A taxonomic revision of the ecologically important *Ochna holstii* (Ochnaceae) complex using molecular and morphological data

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Abstract

Background and aims – *Ochna holstii* and its allies represent an ecologically important group in a variety of lowland to montane habitats in tropical eastern and southern Africa. Identifying and delimiting species within this group has proved challenging due to a lack of variation in morphological characters. We combine genomic-scale data of multiple accessions per species with morphological data to generate a taxonomic revision for the *Ochna holstii* complex using a multi-evidence approach.

Material and methods – A total of 50 samples representing eight species were analysed using target enrichment and a custom bait kit. Phylogenetic analysis was conducted using the multi-species coalescent model and a concatenation maximum likelihood method, and gene tree discordance was investigated. Herbarium specimens of the *O. holstii* complex were studied in detail for informative morphological characters, supplemented where possible from field collections, and a full taxonomic revision is provided.

Key results – Within *Ochna* sect. *Schizanthera* Clade I, our study confirms that all species are monophyletic and supported by morphological data with the exception of *O. holstii*, which is paraphyletic. A new species, *O. mchanga*, previously confused with *O. polyneura*, is described, and the placement of another recently described species, *O. maguirei*, is confirmed for the first time using molecular data.

Conclusion – The widespread montane tree *Ochna holstii* is non-monophyletic in its current circumscription and likely gave rise to the more range-restricted *O. oxyphylla* and *O. stolzii*. We suggest that an integrated taxonomy approach, using both molecular and morphological data, is essential for deciphering difficult species relationships in *Ochna*.

Keywords

African flora**,** incongruence, Malpighiales, non-monophyly, *Ochna*, range restricted, species complex, target enrichment

INTRODUCTION

Ochna L. is a paleotropical genus with ca 80 species distributed across Africa, Madagascar, the Indian subcontinent, and southeast Asia (Shah et al. 2021a). The current classification for the genus recognises four

sections based on targeted sequencing data in combination with diagnostic morphological characters (Shah et al. 2021a): (1) *O.* section *Renicarpus* N.Robson, which has variable anther dehiscence and drupelets that are kidney-shaped and attached centrally (these being ± ellipsoid to subglobose and attached at or towards the base in the

other sections); (2) *O.* section *Ochna*, circumscribed by species having anthers dehiscent through apical pores and a shortly branched style; (3) *O.* section *Schizanthera* Engl., circumscribed by species with longitudinal anther dehiscence and a style united at the apex; and (4) *O.* section *Ramistylus* T.Shah, which has species with apically biporose anthers eventually dehiscing by slits and a prominent deeply divided style.

Specimen identification and species delimitation is challenging within the genus partly due to many herbarium specimens lacking adequate flowers for identification by current literature and several species looking superficially similar to each other (Shah et al. 2021a). Regional accounts have noted difficulties in revising the group, with several treatments listing undescribed taxa. The Flora of Tropical East Africa (FTEA), for example, listed 47 species, including 13 that were not formally described (Verdcourt 2005). These ambiguities in morphology emphasise the need for an in-depth taxonomic revision using an integrated approach with molecular and morphological data. The latest phylogeny for the genus revealed that the second most species-rich section, *O.* sect. *Schizanthera*, is divided into two major clades (Shah et al. 2021a): Clade I consists of several tree and shrub species occurring in montane and dry forest environments, namely *O. holstii* Engl. and related species; whilst Clade II consists largely of species from fire-prone habitats, including several geoxylic suffrutescent species. Findings from Shah et al. (2021a) revealed that the species in Clade I require taxonomic attention, with several nodes in the phylogeny presenting high levels of gene tree conflict and poor support, with apparent paraphyly particularly notable in *O. polyneura* Gilg and *O. holstii*. Specimen misidentification was ruled out as a potential explanation of this relationship with thorough taxonomic work using the voucher and additional herbarium material.

