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## Research Article

# Weda, a new genus with two new species of Euphorbiaceae-Crotonoideae from Halmahera (North Maluku, Indonesia) and phylogenetic relationships of the Australasian tribe Ricinocarpeae

Peter C. van Welzen<sup>1,2\*</sup> , Susana Arias Guerrero<sup>1</sup>, Deby Arifiani<sup>3</sup>, Tjut J.F. Bangun<sup>4</sup>, Roderick W. Bouman<sup>1,2,5</sup>, Marcel C.M. Eurlings<sup>1</sup>, Iska Gushilman<sup>6</sup>, Peter B. Phillipson<sup>7,8</sup>, Iris Tabak<sup>1</sup>, Esmée Winkel<sup>1</sup>, and Kenneth J. Wurdack<sup>9</sup>

<sup>1</sup>Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA, Leiden, The Netherlands

<sup>2</sup>Institute of Biology Leiden, Leiden University, P.O. Box 9505, 2300 RA, Leiden, The Netherlands

<sup>3</sup>Herbarium Bogoriense, Botany Division, Research Center for Biology, Indonesian Institute of Sciences, Cibinong, Bogor, Indonesia

<sup>4</sup>North Gorua Village, RT 006/RW 03, North Tobelo District, North Halmahera, North Maluku, Indonesia

<sup>5</sup>Hortus botanicus, Leiden University, 2311 GJ, Leiden, The Netherlands

<sup>6</sup>Bumi Mekar Wangi Residence, Blok C6 No. 12, RT 04/RW 05, Tanah Sereal, Bogor 16168, Indonesia

<sup>7</sup>Missouri Botanical Garden, St. Louis, MO 63110, USA

<sup>8</sup>Institut de Systématique, Évolution, et Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, École Pratique des Hautes Études, Université des Antilles, C.P. 39, 57 rue Cuvier, Paris 75005, France

<sup>9</sup>Department of Botany, MRC-166, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

\*Author for correspondence. E-mail: peter.vanwelzen@naturalis.nl

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**Abstract** During the environmental impact study for a proposed nickel mine near Weda Bay on Halmahera in North Moluccas (Maluku Utara Province), Indonesia, two unknown Euphorbiaceae were discovered. Morphological comparisons and molecular phylogenetic analyses using four markers (plastid *trnL-F* and *rbcl*, and nuclear ribosomal internal transcribed spacer and external transcribed spacer) indicated that they should be recognized as constituting a new, distinct genus of two species, which are described and illustrated here as *Weda fragarioides* and *Weda lutea*. The new taxa are members of the Australasian tribe Ricinocarpeae in subfamily Crotonoideae, and they are most closely related to *Alphandia*. In contrast with the otherwise mostly sclerophyllous Ricinocarpeae, *Weda* possesses stellate to dendritic hairs, large, long-petiolate, glandular leaves, and inflorescences with a pair of large, leafy, subopposite bracts. The two narrowly distributed species are distinguished from each other by vegetative and floral features, molecular data, and elevational preferences. Leaf elemental analysis of *Weda* indicated manganese, but not nickel, accumulation. Newly resolved generic relationships and potential morphological synapomorphies within Crotonoideae are discussed, and the circumscription of Ricinocarpeae is expanded from 7 to 11 genera.

**Key words:** Crotonoideae, elemental analysis, Euphorbiaceae, Malesia, molecular phylogenetics, Ricinocarpeae.

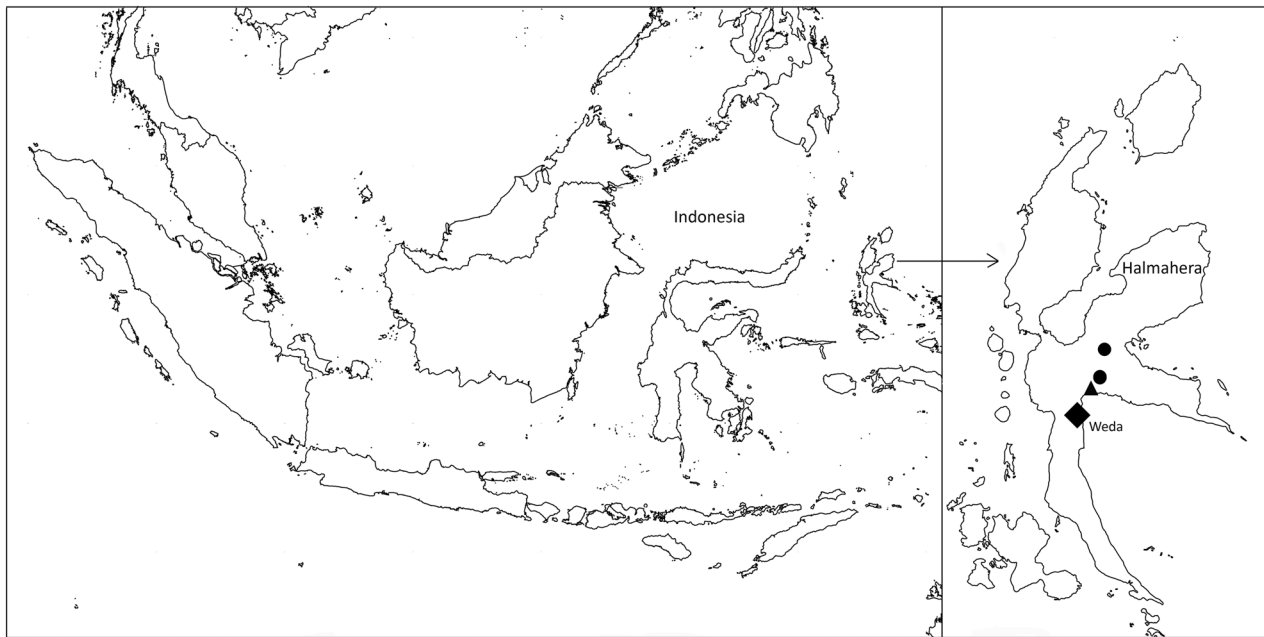
## 1 Introduction

The exploration of remote and ecologically or edaphically unusual environments often yields significant taxonomic novelties, and this pattern is evident in Euphorbiaceae with several genera recently described (i.e., *Gradyana*, Athiê-Souza et al., 2015; *Karima*, Cheek et al., 2016; *Tsaiodendron*, Zhou et al., 2017; *Incadendron*, Wurdack & Farfan-Rios, 2017). The Malay Archipelago (Malesia) with its many islands and

intense tectonic activity (including earthquakes and volcanism) is ecologically diverse and contains a high number of endemic species (van Welzen et al., 2005). Many of these islands are still undercollected and their floras poorly known, including the Moluccas in Indonesia (Fig. 1). Of the 804 gymnosperm and angiosperm species recorded for the Moluccas (from a total of 6616 indigenous Malesian taxa published in Flora Malesiana series 1; van Steenis and others, 1950 and later; see van Welzen et al., 2005), 71 are

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**Fig. 1.** Map of Indonesia, with inset showing the island of Halmahera and the distribution of *Weda*. *Weda*, the district capital of Central Halmahera (diamond), *Weda fragarioides* (dots, with lower dot covering two collections, including the type), and *W. lutea* (triangle, which covers three collections) are indicated.

endemic. A review of the checklists of the Malesian Euphorbiaceae (Airy Shaw, 1982; van Welzen, 2017) shows that 8 of the 81 recorded Moluccan species (in 26 genera) are endemic. The Moluccas are often treated as a monolithic biogeographic unit (i.e., same climate), but recently it was shown that the very different tectonic origins of North and South Moluccas warrant the recognition of two biogeographic provinces (Rutgrink et al., 2018).

Halmahera is the largest island in North Moluccas (Maluku Utara; Fig. 1), and it harbors economically important ores rich in nickel and cobalt. The mining company PT Weda Bay Nickel (PT = Perseroan Terbatas, and it refers in Indonesian to a limited liability company) plans to mine in Halmahera, one of the largest undeveloped nickel deposits in the world, with potential for extraction of 9 million tons nickel. Ultramafic soils, associated with such deposits, are known to harbor higher levels of plant endemism and diverse metal hyperaccumulators (e.g., Cuba, New Caledonia; Reeves et al., 1996; Jaffré et al., 2013). As a part of the procedure to procure mining permissions, an environmental impact study was needed, of which one aspect was a botanical inventory that was conducted under the guidance of the Missouri Botanical Garden. The mine site and neighboring areas in Halmahera were inventoried and the collected specimens were distributed to the herbaria of BO (Herbarium Bogoriense), L (Naturalis Biodiversity Center), and MO (Missouri Botanical Garden), whereas staff of BO and L provided most of the identifications, with further expert identifications obtained as needed. During identification at L, from the set of three separate collections from the vicinity of Weda Bay in the southeastern coast of Halmahera (Fig. 1), unknown Euphorbiaceae appeared with the following characteristics: large, adaxial, basal glands on the leaf blades and fruits with a columella, which had apical remnants of a single ovule/seed per locule. The “*Macaranga*” specimen, referred to by Lopez et al. (2019b, 2019c), and other

three specimens originally identified as “*Pangium edule*” (Achariaceae) proved to be a second new species, overlapping in several distinctive characters. Morphological and molecular analyses have shown that this material from Weda Bay constitutes a new genus comprising two new species within Euphorbiaceae, subfamily Crotonoideae Pax, and they are described below. We provide a generic-level molecular phylogenetic perspective of the core Crotonoideae, which is the most comprehensive perspective to date, illuminating the interesting biogeography, as well as certain problems in existing tribal classification, especially related to tribe Ricinocarpeae Müll.Arg. We also investigated whether the new genus might be a nickel hyperaccumulator, given its presence in other Euphorbiaceae (e.g., *Leucocroton* Griseb.; Reeves et al., 1996) and in other Malpighiales worldwide, including species of Phyllanthaceae (Reeves et al., 1996; van der Ent et al., 2016, 2018; Bouman et al., 2018), Dichapetalaceae, Salicaceae, and Violaceae (van der Ent et al., 2015). For Halmahera, it was recently shown that one of these hyperaccumulators, a *Rinorea* sp. (Violaceae), was even capable of influencing the bacterial community around its roots (Lopez et al., 2019b).

## 2 Material and Methods

### 2.1 Micromorphology and elemental analysis for heavy metals

Scanning electron microscopy (SEM) of untreated herbarium fragments and unacetolyzed pollen was conducted with a Zeiss EVO MA15 (Carl Zeiss SMT, Inc., Peabody, Massachusetts, USA) SEM at 12 kV after sputter coating with 3 nm of C and 8 nm of Au/Pd using a Leica EM ACE600 (Leica Microsystems GmbH, Wetzlar, Germany). An Orbis MC Micro-XRF Analyzer (EDAX Inc., Mahwah, New Jersey, USA), 20 kV, 600  $\mu$ Amp, was

used to scan a dried leaf fragment of 1.28 by 1 cm (Gushilman et al. 777, L) for a non-destructive elemental analysis.

## 2.2 Molecular phylogenetic sampling

To infer broad relationships of the Weda Bay material, we generated orthologous sequences of plastid *rbcl* and *trnL-F* (*trnL* intron and the 3' intergenic spacer), and performed a preliminary analysis in the context of the full 179-tip Euphorbiaceae backbone phylogeny of Wurdack et al. (2005), which indicated nested placement in Crotonoideae. Our final taxon sampling of 102 tips (97 taxa) focused on Crotonoideae and included 47 of ca. 52 genera potentially belonging to clade C2, using sequence data from Wurdack et al. (2005), GenBank, and 149 newly generated sequences. A small outgroup sampling (seven taxa) represented the three other subfamily lineages without greatly increasing *trnL-F* alignment complexity. To improve resolution, especially for the Ricinocarpeae s.l. subclade with which the Weda Bay material grouped, we added nuclear ribosomal internal transcribed spacer (ITS) region and external transcribed spacer (ETS) region data. External transcribed spacer aims to resolve species-level relationships using recently designed primers that amplify multiple groups of Euphorbiaceae (Cardinal-McTeague et al., 2019; Wurdack, unpublished data). To reduce alignment problems with increasing sequence divergence, the ITS taxon sampling was limited to clades C1 and C2 (77 tips, 65 with data) and the ETS to Ricinocarpeae s.l. (28 tips, all with data plus two other clade C2 taxa). In addition, a fragment of plastid *matK* was sequenced for the Weda Bay material to produce DNA barcode reference data. Voucher information and GenBank numbers are provided in the Appendix I.

