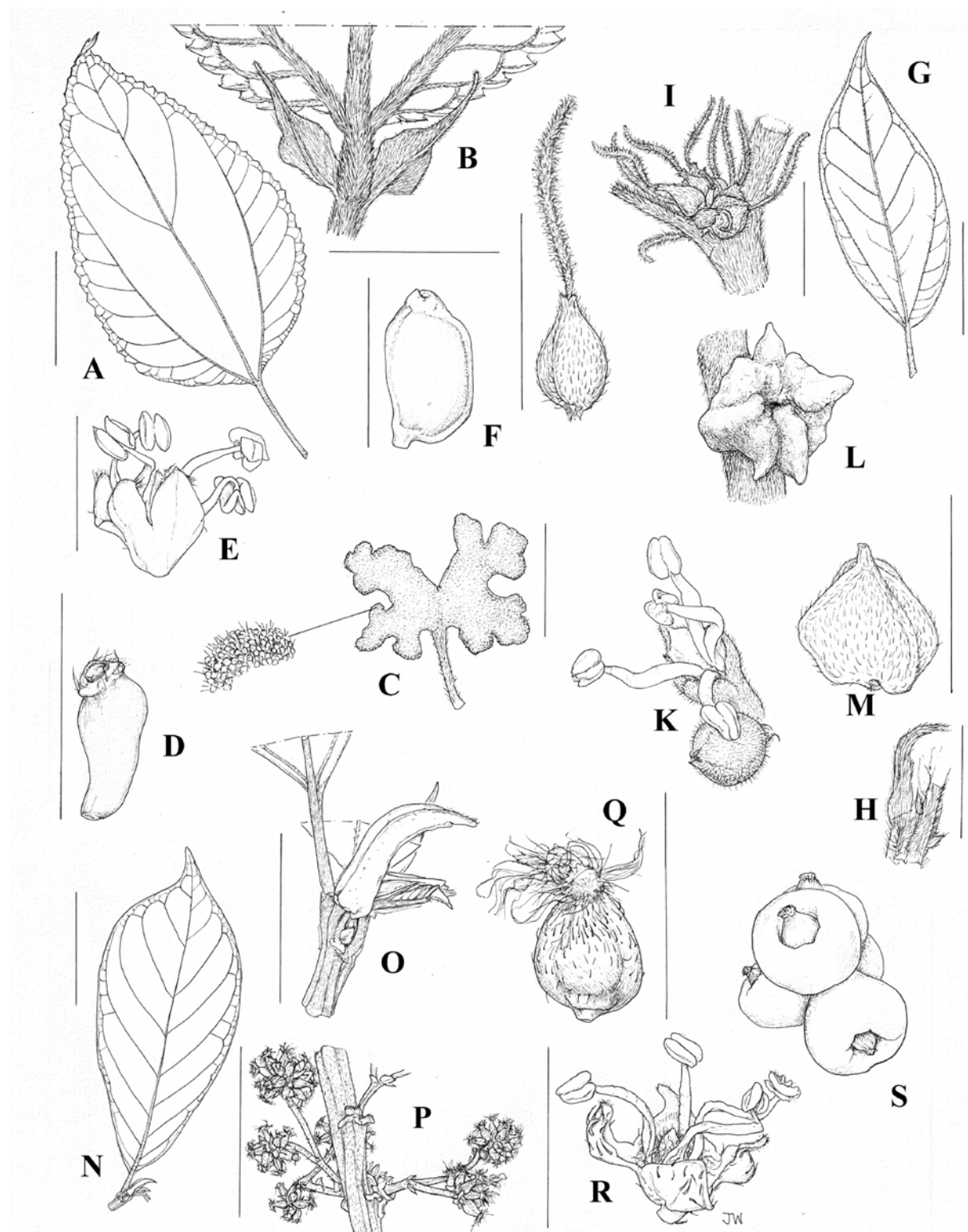


Figure 11. Leukosykeae.