Ochna holstii is a shrub or tree, growing up to 27 meters tall, widespread across tropical eastern Africa. It is a characteristic Afromontane tree, often locally common in habitats of evergreen moist montane forest, sometimes also occurring in drier forest assemblages (Verdcourt 2005), and is distributed from South Sudan through Central Africa and East Africa down to South Africa, broadly corresponding to the Eastern Afromontane hotspot (Burgess et al. 2007; Misned 2014). The species has been treated in several regional floras (Robson 1963; Bamps and Farron 1967; Du Toit and Obermeyer 1976; Verdcourt 2005) and, due to its large distribution range and presence in varying environments, it is known to display notable infraspecific morphological variation (Robson 1963; Verdcourt 2005). However, attempts to recognise these morphological outliers as independent taxa have proved unsuccessful, leading to conflicting species descriptions and circumscriptions in different regional accounts. Furthermore, closely related species in the same clade (*O.* sect. *Schizanthera* Clade I), including *O. polyneura*, *O. puberula* N.Robson, *O. oxyphylla* N.Robson, *O. stolzii* Gilg ex Engl., and *O. afzelioides* N.Robson, also

require taxonomic revision due to uncertain morphology-based species delimitation. As some of these closely allied species look superficially alike and occur in overlapping habitats, species delimitation solely through morphology is difficult. Thus, an integrated taxonomy approach involving both molecular and morphological data is required to adequately resolve species limits within this complex (Shah et al. 2021a).

Resolving relationships between species has greatly advanced through molecular phylogenetics (Willyard et al. 2021). The growing use of genomic scale datasets derived through methods such as target capture (Antonelli et al. 2021; Maurin et al. 2021; Ottenlips et al. 2021; Pérez-Escobar et al. 2021; Thomas et al. 2021; Shah et al. 2021b), RADseq (Razkin et al. 2016; Darbyshire et al. 2020b; Hühn et al. 2022; Comito et al. 2022), and single nucleotide polymorphisms (SNPs) (Eaton and Ree 2013) has opened the possibilities for resolving complex relationships across all levels of the Tree of Life. At the species level, incorporating hundreds of genes and ensuring a dense sampling may enable the unravelling of complex interspecies relationships (Willyard et al. 2021). However, despite these advances, difficulty remains when trying to resolve relationships within recent evolutionary radiations (Nicholls et al. 2015; Harvey et al. 2016; Snak et al. 2016; Fernández-Mazuecos et al. 2018; Larridon et al. 2020; van Kleinwee et al. 2022).

Molecular studies of plant lineages that have experienced recent rapid radiations ≤ 15 million years often result in poorly resolved phylogenetic relationships, with short branch lengths and low support values (Nicholls et al. 2015; Meiklejohn et al. 2016; Fernández-Mazuecos et al. 2018). The genus *Ochna* is estimated to have evolved around 21.5 Ma (millions of years) with a 95% highest posterior density (HPD) interval of 16.0–27.8 Ma, and *O.* sect. *Schizanthera* around 13.5 Ma with an HPD interval between 8–18 Ma (Shah et al. unpubl. data), which is relatively recent in evolutionary terms and may explain the difficulties in delimiting species. Moreover, based on studies of Neotropical plant groups, Pennington and Lavin (2016) hypothesised that recently evolved, widespread species are likely to be non-monophyletic with one or more narrow range species embedded within them.

Furthermore, the use of genomic data to elucidate these species relationships may result in phylogenetic discordance among genes and topological incongruence (Edwards 2008; Rose et al. 2021). Reasons for incongruence may reflect true biological signals (Paetzold et al. 2019) through processes such as incomplete lineage sorting, hybridisation, introgression, and gene duplication events (Maddison 1997; Degnan and Rosenberg 2009).

In this paper, we focus on resolving the evolutionary relationships of *O.* sect. *Schizanthera* Clade I through an integrated taxonomic approach using morphological and molecular evidence. We use this case study to test the hypothesis of Pennington and Lavin (2016) on an Afrotropical plant group. They suggested using numerous

individuals represented by multiple accessions for each species to test if tropical widespread woody species may be non-monophyletic. We apply a targeted capture method with a custom bait kit to generate data for *O. holstii* and seven related species and present the first attempt to resolve inter- and intraspecific relationships of this species complex.