## 2.3 Molecular phylogenetic laboratory methods

Initial DNA extractions of the Weda Bay material were carried out at Leiden from small (ca. 1 cm<sup>2</sup>) pieces of herbarium specimen leaves, using a NucleoMag 96 Tissue kit (Macherey-Nagel GmbH & Co., Düren, Germany) following the manufacturer's protocol on a KingFisher Flex magnetic particle processor (Thermo Fisher Scientific, Waltham, Massachusetts, USA). The samples were ground frozen in a TissueLyser (Qiagen Benelux B.V., Venlo, The Netherlands) two times at 90 s with a frequency of 30 cycles/s. All other new sampling and resulting data, including extractions from duplicate Weda Bay material, used established workflows at the Smithsonian Institution (Wurdack et al., 2005; Dorr et al., 2018). For amplification of *trnL-F*, primers c + f for full length and combinations c + d, e + f, and/or *trnL-intF* + f for degraded templates were used (Taberlet et al., 1991; Wurdack et al., 2005). For amplification of *rbcl*, 1f + 1360r for full length and 1f + 724r and 628f + 1360r for degraded templates were used (Lledó et al., 1998). ITS was amplified using 5a + U4 for full length and the combinations 5a + U2 and P3 + 4 for degraded templates (Stanford et al., 2000; Cheng et al., 2016). ETS was amplified with F2 or F3 (5'-GTGTCGTCTCTCGGATGC-3') and 18s 5'R (Cardinal-McTeague et al., 2019), yielding ca 500 and 200 bp fragments, respectively. Only the shorter 200 bp fragment could be amplified from the Weda Bay material, which may reflect primer binding problems with F2. The barcode portion of *matK* was amplified using primers *matK-1R\_KIMf* + *matK-3F\_KIMr* (Dunning & Savolainen, 2010). Amplifications were conducted in a total volume

of 15–25 µL containing 1–20 ng template DNA, 1× PCR buffer, 100 µM of each dNTP, 0.5 µM of each primer, 1.0 µL of bovine serum albumin (10 mg/mL), and 0.2–0.5 µL of Phire Green Hot Start II DNA Polymerase (Thermo Fisher Scientific) or Biolase™ DNA polymerase (Bioline USA, Taunton, Massachusetts, USA). Amplification conditions included an initial denaturation/activation of 60 s at 98 °C, followed by 35–40 cycles of 10 s denaturation at 98 °C, 10 s annealing at 50 °C (55 °C for ITS and ETS), and 45 s extension at 72 °C, followed by a final 5 min extension at 72 °C. Bi-directional fluorescent Sanger sequencing with the noted primers and BigDye® Terminator v3.1 chemistry (Thermo Fisher Scientific) was performed on ABI 3730xl DNA Analyzers (Thermo Fisher Scientific), and sequences were edited in Geneious ver.8.1.9 (<http://www.geneious.com>, Kearse et al., 2012) or Sequencher ver.5.2 (Gene Codes, Ann Arbor, Michigan, USA).

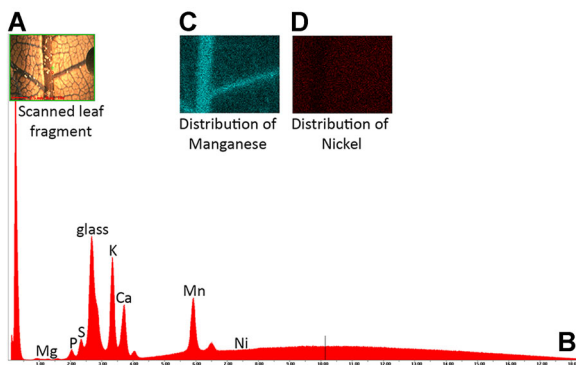
## 2.4 Phylogenetic analyses

For initial analysis, *trnL-F* sequences of the Weda Bay material were inserted into the 179-tip multiple sequence alignment (MSA) of Wurdack et al. (2005) using Mesquite ver.3.4 (Maddison & Maddison, 2018), and global Bayesian inference (BI) was conducted with MrBayes ver.3.2.6 (Ronquist et al., 2012) on the CIPRES gateway (<https://www.phylo.org/>) using standard options (most complicated model, nst = 6, rates = invgamma) and sampling every 1000 generations over 20 000 000 generations. Convergence was assessed with Tracer ver.1.6.0 (Rambaut et al., 2013) for effective sample sizes (ESS) >200, a 20% burn-in implemented, and the maximum clade credibility (MCC) tree (LogCombiner and TreeAnnotator in Beast package; Drummond et al., 2012) viewed with FigTree ver.1.4.2 (Rambaut, 2014). For the final 102-tip matrix, the sampling of Wurdack et al. (2005) was reduced to 66 tips, the *trnL-F* alignment then collapsed empty columns, and the additional data were manually inserted under similarity criteria using Se-AL ver.2.0a11 (Rambaut, 1996–2002). As noted in the study of Wurdack et al. (2005), the *trnL-F* alignment is complex with a mix of discrete indels and hypervariable regions of ambiguous alignment. For ITS and ETS, the MSAs were generated under the Q-INS-i refinement method of MAFFT ver.7.452 (Katoh & Standley, 2013) and then adjusted by eye using Se-AL, similarity criteria, and limiting matrix fragmentation. The ITS and ETS MSAs are relatively compact with mostly 1–3 bp indels. For ITS, the MSA is relatively homogeneous within clades C1 and C2, but it was challenging to align clades with each other; for ETS, the MSA was relatively homogeneous as the taxon sampling included only two tips (*Aleurites*, *Tapoides*) outside of Ricinocarpeae s.l. To examine the impact of ambiguously aligned regions, sensitivity analyses included three masking sets: (i) all data (aligned length 4354 bp and 38.3% total missing data), (ii) a strict set excluding 814 bp, which removed positions with >50% missing data (aligned length 3540 bp and 26.0% total missing data), and (iii) relaxed set excluding 567 bp (aligned length 3787 bp and total 30.6% missing data), which removed *trnL-F* hotspots and overlapping indels (a subset of the 814 bp strict set). All three masking set analyses yielded similar topologies and support values (differing <5%), and the relaxed set (567 bp excluded) was selected for final analyses. To examine the impact of model selection and ML program on results, the 567-matrix was run on PhyML ver.3.0 with Smart Model Selection ver.1.8.1 (GTR + I + G selected; Guindon

et al., 2010; Lefort et al., 2017) and IQ-TREE (567-matrix partitioned by marker; Trifinopoulos et al., 2016). For final trees, the Bayesian MCMC analyses were implemented in MrBayes with two concurrent runs, each with four chains and sampling every 1000 generations over 50 000 000 generations, a 0.2 temperature coefficient, and a conservative 20% burn-in implemented. The final maximum likelihood (ML) analysis was performed with RAxML ver.8.2.12 (Stamatakis, 2014), as implemented on CIPRES XSEDE under GTR + I + G and clade support estimated by 1000 rapid bootstrap (ML-BS) replicates. Each marker was also analyzed separately with ML to determine any strongly supported topological differences that could indicate incongruence. A reduced 30-tip data set (all 28 Ricinocarpeae and rooted with *Aleurites* + *Tapoides*) with no exclusion sets (aligned length 3817 bp and 22.0% total missing data) was analyzed with RAxML as before to test the impact of reduced missing data (especially for ETS), fewer ambiguous regions, and greater computational thoroughness on clade resolution. The final 102-tip MSA with masking details is available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.nvxok6dnw> or <https://datadryad.org>).

### 3 Results

The elemental analysis to assess whether the first Weda Bay species might be a nickel hyperaccumulator showed no increased values (Fig. 2). The nickel present at low concentrations appeared to be evenly distributed, though less so above the major veins, which is consistent with the spread of this metal, as part of water-soluble salts, through the leaf due to evaporation (Antony van der Ent, pers. comm.). However, the leaf had manganese accumulation, especially along the midrib and major veins (Fig. 2). These findings are corroborated by Lopez et al. (2019b, 2019c) for the second species (referred to as “*Macaranga* sp.” in their papers), which accumulates some nickel but mainly manganese.

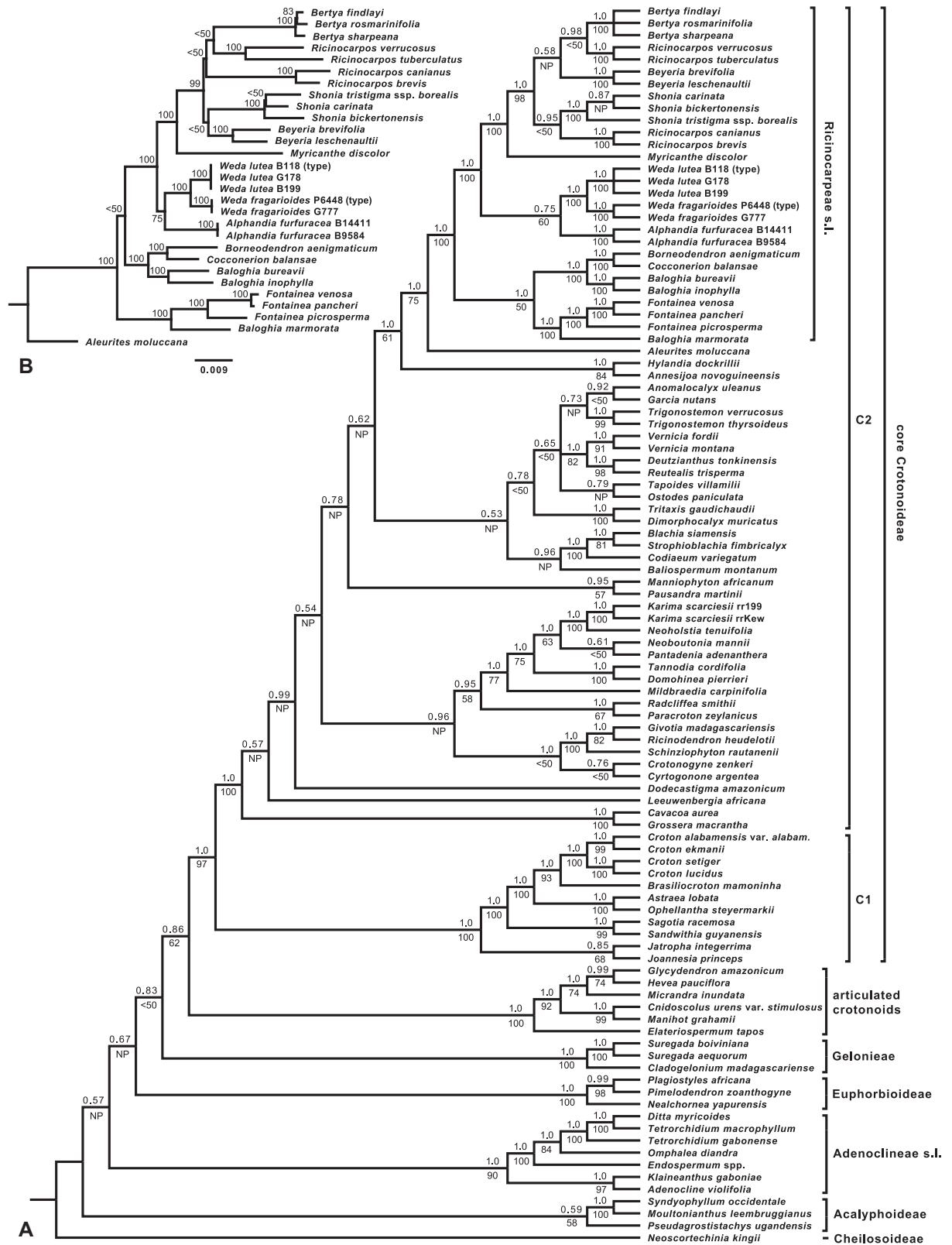


**Fig. 2.** Elemental analysis of *Weda fragarioides* leaf fragment. Sample analyzed (A); white dots are stellate hairs. Spectrum (B) showing high amounts of manganese (Mn) and low amounts of nickel (Ni); the second highest peak is caused by the glass holder of the sample. Elemental maps with manganese (C) concentrated above the midrib and secondary veins (lighter regions), whereas nickel (D) is spread at low concentration throughout the leaf.

Search results of the *matK* and *trnL-F* sequences of the Weda Bay material against GenBank and/or BOLD using BLAST showed best matches with members of tribe Ricinocarpeae. In the 179-tip Euphorbiaceae-wide, 2-marker MCC tree (not shown, but compatible with fig. 4 in Wurdack et al., 2005), the Weda Bay material was recovered as a strongly supported (posterior probability, PP 1.0) sister group to *Ricinocarpos*. In our 102-tip, 4-marker analyses, the major lineages of Euphorbiaceae that represent potential subfamily clades were poorly resolved along the spine of the tree and Crotonoideae was not supported as monophyletic (Fig. 3A). The core Crotonoideae (excluding the articulated crotonoids, Gelonieae, and Adenoclineae s.l.) are strongly supported (PP 1.0, bootstrap percentage, BP 97) and comprise two strongly supported (PP 1.0, BP 100) sister clades C1 and C2 (sensu Wurdack et al., 2005); however, C2 has especially poor backbone resolution with none of its four constituent tribes resolved as monophyletic. The Weda Bay material was strongly supported (PP 1.0, BP 100) as a member of Ricinocarpeae s.l. and as a weakly supported sister group to *Alphandia* Baill. (PP 0.75, BP 60). Although resolution among the genera within Ricinocarpeae s.l. was poor, only *Ricinocarpos* and *Baloghia* were not recovered as monophyletic. The Bayesian and ML analyses were largely congruent with a handful of unsupported (BS <50) topological differences. The Ricinocarpeae s.l. resolution was similar between the 102- and 30-taxon RAxML analyses, with slightly better support for the Weda Bay material + *Alphandia* (BP 75) and a shift in the poorly supported node relating to the two *Baloghia* subclades (see Fig. 3B). There were no topological differences, with BP >70, among analyses of each individual marker or in partial combination as plastid versus ribosomal (see Figs. S1, S2). However, the ribosomal markers did have weakly supported differences in the deepest nodes of Ricinocarpeae s.l., and in particular *Alphandia* and the Weda Bay material had a nested rather than sister relationship (Fig. S2). Our alternative analyses (i.e., differing exclusion sets, IQ-TREE, PhyML, partitioning schemes) showed a little impact of analysis details on topology or support values. The multiple accessions of each Weda Bay taxon have identical sequences for each marker within a species. Variation between species includes 3 differences (1 poly-A indel and 2 substitutions, all in the *trnL* intron) for *trnL-F*, no differences for *rbcL*, 13 differences (11 substitutions and 2 polymorphic sites) for ITS, and 9 differences (8 substitutions and 1 tandem duplication) for ETS.