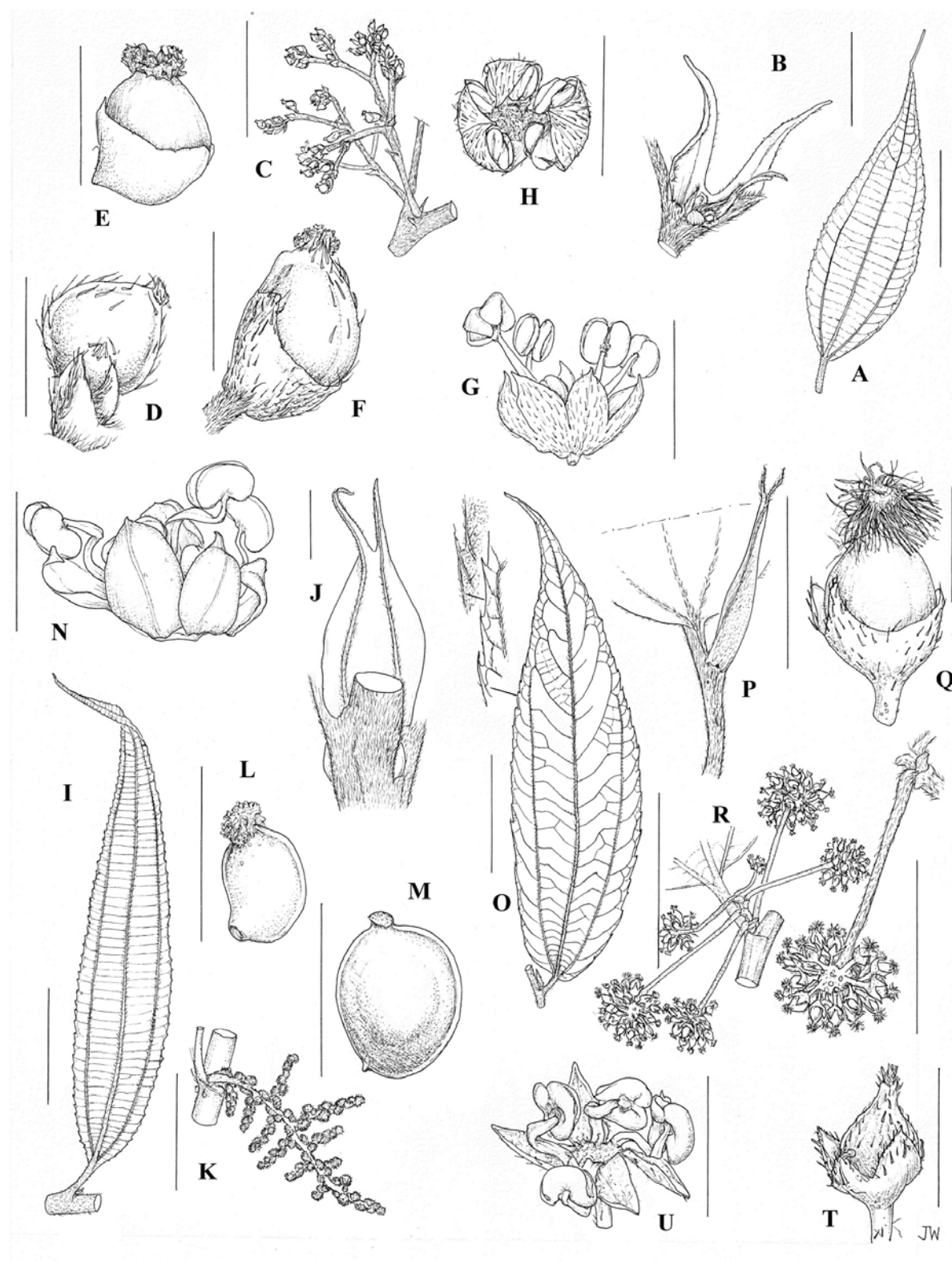


Figure 12. Cecropieae.



Figure 13. *Pouzolziella australis*.