MATERIAL AND METHODS

Molecular analyses

Taxon sampling

In total, 218 samples were included, comprising 50 ingroup and 168 outgroup samples. The ingroup samples span the morphological variation and geographic distribution of the following species in *O*. sect. *Schizanthera* Clade I: *O. holstii*, *O. oxyphylla*, *O. stolzii*, *O. polyneura*, *O. puberula*, *O. afzelioides*, and *O. maguirei* (Supplementary material 1). In this study, 25 additional samples for the ingroup were included compared to Shah et al. (2021a), and all 25 samples were confirmed to fall within *O*. sect. *Schizanthera* Clade I. Outgroup samples included coverage from all other sections of *Ochna*, consisting of the same accessions included in the molecular study of Shah et al. (2021a). Samples were extracted from herbarium specimens or freshly collected silica-dried leaf material.

DNA extraction, library preparation, and sequencing

Molecular lab work to generate targeted sequencing data was conducted in the Jodrell Laboratory at Royal Botanic Gardens, Kew. A modified cetyl-tri-methylammonium bromide (CTAB) approach, with chloroform:isoamyl alcohol (Sevag) and precipitation in isopropanol at -20°C (Doyle and Doyle 1987), was used to extract genomic DNA from leaf tissue samples. Following the manufacturer's protocol, the samples were purified with Agencourt AMPure XP Beads (Beckman Coulter, Indianapolis, IN, USA). All DNA extracts were quantified with a Quantus Fluorometer (Promega, Madison, WI, USA) and run on a 1% agarose gel to assess their average fragment size. DNA extracts with an average fragment size above 350 bp were sonicated using a Covaris M220 Focused-ultrasonicator (Covaris, Woburn, MA, USA) following the manufacturer's protocol. Dual-indexed libraries for Illumina® sequencing were prepared using the NEBNEXT Ultra II DNA Library Prep Kit and the NEBNEXT Multiplex Oligos for Illumina (Dual Index Primers 1 and 2; New England BioLabs, Ipswich, MA, USA) following the manufacturer's protocol, but using half the recommended volumes. We used 200 ng (or a minimum of 50 ng) of the fragmented DNA for the end-preparation reaction. Following the adapter ligation and size selection, the DNA fragments were amplified using eight cycles of PCR. The libraries were quantified using a Quantus™ Fluorometer, and fragment size was assessed with TapeStation using High Sensitivity D1000 ScreenTapes. The final library size, including the adapters, was ca 500 bp on average. For targeted enrichment of nuclear loci, we followed Johnson et al. (2019), samples with similar library concentration and fragment size were pooled and enriched with the Ochnaceae-specific probes (see Schneider et al. 2022; Shah et al. 2021a, for bait design and details). The hybridisation was performed for 24 hours at 65°C, followed by 12 cycles of PCR. Final products were again run on the TapeStation to assess the fragment size so they could be pooled equimolarly for sequencing. Sequencing of library pools was performed on an Illumina® HiSeqX instrument (San Diego, CA, USA) at Macrogen (Seoul, South Korea), producing 2 × 150 bp paired-end reads.

Phylogenetic analyses

The raw sequencing reads were trimmed with Trimmomatic v.0.36 (Bolger et al. 2014) using the settings LEADING:20 TRAILING:20 SLIDINGWINDOW:4:20 MINLEN:36 to remove adapter sequences and portions of low quality. The HybPiper pipeline v.1.31 was implemented (Johnson et al. 2016) using BWA v.07.17-r1188 (Li and Durbin 2009). Mapped reads were then assembled into contigs with SPAdes v.3.13.1 (Bankevich et al. 2012). The retrieve_sequences.py script from the HybPiper suite was used with the .dna flag to produce outputs of a single sequence per gene selected using length, similarity, and coverage. Potential paralogous exons were identified using HybPiper, and the impact of paralogy was subsequently investigated by analysing the dataset with and without paralogous genes, where 19 putatively paralogous genes were removed.

To negate the impact of missing data, we removed samples that had less than 25% overall mean recovery across all loci and removed sequences that had less than 30% of the average sequence length for that gene or, in shorter loci, less than 200 bp.