### 4 Discussion

The subfamily circumscription and the complex tribal and subtribal classification of Crotonoideae need considerable revision in light of the emerging molecular phylogenetic results to date (e.g., Wurdack et al., 2005). Moreover, some generic circumscriptions (i.e., *Ricinodendron* Müll.Arg., *Vernicia* Lour.) differ between recent classifications, with Radcliffe-Smith (2001) recognizing segregate genera not accepted by Webster (2014). Clade C2 of Crotonoideae with inaperturate pollen presently includes 45–52 (varying according to circumscriptions) mostly Old World genera grouped into the non-monophyletic tribes Codiaeae (Pax) Hutch., Ricinocarpeae, Ricinodendreae (Pax) Hutch., and Aleuritidae Hurus. Relatively few molecular phylogenetic studies have



**Fig. 3.** Phylogenetic relationships of *Weda* and Ricinocarpeae s.l. **A**, Bayesian maximum clade credibility tree based on the combined 102-tip, 4-marker data set with posterior probabilities, and ML bootstrap values  $>0.5/50\%$  are indicated above and below branches, respectively. NP = not present in ML analysis. **B**, Phylogram from RAxML analysis of 20-tip, 4-marker data set (*Tapoides* root trimmed); bootstrap values  $>50\%$  are indicated.

sampled within clade C2 (i.e., Wurdack et al., 2005; Tokuoka, 2007; Cheek et al., 2016; Yu et al., 2019). Although our clade C2 taxon sampling is the most comprehensive to date (48 genera, including 10 new to GenBank, but missing *Benoistia* H.Perrier & Leandri, *Loerzingia* Airy Shaw [= *Deutzianthus* Gagnep. fide Webster, 2014], *Oligoceras* Gagnep., and *Parapantadenia* Capuron [= *Pantadenia* fide Webster, 2014]), resolution remains poor, which would benefit from a phylogenomic approach. Among new insights are that *Vernicia* would be paraphyletic if reunited with *Reutealis* Airy Shaw, as was proposed by Webster (2014), unless *Deutzianthus* (with perhaps *Loerzingia* included as synonym) was not also reduced. The relationship between *Annesijoa* Pax & K.Hoffm. and *Hylandia* Airy Shaw is surprising (PP 1.0, BP 84; strong support with ITS alone but also emergent with the plastid markers), given their numerous morphological differences. *Annesijoa* has usually been affiliated with other compound-leaved taxa (i.e., *Joannesia* Vell., *Leeuwenbergia* Letouzey & Hallé, *Ricinodendron* Müll.Arg.), and *Hylandia* affiliated with *Baloghia* Endl. and *Fontainea* Heckel (Radcliffe-Smith, 2001; Webster, 2014). *Hylandia* and *Fontainea* share drupaceous fruits, which are structurally very different (see Rozefelds et al., 2017).

Ricinocarpeae s.l., the focus of this study due to its relevance for placing the Weda Bay material, is the largest supported C2 subclade in our analyses and for which we propose a new tribal circumscription (Fig. 3A) that is expanded from the seven genera of Webster (2014). In our sensu lato circumscription, the tribe contains a distinct Australasian group of nearly 100 species in 11 genera (all 11 sampled), which include the Weda Bay genus (described below) and members of Ricinocarpeae s.s. (*Bertya* Planch., *Beyeria* Miq., *Borneodendron* Airy Shaw, *Cocconerion* Baill., *Myricanthe* Airy Shaw, *Ricinocarpos* Desf., *Shonia* R.J.F.Hend. & Halford), and Codiaeeae subtribe Baloghinae G.L.Webster (*Alphandia*, *Baloghia*, *Fontainea*, but not *Hylandia*). *Dimorphocalyx* Thwaites, which was closely associated with *Fontainea* by Radcliffe-Smith (2001), is excluded from Ricinocarpeae s.l. We have refrained from revising the subtribal taxonomy due to low support at the deepest nodes. However, the Weda Bay taxa can be accommodated in subtribe Bertyinae Müll.Arg. Members of the tribe, and they present the following characteristics: even though morphologically diverse, frequently (but see exceptions below) share monoecy (rarely dioecious), reddish latex, stipules absent (rarely present), indumentum stellate (rarely simple or dendritic), inflorescences terminal (sometimes axillary or pseudoterminal), pistillate flowers with well-developed petals (rarely absent), stamens numerous (mostly 20–100), filaments often partly connate, anthers extrorse, and seeds carunculate (or fruit drupaceous). These features in combination distinguish Ricinocarpeae s.l. from other clade C2 taxa, and stipules appear especially diagnostic. Genera of clade C2 possess stipules except for *Codiaeum* Rumph. ex A.Juss., *Garcia* Vahl. and nearly all Ricinocarpeae s.l. (except *Borneodendron*), which are exstipulate. *Oligoceras*, known only from the type collection of flowering branches, is described as exstipulate (Radcliffe-Smith, 2001; Webster, 2014) but needs further study to rule out small, caducous stipules. The apical bud in *Borneodendron* is covered by a caducous, circum-axillary sheath, associated

with the youngest verticillate whorl of three leaves, enclosing suppressed axillary buds (each apparently covered in tiny bud scales) and the younger leaf primordia (SAN 109845, L, US). This sheath has been interpreted as united interpetiolar stipules with similarities to *Baloghia inophylla* (G.Forst.) P.S.Green (Airy Shaw, 1963; van Welzen, 2012). *Baloghia* is usually described as exstipulate (Radcliffe-Smith, 2001; Webster, 2014), but some species bear structures that have been described as stipules (Baillon, 1858; Pax & Hoffmann, 1911) or caducous bud scales (“perulae pseudostipuliform, soon deciduous,” fide Radcliffe-Smith, 2001). *Baloghia* spp. have a range of shoot apex morphologies, from clearly naked with no appendages in the New Caledonian taxa (e.g., *B. alternifolia* Baill., *Baummann* 15305, US; *B. drimiflora* (Baill.) Schltr., *Bernardi* 12534, US; *B. pulchella* Schltr. ex Pax, *Franc* 2486, US) to variously sheathed. In *B. inophylla* (Johnson & Constable 52338, US), there are two decussate pairs of valvate axillary appendages enclosing a single pair of opposite leaves and leaving annular scars. The appendage pairs are dimorphic and perhaps not homologous, with the proximal pair (bud scales) scale-like and containing axillary buds, and the much larger distal pair (stipules), with hirsute margins and lacking axillary buds. In Australian *Baloghia marmorata* C.T.White, a cluster of 6–8+ imbricate scales with axillary buds, encloses a seasonal flush of otherwise naked leafy nodes (4–6 alternate to sub-opposite leaves), leaving annular scars (White 3588, US). In Australian *Baloghia parviflora* C.T.White, which otherwise vegetatively resembles *B. marmorata*, there are no imbricate scales (*McPherson* 6670, MO). The nature of stipules has been debated by morphologists; stipule axils are not expected to contain axillary buds (see Rutishauser & Sattler, 1986). However, other apical interpetiolar appendages containing axillary buds, similar to *Borneodendron*, are described as stipules (e.g., Rhizophoraceae; Gill & Tomlinson, 1969). *Cocconerion* spp., the strongly supported sister group to *Borneodendron*, possess verticillate whorls, densely packed with 6–10 leaves per node, which before leaf expansion form a tight stockade of abaxial midribs (vernation is involute, with blade rolls inside the bud), protecting the shoot apex without additional appendages (i.e., exstipulate).

Details of the intergeneric relationships recovered within Ricinocarpeae s.l. differ from the more sparsely sampled study of Tokuoka (2007). Webster (2014) excluded *Alphandia* from his Ricinocarpeae and classified it as an aberrant member of tribe Codiaeeae. The pollen evidence used to justify this exclusion is less compelling than morphology, which unites them, and our results also support the inclusion of *Alphandia* within Ricinocarpeae, as circumscribed by Radcliffe-Smith (2001). *Baloghia* (3 of 15 species sampled) is clearly not monophyletic as Australian endemic *B. marmorata* groups with *Fontainea* (PP 1.0, BP 100). *Baloghia* has typical explosively dehiscent capsular fruit versus *Fontainea* with drupes. The fruiting voucher for *B. marmorata*, from which the leaf sample was directly obtained, appears to be correctly identified and has the characteristic dehiscent fruits of that species. The sclerophyllous Australian genera (i.e., *Bertya*, *Beyeria*, *Ricinocarpos*, *Shonia*) of Ricinocarpeae s.l. present many overlapping morphological characters (see table 1 in Halford & Henderson, 2005). Our results, though limited in power due to sparse species sampling

and relatively poor resolution, suggest that the generic circumscriptions need further study. *Shonia* (three of four species sampled here) was described to accommodate taxa formerly in *Beyeria* that were considered morphological intermediates between *Beyeria* and *Ricinocarpos* (Halford & Henderson, 2005). They form a strongly supported clade (PP 1.0, BP 100), but the continued recognition of *Shonia* as a distinct genus will depend on relationships among the related sclerophyllous genera. *Borneodendron*, *Cocconerion*, and *Myricanthe* clearly fall within *Ricinocarpeae* s.l. and have no relationships with *Picrodendraceae* (formerly *Euphorbiaceae*, subfamily *Oldfieldioideae*), as had been suggested by Airy Shaw (1971, 1980) and Radcliffe-Smith (2001), based on some morphological similarities and biogeography. This hypothesis had discounted the major differences in ovule number and palynology between *Picrodendraceae* (two ovules per locule; pollen echinate) and *Euphorbiaceae* (one ovule per locule; pollen not echinate except in *Cheilosoidae*). The close relationship between *Borneodendron* and *Cocconerion* is well supported by morphology including the unusual shared features of whorled leaves and hairy anthers (Airy Shaw, 1971).

The *Ricinocarpeae* s.l. genera are discussed below, highlighting major morphological differences from and similarities to the new genus established for the Weda Bay material.

*Alphandia* (three species, New Guinea, New Caledonia, Vanuatu). Differences: sticky latex; inflorescences terminal or subterminal, racemosely thyrsoid; disc glands/ring present; inner filaments united; anthers geniculate; seeds carunculate. Similarities: two leaf glands, long petioles (2–6 cm; to 1/2 length of blade).

*Baloghia* (15 species, Australasian, including 12 in New Caledonia). Differences: sometimes dioecious; indument simple (or glabrous), leaves sometimes opposite, mostly sessile to shortly petiolate (to 5 cm in *B. parviflora*; 1/3 length of blade); inflorescences terminal (rarely lateral), racemose or narrowly paniculate, uni- or bi-sexual; flowers large; filaments connate, thick. Similarities: disc sometimes absent in staminate flowers, always absent in pistillate flowers; caruncle absent or minute.

*Bertya* (28 species, Australia). Differences: often resinous; leaves sometimes opposite, sessile to shortly petiolate; lacking glands; inflorescences of paired, solitary, or clustered flowers; calyx petaloid; petals absent; filaments united into column; pistillate sepals sometimes accrescent; stigmas entire to seven-fid; fruit one-locular by abortion; seeds carunculate. Similarities: inflorescences axillary; disc absent; filaments short.

*Beyeria* (24 species, Australia). Differences: resinous; leaves sessile to shortly petiolate; flowers fascicled or solitary; petals smaller than sepals or absent; disc glands usually present; stigma lobed/peltate; seeds carunculate. Similarities: inflorescences axillary; filaments very short and free; staminate receptacle hemispherical.

*Borneodendron* Airy Shaw (monotypic, north Borneo). Differences: stipules present (united, caducous); leaves verticillate in groups of three; inflorescences terminal, staminate racemose, three flowers per node; calyx three-lobed; petals absent; stamens united in column; anthers hairy; ovary two-locular; seeds carunculate. Sim-

ilarities: two or more leaf glands, large, petiolate leaves (to 2.5 cm; 15% length of blade); bracts conspicuous (but not as large as basal ones in the Weda Bay material); disc absent; filaments very short.