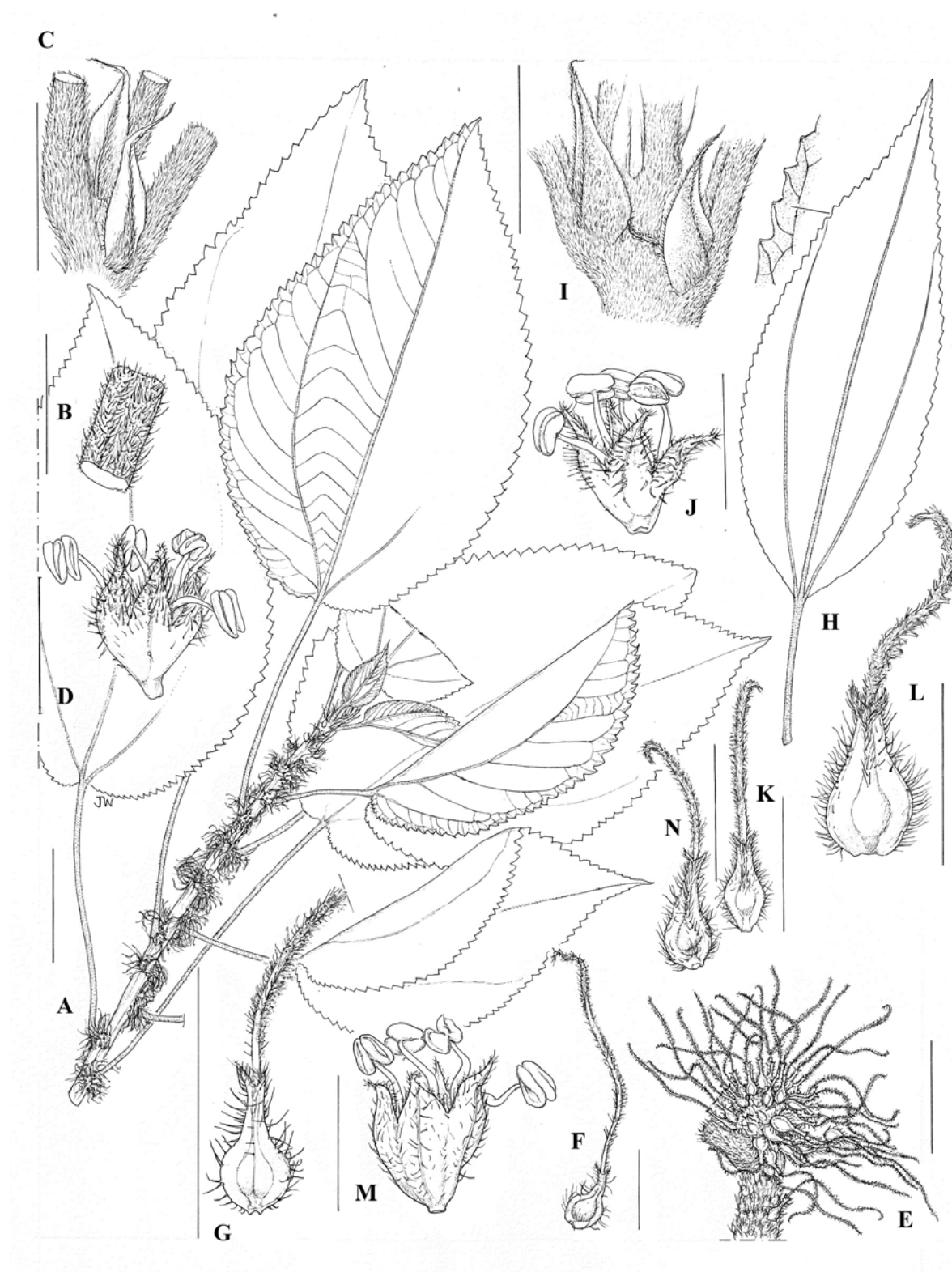


Figure 14. *Margarocarpus*.



Figure 15. *Leptocnide rubricaulis*



Figure 16. *Muimar*.