*Cocconerion* (two species, New Caledonia). Differences: latex distinct; leaves verticillate in groups of 6–10, subsessile, lacking glands; flowers solitary or in fascicles; petals absent; filaments united in column; anthers hairy; seeds carunculate. Similarities: inflorescences axillary; disc absent; filaments short.

*Fontainea* (six species, of which one widespread, rest in Australia). Differences: dioecious; hairs simple; leaves mostly relatively short-petiolate (to 4.5 cm; 20% length of blade); petals densely hairy; disc present; filaments connate; fruits drupaceous. Similarities: basilar glands often present; inflorescences axillary (or terminal), cymose.

*Myricanthe* Airy Shaw (one species, New Caledonia). Differences: leaves opposite, lacking glands; shortly petiolate (0.5–1.5 cm; to 20% length of blade); inflorescences terminal, racemose; calyx three-lobed (lobes split variously); petals absent; filaments united in column; stigmas 10-palmatifid; seeds carunculate. Similarities: disc absent; filaments short.

*Ricinocarpos* (28 species, Australia). Differences: leaves sessile to shortly petiolate, lacking glands; inflorescences terminal or pseudo-axillary, flowers usually in fascicles or solitary; disc present; filaments usually connate, anthers reflexed; fruits often not smooth; seeds carunculate.

*Shonia* (four species, Australia). Like *Beyeria*, but petals longer than sepals; inflorescences terminal or axillary, racemose; disc present (unlike Halmahera material).

Most *Ricinocarpeae* s.l. and the Weda Bay material agree in the absence of stipules (see above for comments on *Borneodendron*) and the presence of stellate hairs (but also dendritic in the new genus). Unlike the Weda Bay material, the Australian and New Caledonian taxa are mostly reduced variously and are sclerophyllous, with leaf blades lacking the basal glands, being sessile to shortly petiolate, and being very narrow and small. The other taxa sampled across clade C2 all differ from the Weda Bay material in their very different inflorescences, and most of them possess stipules and/or a floral disc. Neotropical *Garcia* has no stipules and an ill-defined disc, but it only has simple hairs and completely different inflorescences with terminal clusters of large flowers.

Within the mainly Australian/New Caledonian *Ricinocarpeae* s.l., *Borneodendron* (N Borneo) and the Weda Bay genus are the biogeographic outliers. The presence of the latter in North Moluccas is likely the result of plate tectonic movements. Halmahera consisted of an eastern and a western half for a long time, and it was a part of the Outer Melanesian Arc, which was close to northeastern New Guinea around 24 Ma (Coleman, 1997; Hall, 2002). Dispersal from Australia likely involved New Guinea. During the last 24 million years, parts of Halmahera moved along the north coast of New Guinea to their present position, west of New Guinea, where they united, and similar to the rest of North Moluccas, they differed in floristic composition from South Moluccas, which moved to the north from Australia (Rutgrink et al., 2018). The Weda Bay plants, endemic to Halmahera, likely originated prior to the union with South Moluccas, but a divergence dating analysis is needed to test



this hypothesis. Due to the distinctiveness of the Weda Bay material with morphological and molecular divergence from potential close relatives (Fig. 3), we describe the specimens from Halmahera as a new genus with two new species and classify the genus in the subfamily Crotonoideae, tribe Ricinocarpeae, as circumscribed herein.

Some morphological features of the new genus, especially in the flowers and fruits, are poorly understood due to the few, sparsely reproductive specimens available (one flower per inflorescence branch). We therefore refrained as much as possible from dissecting flowers. Uncertainty remains in the interpretation of the receptacle of the staminate flowers. In the first species, it appears as a highly domed receptacle, and in the second species, it seems more as a union of the basal part of the filaments into an androphore. In the sexes of both species, no typical floral disc or disc glands were discovered. However, a narrow tissue band with a hirsute margin is present in the staminate flowers of the second species and may be a reduced disc (Fig. 4A). Finally, the very young seeds, as seen in the material of the second species, had an apical appendage with caruncle-like tissue, which was not seen in the far more mature seeds of the first species. This difference could be another factor to separate the two species or the appendage may disappear during seed development. Caruncles are usually present in Ricinocarpeae, but rare elsewhere in clade C2.

The trichome diversity in the new genus spans three basic types (simple, stellate, and dendritic), with clear differences between the species, notably in the presence/absence of long, simple trichomes (Figs. 4G–4J). The dendritic trichomes, each containing a variously elongate central axis with numerous arms (radii), are especially well developed in the second species. The stellate trichomes can have long, thin or shorter, fatter arms, or occasionally have a long central arm (Fig. 4H; *porrect sensu Webster et al., 1996*). The stellate and dendritic trichomes have a large multicellular attachment to the leaf surface, but they are easily detached and they mostly weather off from older leaves (Fig. 4F). The pollen of both species is virtually identical and spheroidal, 40–48  $\mu\text{m}$  dia. (polar:equatorial ratio 1.03;  $n = 10$ , via SEM), inaperturate, and with subunits at the surface densely spaced, free, and rounded at their tips (Figs. 4D, 4E). The pollen has a typical Croton structure, closely resembling that of *Alphandia* (see Nowicke, 1994; fig. 49). Based on our present floristic inventories, the two new species have a very limited distribution, and they only occur in ultramafic areas, which have a patchy distribution (Cock & Lynch, 1999; Lopez et al., 2019a). This means that their continued existence is extremely vulnerable to habitat destruction, especially when nickel mining commences. Protection of the Weda Bay area is of eminent importance, given the growing list of endemic taxa (e.g., *Nepenthes*, Cheek, 2015; *Pandanus*, Callmander et al., 2015).

## 5 Taxonomic treatment

*Weda* Welzen, gen. nov., Figs. 4–8

Type: *W. fragarioides* Welzen

Diagnosis: Monoecious trees with stellate to dendritic hairs and often long, simple patent hairs. Stipules lacking. Leaves alternate with long petioles, base of blades with two large, adaxial, basal glands or these at end of

narrow lobes, venation raised, very distinct. Inflorescences axillary, cymose, functionally unisexual, with long peduncle and apically two unequal, subopposite, leaf-like, (sub)sessile, late-caducous bracts. Flowers with calyx and corolla, apparently lacking a disc. Staminate flowers with highly domed, hirsute receptacle with many short stamens or an androphore with a short free-filament part per stamen. Pistillate flowers with three-locular ovary, stigmas split, smooth adaxially. Fruits capsular, smooth, dehiscent loculicidally and septicidally. Seeds naked, marbled.

Trees, monoecious; latex unknown. Indumentum of pale brown, short, stellate to somewhat lepidote to dendritic hairs, parts also with long, whitish, simple hairs (especially in *W. lutea*). Stipules absent. Leaves alternate to sub-opposite, simple; petioles long, cylindrical, basally slightly pulvinate, apically hardly thickened; blade at insertion (not peltate) or at base of peltation (blade peltate) with two adaxial large elongate glands, margin entire with an occasional extending gland, surfaces smooth, penninerved or basally palmately nerved, venation raised on both sides, especially beneath, secondary veins looped and closed near the margin, higher order veins laxly reticulate. Inflorescences axillary, erect, cymose, bisexual, but usually unisexual functionally, basically dichotomous and first pistillate with a single, central pistillate flower, after fruit dehiscence, when the more horizontal, scorpioid branches develop, with per branch only staminate flowers with one or two flowering at a time; peduncle long, somewhat flattened, with two leaf-like, slightly subopposite bracts of unequal size at the distal end, lower one smaller, both late caducous during staminate phase; floral bracts either vestigial, hairy enations or acicular and apically glandular. Flowers five-merous, actinomorphic, pedicellate; sepals four or five, basally united, lobes imbricate, outer three smaller than inner one or two, apices rounded; petals ovate, five or six, contorted, fleshy, glabrous, apex rounded. Staminate flowers, highly dome-shaped receptacle or filaments partly united in an androphore, densely hairy with simple hairs; disc absent or not obvious to a vague ring around dome/androphore in *W. lutea*; stamens more than 30, filaments free, thread-like, with few hairs, anthers two-lobed, dorsibasifixed, connective very short and indistinct, thecae almost completely separate, opening extrorsely with longitudinal slits, glabrous; pistillode absent; pollen spheroidal, inaperturate, crotonoid. Pistillate flowers, partly seen in bud and in young fruit; sepals five; petals five; disc not seen; ovary three-locular, densely hairy, with a single ovule per locule, style short, hairy, stigmas three, broad, mostly bifid, glabrous, smooth, not papillate above. Fruits capsular, ellipsoid, slightly lobed, lobes higher than wide, smooth, dehiscent completely loculicidally and septicidally into six mericarps; wall thin, with a thin exocarp and a woody meso- and endocarp when dry; columella three-quetrous, persistent. Seeds three per fruit, smooth, marbled, naked, with an apical appendage with carunculoid tissue in the young material of *W. lutea* but without appendage (disappeared) in the mature seeds of *W. fragarioides*; hilum small; embryo unknown.

Distribution: The two species are each discovered from three collections made in central Halmahera (Indonesia, N Moluccas; Fig. 1).



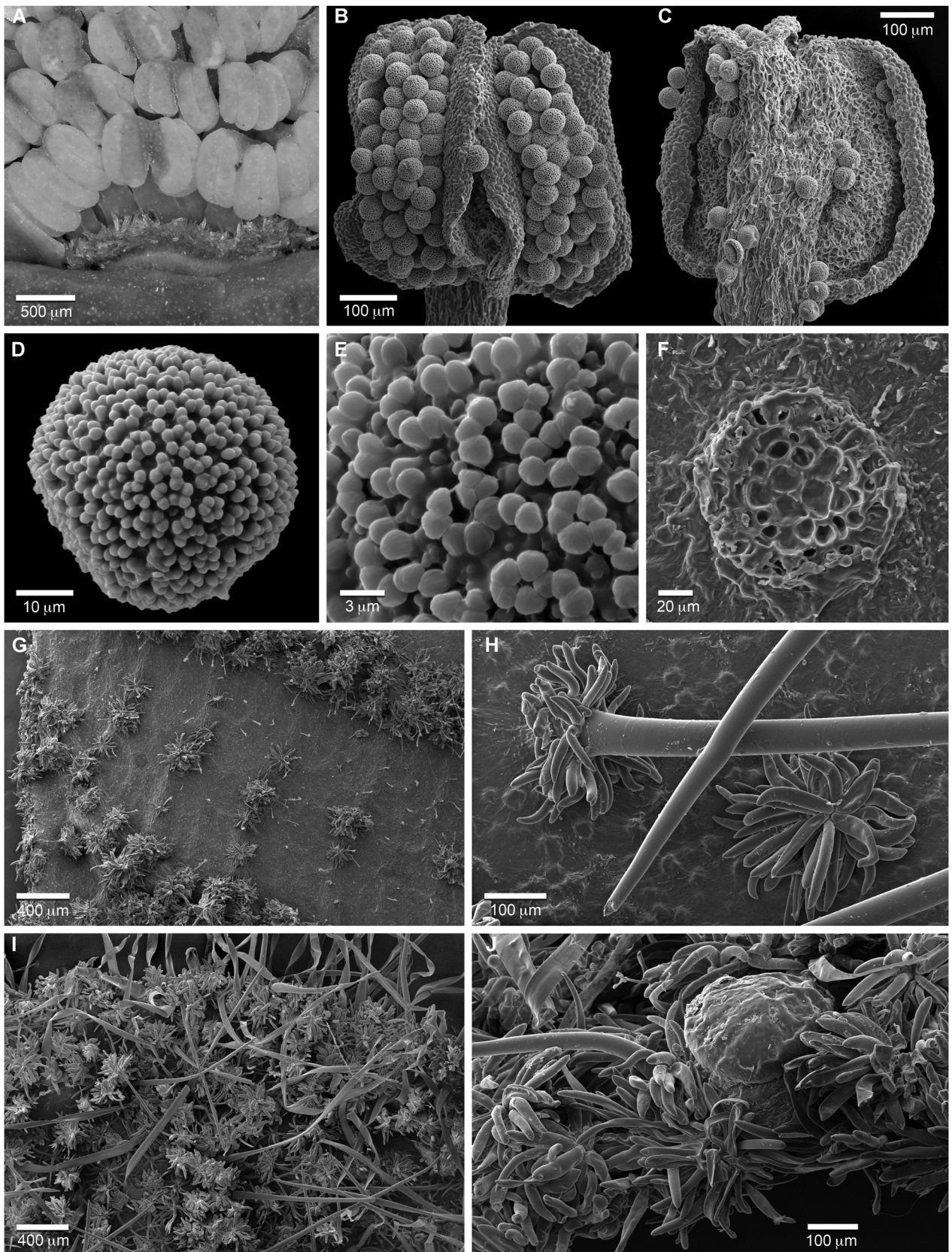
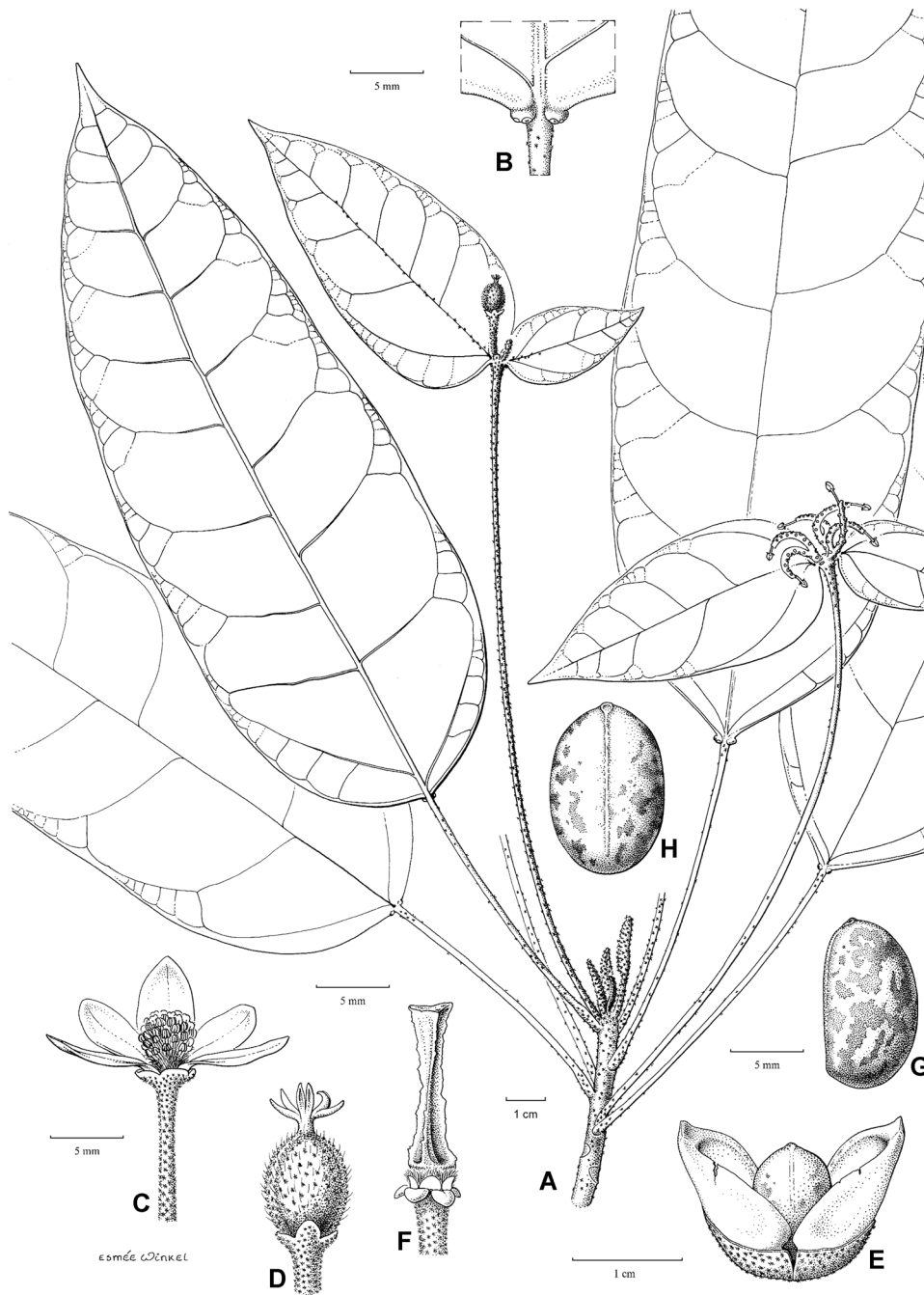
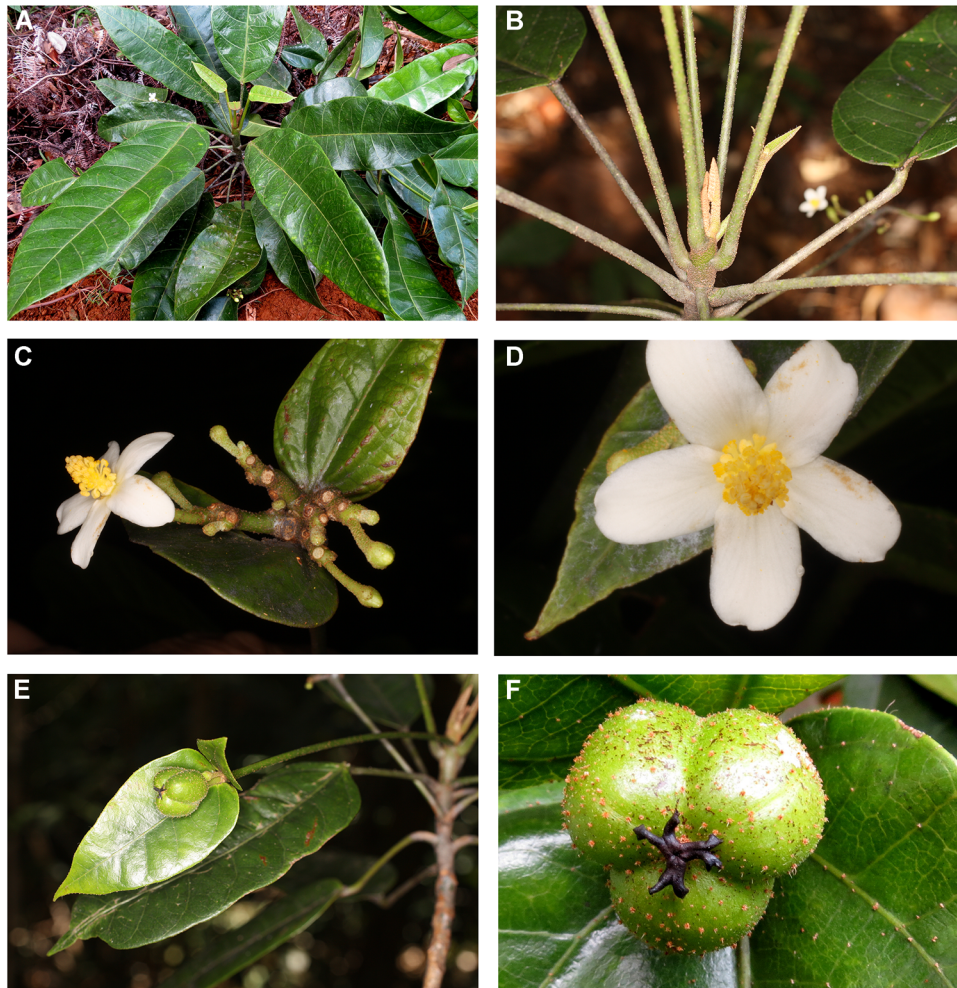


Fig. 4. Continued



**Fig. 5.** *Weda fragarioides* Welzen. **A**, Habit. **B**, Basal leaf blade glands. **C**, Staminate flower with front petal removed. **D**, Pistillate flower with petals removed. **E**, Partly loculicidally split mericarps and seed. **F**, Columella remaining after fruit dehiscence. **G**, Seed, lateral (profile) view. **H**, Seed, ventral view. (based on: **A–D**, Phillipson et al. 6448, L; **E–H**, Bangun et al. 971, L). Illustration by Esmée Winkel (2018).

**Fig. 4.** Micromorphology of *Weda fragarioides* (**B–D**, **G**) and *W. lutea* (**A**, **E**, **F**, **H–J**). **A**, Mature staminate bud with hirsute margin disc (middle), tightly packed extrorse anthers, and petals (bottom). **B**, Dehiscing anther with pollen, dorsal. **C**, Dehiscing anther, ventral. **D**, Pollen. **E**, Exine sculpture with clusters of rounded subunits. **F**, Multicellular attachment site of dendritic leaf trichome, adaxial. **G**, Young leaf at margin with stellate trichomes tracking secondary and tertiary venation, abaxial (thin, simple structures are fungal thalli). **H**, Simple, stellate, and intermediate (porrect) trichomes, adaxial. **I**, Young leaf at margin with three types of trichomes (simple, dendritic, and understory of stellate), abaxial. **J**, Marginal gland on young leaf, abaxial. *Weda lutea* Welzen (from: **A**, **E**, Gushilman & Haris 178; **B–D**, Bangun et al. 971; **F**, **H–J**, Bangun et al. 199; **G**, Gushilman et al. 777, all MO; imaged by **A**, light microscopy of rehydrated, partly dissected mature bud, or **B–J**, SEM).



**Fig. 6.** *Weda fragarioides* Welzen. **A**, Habit (Gushilman et al. 777, photo IG 5481). **B**, Branch tip with long petioles, exstipulate developing leaf, stellate hairs and glands at base of leaf blade (Phillipson et al. 6448, photo PBP 5058). **C**, Bracteate inflorescence with a single developed staminate flower (Phillipson et al. 6448, photo PBP 5079). **D**, Staminate flower with androecium of many free, short stamens and white petals (Phillipson et al. 6448, photo PBP 5072). **E**, Bracteate infructescence with young fruit (Phillipson et al. 6448, photo PBP 5059). **F**, Young fruit with smooth bifid stigmas and brown stellate hairs (Gushilman et al. 777, photo IG 5487).

**Etymology:** The genus name refers to Weda Bay where the specimens were collected.

**Note:** The leaf blade glands are typical, with the long peduncled inflorescences having two leaf-like large bracts, the highly domed receptacle or androphore of the staminate flowers, and the stellate to dendritic indumentum.

### 5.1 Key to the species

- 1a. Leaf blades basally attached, glands at insertion, margin without glands, simple hairs absent; venation pinnate. Floral bracts vestigial, hairy enations. Petals white ..... ***W. fragarioides***
- 1b. Leaf blades peltate, glands at base of peltation, margin with occasional somewhat smaller glands, simple hairs present; venation basally palmate. Floral bracts acicular, up to 2.5 mm long, ending in a globose gland. Petals yellow ..... ***W. lutea***

### 1. *Weda fragarioides* Welzen, sp. nov., Figs. 4B–4D, 4G, 5, 6.

**Diagnosis:** Leaf blades not peltate, large glands at blade insertion. Inflorescence branches short, less than 5 cm long. Floral bracts vestigial, hairy enations. Petals white.

**Type:** PB Phillipson, M Merello, B Sau, R Mahroji, I Haris 6448 (holotype, L; isotypes, BO, MO-6582852), Indonesia, central Halmahera, Weda Bay, Bukit Limber, 00°32'07"N, 128°00'17"E, 761 m alt., 2 October 2012.

**Other material:** TJF Bangun, I Haris, M Soleman, A Yani 971 (BO, L, MO), Indonesia, East Halmahera, Weda Bay, Blikep Nu, Camp 3, 00°42'55"N 128°02'11"E, 566 m alt., 7 June 2014; I Gushilman, R Mahroji, PB Phillipson, TJF Bangun, B Fabanyo 777 (BO, L, MO), Indonesia, Central Halmahera, Weda Bay, Bukit Limber, 00°31'39"N, 128°00'19"E, 777 m alt., 12 September 2013.

**Habit:** trees, 12 m high, dbh at least 7 cm; flowering branches 6–8 mm diameter. Outer bark brown. Leaves spotted brown with stellate hairs when young; petioles



5.5–12 cm long, 2–3 mm thick in middle, with stellate to somewhat lepidote hairs when young, soon glabrescent, gray; blade ovate-oblong to elliptic-oblong, 10.5–30 by 3.8–12 cm, 2.42–4.7 times as long as wide (mean = 3.08, SD = 0.440,  $n = 32$ ), base rounded to cuneate, shortly attenuate near the basal adaxial (acropetiole) glands; glands ca. 2 by 1.3 mm and ca. 1 mm high with long axis perpendicular to petiole; lamina margin recurved to flat, apex acuminate, acumen ca. 1.5 cm long, upper surface glabrous, margin and lower surface glabrescent with mainly main veins and margin remaining slightly hairy, venation pinnate, secondary veins 10–14 pairs, basal pair under slightly steeper angle with midrib. *Inflorescences*: peduncle 7.5–17 cm long, mainly glabrous except apically few stellate hairs (on specimen from Blipek Nu also long, white simple hairs); bracts ovate, 3.7–10.7 by 1.9–5 cm, sessile, without glands, basally emarginate, margin entire, apex acute to acuminate, venation well developed, like leaf blades, but generally fewer secondary veins; other bracts on branches present as vestigial, hairy enations below the flowers. Flowers, petals white. Staminate flowers ca. 16 mm diameter, receptacle highly domed; buds green; pedicel up to 10 mm long, with stellate hairs; sepals ovate, fleshy, margins with simple hairs, inside glabrous; outer ones ca. 2.2 by 2 mm, externally bearing stellate hairs; inner ones ca. 3 by 3 mm, outside lower half with stellate hairs; petals ca. 9 by 4.5 mm; disc absent or indistinct, filaments thread-like, ca. 1 by 0.1 mm, pale yellow, glabrous or rarely with scattered simple hairs, anthers elliptic, ca. 0.7 by 0.7 mm, yellow, glabrous. Pistillate flowers, seen in bud and in young fruit; pedicel ca. 6 mm long in young fruit, hairy; sepals ovate, ca. 1.8 by 1.8 mm, with stellate hairs outside; petals seen young or caducous, somewhat hairy outside when in bud; disc not seen; ovary: styles shortly connate, ca. 1 mm high in young fruit, hairy, stigmas ca. 3 mm long, bifid except basal ca. 0.5 mm, dark gray. Fruits ca. 1.3 cm high by 1.5 cm wide when nearly mature, sulcate along sutures, mericarps ca. 2 cm high; pedicel 14–18 mm long; wall ca. 0.8 mm thick, with brown stellate hairs with central arm longer and setaceous in Bukit Limber material; sepals persistent; columella ca. 1.2 cm high, narrowly hour-glass shaped, apically not much widened, trigonous in outline. Seeds seen immature (embryo not developed), ellipsoid but flattened on dorsal side, ca. 12 by 7–8 by 5.5–6 mm, light brown and marbled with dark brown irregular spots, apically without appendage.

*Distribution*: Indonesia, N Moluccas (Maluku Utara), Halmahera, north of Weda Bay, Bukit Limber, 00°32'07"N, 128°00'17"E and Blipek Nu, Camp 3, 00°42'55"N 128°02'11"E (Fig. 1).

*Habitat and Ecology*: Common on Blipek in primary to secondary forest along the road at 566–777 m altitude. Flowering in September–October and fruiting in June.

*Etymology*: Due to the arched receptacle in the staminate flowers, the epithet refers to the strawberry (*Fragaria* L.), where the receptacle becomes a highly domed fruit.

*Conservation*: The known distribution of the new taxon is limited, as exploration of Halmahera and nearby islands is highly incomplete (see Callmander et al., 2015).

It appears to be a local endemic and might at least be vulnerable, especially when the planned nickel mine begins operation.

*Note*: The specimen from Blipek Nu is slightly different, as the leaf blades are more elliptic, whereas the specimens of Bukit Limber are more ovate. In addition, the peduncle of the pistillate inflorescence of Blipek Nu has (next to stellate hairs) long simple hairs, not seen in the specimens of Bukit Limber, whereas many stellate hairs on the fruits in Bukit Limber have a central, much longer and stiffer arm, not seen in the fruits of Blipek Nu.

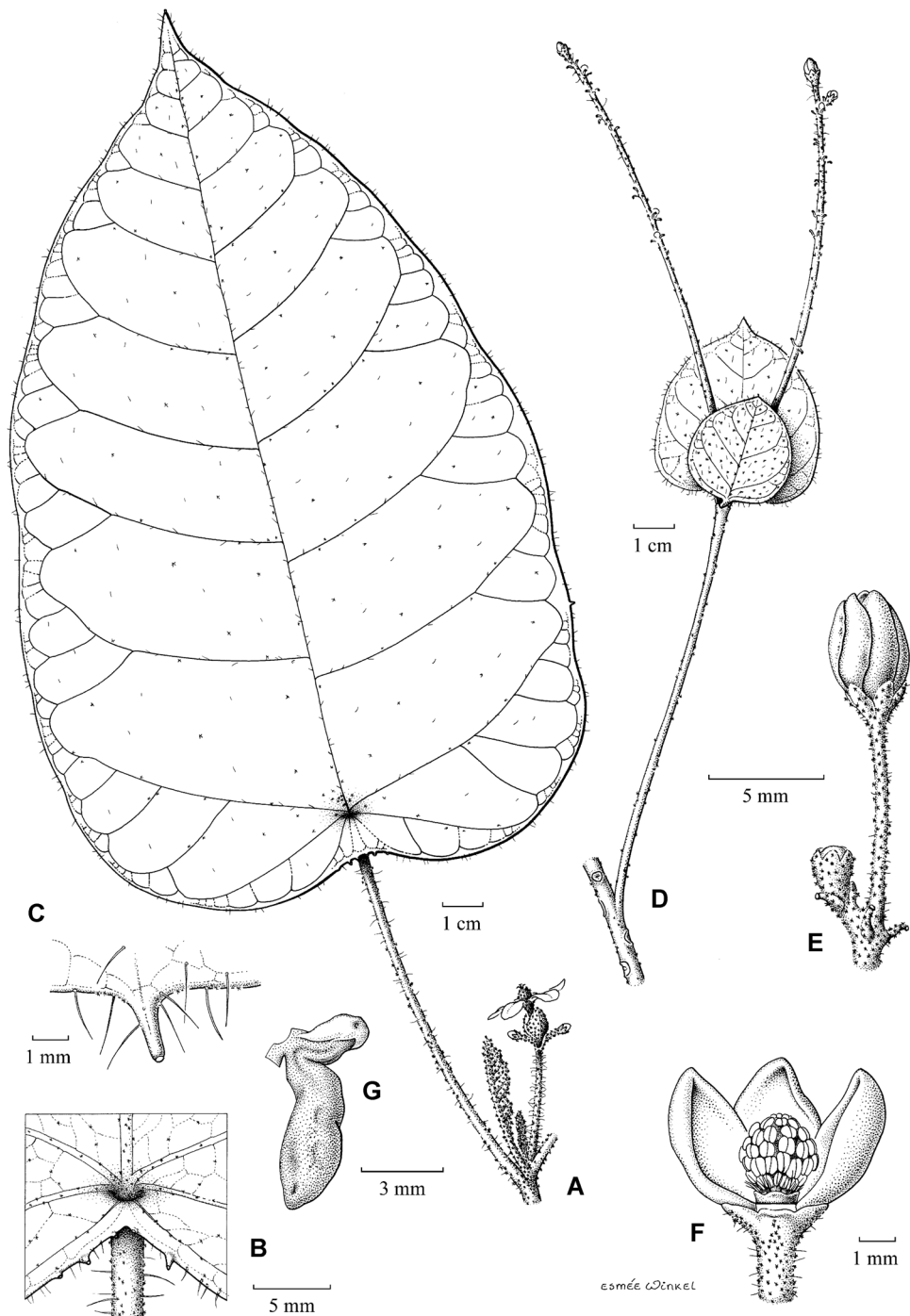
## 2. *Weda lutea* Welzen, sp. nov., Figs. 4A, 4E, 4F, 4H–4J, 7, 8

*Diagnosis*: Leaf blades peltate, glands at base of peltation, margin with occasional somewhat smaller glands; venation basally palmate. Inflorescence branches up to more than 18 cm long (broken). Floral bracts acicular, up to 2.5 mm long, ending in a globose gland. Petals yellow.

*Type*: TJJ Bangun, M Merello, I Gushilman, I. Haris 118 (holotype, L; isotypes, BO, MO-6615796, MO-6615795), Indonesia, central Halmahera, Weda Bay, road to Sake South, 00°29'22"N, 127°58'48"E, 103 m alt., 18 October 2012.

*Other material*: TJJ Bangun, L Andriamahefarivo, R Razakamalala, R Mahroji, D Loha 199 (BO, L, MO), Indonesia, central Halmahera, Weda Bay, Sake South, 00°29'09"N 127°58'56"E, 81 m alt., 30 November 2012; I Gushilman, I Haris 178 (BO, L, MO), Indonesia, central Halmahera, Weda Bay, Sake South, 00°29'07"N, 127°58'53"E, 78 m alt., 30 November 2012.

*Habit*: small trees (reported by Bangun et al. 118 as a 3 m long liana), 10 m high, dbh to at least 10 cm; flowering branches 3–5 mm diameter, branchlets rather densely covered with stellate to dendritic hairs, rather persistent, and long (to 2.2 mm) simple hairs, latter caducous. Outer bark brown to brownish gray, rugose; inner bark pale green to red; sap clear or red and oxidizing black. Leaves dark brown from dense indumentum when young; petioles 8–12.8 cm long, 1–1.8 mm thick in middle, with brown stellate to dendritic hairs and yellow simple hairs; blade ovate-oblong, 8–25.5 by 4.8–16 cm, 1.2–1.7 times longer than wide (mean = 1.58, SD = 0.145,  $n = 17$ ), base peltate for less than 1 cm or cordate, emarginate, with one or usually two elongated slender glands, often to one side, ca. 1.3 by 0.5 mm, often with a flat gland next to the base; lamina margin somewhat recurved, often with several, somewhat shorter glands (Fig. 4J), apex acuminate, acumen up to 2 cm long and minutely gland tipped, upper surface with stellate and simple hairs when young, stellate hairs persistent on midrib and basal part of major veins, lower surface slightly hairy with stellate to dendritic hairs and simple patent hairs, venation basally palmate, secondary veins 8–10 pairs to apex. *Inflorescences*, peduncle 8.4–14.4 cm long, with stellate hairs and often long simple hairs and few dendritic hairs; bracts ovate, 4.2–8 by 3.2–5.8 cm, subsessile, petiole up to 5 mm long, basally emarginate, margin entire, apex acuminate, venation well developed, like leaf blades, but fewer secondary veins, indumentum like leaves; branches at least 18 cm long (broken), along with branches acicular bracts, one or two per node, up to 2.5 mm long by 0.2–0.4 mm diam., ending in a globose gland, apically bent downward. Flowers, sepals basally more united than in other species, petals



**Fig. 7.** *Weda lutea* Welzen. **A**, Habit. **B**, Peltate leaf base with glandular appendages. **C**, Basal laminar gland. **D**, Cymose inflorescence with long branches. **E**, Staminate bud. **F**, Staminate flower, two petals removed, showing androecium. **G**, Young seed with apical caruncule-like appendage, lateral (profile) view. (based on **A–C**, Bangun et al. 199, L; **D–F**, Gushilman & Haris 178, L; **G**, Bangun et al. 118, L). Illustration by Esmée Winkel (2019).

yellow. Staminate flowers ca. 12 mm diameter, receptacle highly domed or androphore; bud green; pedicel up to 11 mm long, with stellate hairs and some long simple hairs; calyx pale green, ca. 3.8 mm long, lobes ovate to oblong, ca. 2.3 by 1.2–1.4 mm, fleshy, outside with stellate hairs, especially in middle, inside glabrous; petals ca. 7 by 3.5 mm; narrow hirsute band (disc) at base of androecium (Fig. 4A); stamens

yellow, filaments seemingly united in an androphore, free part of filaments thread-like, ca. 1 by 0.1 mm, glabrous, anthers elliptic, ca. 0.8 by 0.5 mm, glabrous. Pistillate flowers ca. 21 mm diameter; pedicel ca. 7.5 mm long, hairy; calyx with five lobes, lobes ovate, ca. 4.2 by 2 mm, with stellate hairs outside; petals oblong-obovate, ca. 11 by 5 mm; disc not observed; ovary densely stellate-hairy, ca. 3 mm high,



**Fig. 8.** *Weda lutea* Welzen. **A**, Habit with hairy, slightly peltate leaves (Gushilman et al. 178, photo IG 820). **B**, Young shoot with exstipulate developing leaves, stellate (brown) hairs and long white simple hairs (Bangun et al. 199, photo TF 2517). **C**, Cymose inflorescence with basal young fruit and terminal staminate flowers and buds (Bangun et al. 199, photo TF 2520). **D**, Staminate flower with yellow petals (Bangun et al. 199, photo TF 2510). **E**, Pistillate flower (Bangun et al. 118, photo TF 1228). **F**, Young fruit subtended by sessile bracts (Bangun et al. 199, photo TF 2521).

tapering into a hairy style; stigmas ca. 4 mm long, seemingly only apically split. Fruits dehiscing, ellipsoid, ca. 15 by 14 mm, green, stellate and dendritic hairs brown, hairs with arms all of same length (no longer central arm); wall ca. 1 mm thick; sepals persistent; columella ca. 1.2 cm high, narrow, apically not much widened. Seeds very immature, apically with an extension of a white two-lobed caruncle-like structure.

**Distribution:** Indonesia, N Moluccas (Maluku Utara), Halmahera, northeast of Weda, vicinity of Weda Bay at Sake South (Fig. 1).

**Habitat and Ecology:** (Open) secondary forest at 78–103 m altitude. Flowering in October and November, fruiting in October.

**Etymology:** The epithet refers to the yellow color of the petals.

**Conservation:** The distribution of the *Weda lutea* is not adequately known, as species inventories of other areas in Halmahera and nearby islands are incomplete (see Callmender et al., 2015). It appears to be a local endemic and might at least be vulnerable; it is especially at risk

because it seemingly occurs only at low altitude and will be especially endangered when the planned nickel mine begins operation.

**Note:** The stamens of *W. lutea* were difficult to observe due to the very few open staminate flowers. It is unclear as to whether the stamens are inserted on a highly domed receptacle (as is more the case in *W. fragarioides*) or form an androphore around whose base is a vague circular, very regular annular hirsute disc. The seeds have a poorly understood caruncle-like appendage, not observed in *W. fragarioides*.

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## Author contributions

Peter van Welzen (L) identified and described the taxon and conducted phylogenetic analyses; Susana Arias Guerrero (L) and Deby Arifiani (BO) managed the identification of the specimens in Leiden and Bogor, respectively; Roderick Bouman (L) helped with molecular data; Iris Tabak (L), under the guidance of Marcel Eurlings (L), did the Leiden-based lab work; Peter Phillipson (MO) was one of the organizers of the inventory program and collected specimens with Tjut Bangun and Iska Gushilman (BO); Phillipson also provided photos of living plants; Esmée Winkel (L) drew the illustrations; and Kenneth Wurdack (US) generated the Smithsonian data, developed the final molecular data sets and alignments, and did the final molecular analyses. All the abovementioned researchers helped to write the manuscript.

## References

- Airy Shaw HK. 1963. Notes on Malaysian and other Asiatic Euphorbiaceae. *Kew Bulletin* 16: 341–372.
- Airy Shaw HK. 1971. Notes on Malesian and other Asiatic Euphorbiaceae. *Kew Bulletin* 25: 473–553.
- Airy Shaw HK. 1980. Notes on Euphorbiaceae from Indomalaysia, Australia and the Pacific. *Kew Bulletin* 35: 383–399.
- Airy Shaw HK. 1982. The Euphorbiaceae of Central Malesia (Celebes, Moluccas, Lesser Sunda Is.). *Kew Bulletin* 37: 1–40.
- Athiê-Souza SM, de Melo AL, da Silva MJ, dos Santos Dias de Oliveira L, Ferreira, de Sales M. 2015. Gradyana (Euphorbiaceae): A new genus from northeastern Brazil. *Systematic Botany* 40: 527–533.
- Baillon H. 1858. *Étude Générale du Groupe des Euphorbiacées*. Paris: Victor Masson.
- Bouman R, van Welzen PC, Sumail S, Echevarria G, Erskine PD, van der Ent A. 2018. *Phyllanthus rufuschaneyi*: A new nickel hyperaccumulator from Sabah (Borneo Island) with potential for tropical agromining. *Botanical Studies* 59: 12.
- Callmender MW, Keim AP, Buerki S, Phillipson PB. 2015. The genus *Pandanus* Parkinson (Pandanaeae) on Halmahera Island (Moluccas, Indonesia) with descriptions of three new species and a key to the species on the island. *Candollea* 70: 179–196.
- Cardinal-McTeague WM, Wurdack KJ, Sigel EM, Gillespie LJ. 2019. Seed size evolution and biogeography of *Plukenetia* (Euphorbiaceae), a pantropical genus with oilseed species. *BMC Evolutionary Biology* 19: 29.
- Cheek M. 2015. *Nepenthes* (Nepenthaceae) of Halmahera, Indonesia. *Blumea* 59: 215–225.
- Cheek M, Challen G, Lebbie A, Banks H, Barberá P, Riina R. 2016. Discovering *Karima* (Euphorbiaceae), a new crotonoid genus from West Tropical Africa long hidden within *Croton*. *PLoS One* 11: e0152110.
- Cheng T, Xu C, Lei L, Li C, Zhang Y, Zhou S. 2016. Barcoding the kingdom Plantae: New PCR primers for ITS regions of plants with improved universality and specificity. *Molecular Ecology Resources* 16: 138–149.
- Cock GC, Lynch JE. 1999. Discovery and evaluation of the Weda Bay nickel/cobalt deposits, central Halmahera, Indonesia. *Australasian Institute of Mining and Metallurgy Publication Series* 4: 197–206.
- Coleman PJ. 1997. Australia and the Melanesian arcs: A review of tectonic settings. *AGSO Journal of Australian Geology and Geophysics* 17: 113–125.
- Dorr LJ, Romero-Hernández C, Wurdack KJ. 2018. A new large-flowered species of *Andeimalva* (Malvaceae: Malvoideae) from Peru. *PhytoKeys* 111: 11–16.
- Drummond AJ, Suchard MA, Dong X, Rambaut A. 2012. Bayesian phylogenetics with BEAUTi and the BEAST 1.7. *Molecular Biology and Evolution* 29: 1969–1973.
- Dunning LT, Savolainen V. 2010. Broad-scale amplification of *matK* for DNA barcoding plants, a technical note. *Botanical Journal of the Linnean Society* 164: 1–9.
- Gill AM, Tomlinson PB. 1969. Studies on the growth of red mangrove (*Rhizophora mangle* L.) I. Habit and general morphology. *Biotropica* 1: 1–9.
- Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology* 59: 307–321.
- Halford DA, Henderson RJF. 2005. Studies in Euphorbiaceae s. lat. 7. Shonia R.J.F. Hend. & Halford (Ricinocarpeae, Ricinocarpiinae), a new Australian endemic genus. *Austrobaileya* 7: 215–228.
- Hall R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: Computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences* 20: 353–431.
- Jaffré T, Pillon Y, Thomine S, Merlot S. 2013. The metal hyperaccumulators from New Caledonia can broaden our understanding of nickel accumulation in plants. *Frontiers in Plant Science* 4: 279.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A. 2012. Geneious Basic: An



- integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649.
- Lefort V, Longueville JE, Gascuel O. 2017. SMS: Smart model selection in PhyML. *Molecular Biology and Evolution* 34: 2422–2424.
- Lledó MD, Crespo MB, Cameron KM, Fay MF, Chase MW. 1998. Systematics of Plumbaginaceae based upon cladistic analysis of *rbcl* sequence data. *Systematic Botany* 23: 21–29.
- Lopez S, Benizri E, Erskine PD, Cazes Y, Morel JL, Lee G, Permana E, Echevarria G, van der Ent A. 2019a. Biogeochemistry of the flora of Weda Bay, Halmahera Island (Indonesia) focusing on nickel hyperaccumulation. *Journal of Geochemical Exploration* 202: 113–127.
- Lopez S, Goux X, van der Ent A, Erskine PD, Echevarria G, Calusinska M, Morel JL, Benizri E. 2019b. Bacterial community diversity in the rhizosphere of nickel hyperaccumulator species of Halmahera Island (Indonesia). *Applied Soil Ecology* 13: 70–80.
- Lopez S, van der Ent A, Erskine PD, Echevarria G, Morel JL, Lee G, Permana E, Benizri E. 2019c. Rhizosphere chemistry and above-ground elemental fractionation of nickel hyperaccumulator species from Weda Bay (Indonesia). *Plant and Soil* 436: 543–563.
- Maddison WP, Maddison DR. 2018. Mesquite: A modular system for evolutionary analysis, version 3.40 [online]. Available from <http://mesquiteproject.org> [accessed 20 March 2020].
- Nowicke JW. 1994. A palynological study of Crotonoideae (Euphorbiaceae). *Annals of the Missouri Botanical Garden* 81: 245–269.
- Pax F, Hoffmann K. 1911. Euphorbiaceae–Cluytieae. In: Engler A ed. *Das Pflanzenreich IV.147. III (Heft 47)*. Leipzig: Wilhelm Engelmann. 1–124.
- Radcliffe-Smith A. 2001. *Genera Euphorbiacearum*. Kew: Royal Botanic Gardens.
- Rambaut A. 1996–2002. Se-AL: Sequence alignment editor ver. 2.0 [online]. Available from <http://tree.bio.ed.ac.uk/software/> [accessed 20 March 2020].
- Rambaut A. 2014. FigTree version 1.4.2 [online]. Available from <http://tree.bio.ed.ac.uk/software/figtree/> [accessed 20 March 2020].
- Rambaut A, Suchard MA, Xie W, Drummond AJ. 2013. Tracer version 1.6.0 [online]. Available from <http://tree.bio.ed.ac.uk/software/tracer/> [accessed 20 March 2020].
- Reeves RD, Baker AJM, Borhidi A, Berazaín R. 1996. Nickel-accumulating plants from the ancient serpentine soils of Cuba. *New Phytologist* 133: 217–224.
- Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.
- Rozefelds AC, Milroy AK, Dettmann ME, Clifford HT, Maksimenko A. 2017. Synchrotron computer tomographic (CT) scans complement traditional techniques in understanding the internal anatomy of permineralised *Fontainocarpa* (Crotonoideae, Euphorbiaceae) fruits from the Oligocene of eastern Australia. *Review of Palaeobotany and Palynology* 242: 43–57.
- Rutgrink ALJ, Visser M, van Welzen PC. 2018. Differences between the floras of the North and South Moluccas (Indonesia). *Journal of Systematics and Evolution* 56: 652–662.
- Rutishauser R, Sattler R. 1986. Architecture and development of the phyllode–stipule whorls of *Acacia longipedunculata*: Controversial interpretations and continuum approach. *Canadian Journal of Botany* 64: 1987–2019.
- Stamatakis A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
- Stanford AM, Harden R, Parks CR. 2000. Phylogeny and biogeography of *Juglans* (Juglandaceae) based on *matK* and *ITS* sequence data. *American Journal of Botany* 87: 872–882.
- Taberlet P, Gielly L, Pautou G, Bouvet J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
- Tokuoka T. 2007. Molecular phylogenetic analysis of Euphorbiaceae sensu stricto based on plastid and nuclear DNA sequences and ovule and seed character evolution. *Journal of Plant Research* 120: 511–522.
- Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ. 2016. W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44: W232–W235.
- van der Ent A, Erskine P, Sumail S. 2015. Ecology of nickel hyperaccumulator plants from ultramafic soils in Sabah (Malaysia). *Chemoecology* 25: 243–259.
- van der Ent A, van Balgooy MMJ, van Welzen PC. 2016. *Actephila alanbakeri* (Phyllanthaceae): A new nickel hyperaccumulating plant species from localised ultramafic outcrops in Sabah (Malaysia). *Botanical Studies* 57: 6.
- van der Ent A, Mark R, de Jong MD, Harris HH. 2018. Simultaneous hyperaccumulation of Nickel and cobalt in the tree *Glochidion cf. sericeum* (Phyllanthaceae): Elemental distribution and chemical speciation. *Scientific Reports* 8: 9683.
- van Steenis CCGJ and others eds. 1950 and later. *Flora Malesiana Series 1, 1 and later volumes*. Djakarta: Noordhoff-Kolff n.v. (and others).
- van Welzen PC. 2012. Five rare genera of Euphorbiaceae (sensu lato) in the Malay Archipelago: *Alphandia*, *Ashtonia*, *Borneodendron*, *Cladogynos* and *Tapoïdes*. *Edinburgh Journal of Botany* 69: 389–411.
- van Welzen PC. 2017. (and updates). Euphorbiaceae of Malesia [online]. Available from [www.nationaalherbarium.nl/euphorbs](http://www.nationaalherbarium.nl/euphorbs) [accessed 20 March 2020].
- van Welzen PC, Slik JWF, Alahuhta J. 2005. Plant distribution patterns and plate tectonics in Malesia. *Biologische Skrifter* 55: 199–217.
- Webster GL. 2014. Euphorbiaceae. In: Kubitzki K ed. *The families and genera of vascular plants 11, Malpighiales*. Berlin: Springer Verlag. 51–216.
- Webster GL, Del Arco Aguilar MJ, Smith BA. 1996. Systematic distribution of foliar trichome types in *Croton* (Euphorbiaceae). *Botanical Journal of the Linnean Society* 121: 41–57.
- Wurdack KJ, Farfan-Rios W. 2017. *Incadendron*: A new genus of Euphorbiaceae tribe Hippomaneae from the sub-Andean cordilleras of Ecuador and Peru. *PhytoKeys* 85: 69–86.
- Wurdack KJ, Hoffmann P, Chase MW. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbcl* and *trnL-F* DNA sequences. *American Journal of Botany* 92: 1397–1420.
- Yu R-Y, Slik FJW, van Welzen PC. 2019. Molecular phylogeny of *Trigonostemon* Blume and its relatives (Euphorbiaceae). *Taxon* 68: 918–936.
- Zhou Z, Gu B-J, Sun H, Zhu H, Tan Y-H. 2017. Molecular phylogenetic analyses of Euphorbiaceae tribe Epiptirineae, with the description of a new genus, *Tsaiodendron* gen. nov. from south-western China. *Botanical Journal of the Linnean Society* 184: 167–184.

**Appendix I.** Taxon sampling for the 102-tip analyses including GenBank sequence accession numbers and voucher information. Name changes relating to previously published data are noted with prior names in brackets. **Taxon;** Origin; Source/Voucher (for new data); GenBank numbers, ordered *rbcl*, *trnL-F*, ITS, ETS. An en-dash (–) indicates missing data; new data includes MT040346–MT040494.

**Adenocline violifolia** (Kunze) Prain; AY794870, AY794669, –, –, **Aleurites moluccana** (L.) Willd.; AY794883, AY794709, MT040409, –, **Alphandia furfuracea** Baill., New Caledonia, M Baumann-Bodenheim 14411 (US); MT040346, MT040374, MT040410, MT040466. **Alphandia furfuracea** Baill., New Caledonia, M Baumann-Bodenheim & A Guillaumin 9584 (US); MT040347, MT040375, MT040411, MT040467. **Annesijoa novoguineensis** Pax & K.Hoffm., Indonesia, A Polak 960 (L); MT040348, MT040376, MT040412, –, **Anomalocalyx uleanus** (Pax & K.Hoffm.) Ducke, Brazil, J Ribeiro 1627 (NY); MT040349, MT040377, –, –, **Astraea lobata** (L.) Klotzsch [as *Croton lobatus*]; AY794905, AY794689, AY971172, –, **Baliospermum montanum** (Willd.) Müll.Arg., Laos, J Munzinger 169 (MO); AY794884, AY794726, MT040413, –, **Baloghia bureavii** (Baill.) Schltr., New Caledonia, J Munzinger & G McPherson 529 (MO); MT040350, MT040378, MT040414, MT040468. **Baloghia inophylla** (G.Forst.) P.S.Green, Australia, M Chase 3062 (K; Kew DNA bank K3062); AY794880, AY794707, MT040415, MT040469. **Baloghia marmorata** C.T.White, Australia, P Forster 38364 (BRI); MT040351, MT040379, MT040416, MT040470. **Bertya findlayi** F.Muell., Australia, J Bruhl 2029A (MO); MT040352, MT040380, MT040417, MT040471. **Bertya rosmarinifolia** Planch., Australia, M Chase 1938 (K; Kew DNA bank K1938); AY794878, AY794705, MT040418, MT040472. **Bertya sharpeana** Guymmer, Australia, G Guymmer 1768, AQ0424640 (US); MT040353, MT040381, MT040419, MT040473. **Beyeria brevifolia** (Müll.Arg.) Benth., Australia, D Halford & G Cockerton Q9136, AQ0870743 (BRI); MT040354, MT040382, MT040420, MT040474. **Beyeria leschenaultii** (DC.) Baill., Australia, M Chase 1939 (K; Kew DNA bank K1939); AY794879, AY794706, MT040421, MT040475. **Blachia siamensis** Gagnep., Thailand, M Newman et al. 1137 (L); AY794888, AY794727, MT040422, –, **Borneodendron aenigmaticum** Airy Shaw, Malaysia, Sabah, SAN 145393 (L); –, MT040383, MT040423, MT040476. **Brasilicocron mamoninha** P.E.Berry & I.Cordeiro; AY794907, AY794691, AY971174, –, **Cavacoa aurea** (Cavaco) J.Léonard, Kenya, W Luke & S Robertson 1922 (US); AY794889, AY794718, MT040424, –, **Cladogelonium madagascariense** Leandri; AY794868, AY794667, –, –, **Cnidocolus urens** (L.) Arthur var. **stimulosus** (Michx.) Govaerts; AY794874, AY794679, –, –, **Cocconerion balansae** Baill., New Caledonia, L Thien 130 (NY); MT040355, MT040384, MT040425, MT040477. **Codiaeum variegatum** (L.) Blume, cult. USA, K Wurdack D033 (US); AY788169, AY794729, MT040426, –, **Croton alabamensis** E.A.Sm. ex Chapm. var. **alabamensis**; AY788171, AY794692, DQ227515, –, **Croton ekmanii** Urb. [as *Moacroton ekmanii*]; AY794908, AY794693, EF421763, –, **Croton lucidus** L.; AY794909, AY794701, EF421765, –, **Croton setiger** Hook. [as *Eremocarpus setiger*]; AY794910, AY794697, HM564097, –, **Crotonogyne zenkeri** Pax [as *Crotonogyne* sp.], Gabon, S Smith 1742 (US); AY794893, AY794717, –, –, **Cyrtogonone argentea** (Pax) Prain, B Daramola 19 (K); AY794974, MT040385, MT040427, –, **Deutzianthus**

**tonkinensis** Gagnep., Vietnam, L Gillespie 7401 (CAN); MT040356, MT040386, MT040428, –, **Dimorphocalyx muricatus** (Hook.f.) Airy Shaw, Indonesia, Borneo, A Church et al. 1722 (A); MT040357, MT040387, MT040429, –, **Ditta myricoides** Griseb.; AY794871, AY794675, –, –, **Dodecastigma amazonicum** Ducke, French Guiana, S Mori 22811 (US); AY794885, AY794711, MT040430, –, **Domohinea perrieri** Leandri; AY794895, AY794720, –, –, **Elateriospermum tapos** Blume; AY794873, AY794678, –, –, **Endospermum diadenum** (Miq.) Airy Shaw; AF530849; **Endospermum moluccanum** (Teijsm. & Binn.) Kurz, AY794671, –, –, **Fontainea pancheri** (Baill.) Heckel, New Caledonia, J Munzinger et al. 3414 (MO); MT040358, MT040388, MT040431, MT040478. **Fontainea picrosperma** C.T.White, Australia, P Forster 38363 (BRI); MT040359, MT040389, MT040432, MT040479. **Fontainea venosa** Jessup & Guymmer, Australia, G Guymmer 1861 (MO); AY794881, AY794708, MT040433, MT040480. **Garcia nutans** Vahl ex Rohr, cult. USA, K Wurdack D051 (US); AY794890, AY794714, MT040434, –, **Givotia madagascariensis** Baill., Madagascar, P Phillipson et al. 3767 (MO); AY794891, AY794715, MT040435, –, **Glycydendron amazonicum** Ducke; AY794876, AY794681, –, –, **Grossera macrantha** Pax, Cameroon, D Harris & J Fay 1514 (K); AY74976, MT040390, –, –, **Hevea pauciflora** (Spruce ex Benth.) Müll.Arg.; AY788175, AY794684, –, –, **Hylandia dockrillii** Airy Shaw, Australia, M Luckow 3806 (NY); AY794882, AY794710, MT040436, –, **Jatropha integerrima** Jacq.; AY794902, AY794685, AY971261, –, **Joannesia princeps** Vell., cult. Indonesia, M Chase 1262 (K; Kew DNA bank K1262); AJ418808, AY794686, MT040437, –, **Karima scarcesii** (Scott Elliot) Cheek, rr199; –, KU213659, –, –, **Karima scarcesii** (Scott Elliot) Cheek, rrKew; –, KU213658, –, –, **Klaianeanthus gabonae** Pierre; AY794869, AY794668, –, –, **Leeuwenbergia africana** Letouzy & N.Hallé, N Ekema 11176 (K); AY794979, MT040391, MT040438, –, **Manihot grahamii** Hook.; AY794875, AY794680, –, –, **Manniophyton africanum** Müll.Arg., Gabon, L White 3366 (MO); AY794886, AY794712, MT040439, –, **Micrandra inundata** P.E.Berry & A.Wiedenhoft; AY794877, AY794683, –, –, **Milddraedia carpinifolia** (Pax) Hutch. var. **strigosa** Radcl.-Sm., Tanzania, P Phillipson 4942 (MO); MT040360, AY794722, MT040440, –, **Moultonianthus leembruggianus** (Boerl. & Koord.) Steenis, Brunei, G Challen et al. 3 (K); AY794982, MT040392, –, –, **Myrcanthe discolor** Airy Shaw, New Caledonia, J Munzinger 3418 (P; Kew DNA bank K24717); MT040361, MT040393, MT040441, MT040481. **Nealchornea yapurensis** Huber; AY794865, AY794662, –, –, **Neoboutonia mannii** Benth. & Hook.f., Central African Republic, J Fay 6701 (MO); AY794896, AY794723, MT040442, –, **Neoholstia tenuifolia** (Pax) Rauschert, Malawi, E Tawakali & I Nachamba 1706 (NY); AY794898, MT040394, –, –, **Neoscortechinia kingii** (Hook. f.) Pax & K.Hoffm.; AJ402977, AY794806, –, –, **Omphalea diandra** L.; AY788183, AY794672, –, –, **Ophellantha steyermarkii** Standl.; AY794906, AY794690, –, –, **Ostodes paniculata** Blume, Indonesia, M Chase 1267 (K; Kew DNA bank K1267); AY794900, AY794725, MT040443, –, **Pantadenia adenanthera** Gagnep., Laos, J Maxwell 98–427 (A); MT040362, MT040395, MT040444, –, **Paracroton zeylanicus** (Müll.Arg.) N.P.Balacr. & Chakrab., cult. USA, C Annable 3575 (NY); AY794894, AY794719, MT040445, –, **Pausandra martinii** Baill., Venezuela, P Berry & G Aymard 7466 (MO); AY794887, AY794713, MT040446, –, **Pimelodendron zoanthogyne** J.J.Sm.;

AJ418812, AY794661, –, –. *Plagiostyles africana* (Müll.Arg.) Prain; AY794864, AY794660, –, –. *Pseudagrostistachys ugandensis* (Hutch.) Pax & K.Hoffm.; AY794966, AY794804, –, –. *Radcliffea smithii* Petra Hoffm. & K.Wurdack, Madagascar, C Jongkind 3598 (WAG); MT040363, MT040396, MT040447, –. *Reutealis trisperma* (Blanco) Airy Shaw; –, HG971930, –, –. *Ricinocarpos brevis* R.J.F.Hend. & Mollemans, Australia, B Eckermann LCS20640 [LCS=Landcare Services], AQ0790875 (BRI); MT040364, MT040397, MT040448, MT040482. *Ricinocarpos canianus* Halford & R.J.F.Hend., Australia, I Telford 12320, AQ0730498 (BRI); MT040365, MT040398, MT040449, MT040483. *Ricinocarpos tuberculatus* Müll.Arg., Australia, M Chase 2164 (K; Kew DNA bank K2164); AJ418817, AY794704, MT040450, MT040484. *Ricinocarpos verrucosus* Halford & R.J.F.Hend., Australia, R Jensen 2004, AQ0872581 (BRI); MT040366, MT040399, MT040451, MT040485. *Ricinodendron heudelotii* (Baill.) Heckel, cult. Indonesia, M Chase 1269 (K; Kew DNA bank K1269); AY794892, AY794716, MT040452, –. *Sagotia racemosa* Baill.; AY794903, AY794687, AY971264, –. *Sandwithia guyanensis* Lanj.; AY794904, AY794688, –, –. *Schinziophyton rautanenii* (Schinz) Radcl.-Sm., Zimbabwe, P van Wyk BSA3100 (MO); AF530874, –, MT040453, –. *Shonia bickertonensis* (Specht) Halford & R.J.F.Hend., Australia, D Lucas 73, AQ511632 (BRI); –, MT040400, MT040454, MT040486. *Shonia carinata* Halford & R.J.F.Hend., Australia, M Thomas 3813, AQ0830083 (BRI); MT040367, MT040401, MT040455, MT040487. *Shonia tristigma subsp. borealis* Halford & R.J.F.Hend., Australia, P Forster 33982, AQ0792756 (BRI); MT040368, MT040402, MT040456, MT040488. *Strophoblachia fimbriicalyx* Boerl., Indonesia, M Chase 1270 (K; Kew DNA bank K1270); AY794901, AY794728, MT040457, –. *Suregada aequoreum* (Hance) Seem.; AY794867, AY794666, –, –. *Suregada boiviniana* Baill.; AY788189, AY794663, –, –. *Syndyophyllum occidentale* (Airy Shaw) Welzen; AY794967, AY794805, –, –. *Tannodia cordifolia* (Baill.) Baill., Mayotte, O Pascal 656 (NY); AY794897, AY794721, MT040458, –.

*Tapoides villamilii* (Merr.) Airy Shaw, Malaysia, W Meijer & Aban 128772 (US); MT040369, MT040403, MT040459, MT040489.

*Tetrorchidium gabonense* Breteler; AY794872, AY794674, –, –. *Tetrorchidium macrophyllum* Müll.Arg.; AY788191, AY794676, –, –. *Trigonostemon thyrsoideus* Stapf, Vietnam, L Gillespie 7402 (CAN); MT040370, MT040404, –, –. *Trigonostemon verrucosus* J.J.Sm., Indonesia, M Chase 1274 (K; Kew DNA bank K1274); AY788192, AY794703, MT040460, –. *Tritaxis gaudichaudii* Baill.; –, MK876624, MK876518, –. *Vernicia fordii* (Hemsl.) Airy Shaw; NC\_034803, NC\_034803, –, –. *Vernicia montana* Lour., cult. Indonesia, M Chase 2105 (K; Kew DNA bank K2105); AY794899, AY794724, MT040461, –. *Weda fragarioides* Welzen, Indonesia, P Phillipson et al. 6448 (L); –, MT040405, MT040462, MT040490, matK: MT063192. *Weda fragarioides* Welzen, Indonesia, I Gushilman et al. 777 (L); MT040371, MT040407, MT040463, MT040491, matK: MT063191. *Weda lutea* Welzen, Indonesia, T Bangun et al. 118 (BO); –, –, –, MT040492. *Weda lutea* Welzen, Indonesia, T Bangun et al. 199 (BO); MT040373, MT040408, MT040465, MT040494. *Weda lutea* Welzen, Indonesia, I Gushilman & I Haris 178 (BO); MT040372, MT040407, MT040464, MT040493.

## Supplementary Material

The following supplementary material is available online for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.12581/supinfo>:

**Fig. S1.** Phylogram from RaxML analysis of plastid markers (*trnL-F* and *rbcL*) from *Weda* 4-marker data set.

**Fig. S2.** Phylogram from RaxML analysis of rDNA markers (ITS and ETS) from *Weda* 4-marker data set.

**Data S1.** Aligned molecular matrix for four markers (plastid: *trnL-F* and *rbcL*; rDNA: ITS, ETS), available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.nvxok6dnw>.