For the multi-species coalescent approach, individual maximum likelihood gene trees were constructed from the aligned exon regions with IQTREE v.2.0 (Nguyen et al. 2015) with 1000 ultrafast bootstraps using the "-B" option. Each gene was treated as a single partition with optimum model selection implemented by the program. Internal branches with bootstrap support values below 10% were collapsed with "nw_ed" in Newick utilities v.1.6 (Junier and Zdobnov 2010). Species trees were then inferred from the gene trees using ASTRAL-III v.5.6.3 (Zhang et al. 2018). Species trees were rooted using the outgroup taxa *Touroulia guianensis* Aubl. (Ochnaceae, Quiinoideae) and *Medusagyne oppositifolia* Baker (Ochnaceae, Medusagynoideae) with "nw_reroot" in Newick utilities v.1.6 (Junier and Zdobnov 2010). Furthermore, DiscoVista (Sayyari et al. 2018) was used to test and visualise discordance between the gene trees and the multi-species coalescent species tree.

For the concatenation approach, the alignments of each locus were concatenated using AMAS for the exon

and supercontig datasets separately. A species tree was generated using maximum likelihood analysis with the concatenated supermatrix of exon alignments using IQTREE v.2.0 with 1000 ultrafast bootstraps using the "-B" option (Nguyen et al. 2015). The data were treated as a single partition, and the optimum model was selected automatically by the program.

Morphology and distribution

Traditional methods of herbarium taxonomy were followed in the morphological analyses. Herbarium specimens, primarily held at BM, E, EA, and K (herbarium acronyms follow Thiers 2023), were examined and measured for the taxonomic descriptions. For completeness additional material from BR, G, HBG, LISC, NHT, SRGH, and WAG, especially type specimens, was viewed via JSTOR Global Plants. Measurements were taken with a ruler and binocular microscope graticule (Leica Microsystems MZ6, Wetzlar, Germany) on dry herbarium specimens. To try to recognize only monophyletic groups, we examined numerous herbarium specimens (ca 120) across the range of *O. holstii* to compare vegetative and reproductive features, including micromorphological characters such as position, size, and shape of the embryo. Drupelets from four specimens of *O. holstii*, *O. oxyphylla*, and *O. stolzii* were rehydrated and dissected to inspect the embryos. Label data from herbarium specimens were digitised, and geographic localities were georeferenced using regional gazetteers (Polhill 1988; Pope and Pope 1998) and Google Earth. Distribution maps were generated in ArcGIS Pro v.2.5.0 (Esri 2020); all maps are built from specimens seen at BM, EA, and K, with the exception of *O. maguirei*, which was adapted from Balkwill (2020). All specimens cited in the taxonomic treatment have been seen.

Conservation assessments

Preliminary conservation assessments were carried out according to the IUCN Red List categories and criteria (IUCN 2012). The extent of occurrence (EOO) and area or occupancy (AOO) of the species were calculated in GeoCAT (Bachman et al. 2011), where the AOO was based on a user-defined cell width of 2 km in line with IUCN Red List criteria (IUCN Standards and Petitions Subcommittee 2022).

RESULTS

Molecular analysis

Target capture success

Gene recovery from the Ochnaceae probe kit was extremely high, with all 275 loci recovered. Reads mapped on target ranged from 89410 to 12091738, with an average of 2524071 (Supplementary material 2). Ingroup taxa had 85% reads mapped on target, with no taxonomic bias observed across the genus and all sections and outgroup taxa equally well recovered.

Phylogenetic relationships

Both multi-species coalescent (MSC) and concatenation phylogenetic inference methods resolved similar topologies. In the MSC inference, *O.* sect. *Schizanthera* Clade I is retrieved as a strongly supported clade with local posterior probability (LPP) = 1 (Fig. 1A), although within it, *O. holstii* is resolved as paraphyletic. In the ML inference, both *O. holstii* and *O. oxyphylla* are resolved as paraphyletic (Supplementary material 3).

In detail, in the MSC results (Fig. 1A), the "mchanga" clade is sister to the rest of *O.* sect. *Schizanthera* Clade I, with strong support (LPP = 1). The accessions from south-eastern Tanzania and north-eastern Mozambique placed in this clade have previously been identified as *O. polyneura*. However, they are clearly distinct from the true *O. polyneura*, represented as the "polyneura" clade. The second is the "puberula" clade with accessions of *O. puberula*, in which its nine accessions are here resolved as monophyletic with broad sampling and strong support (LPP = 1). Our study includes nine accessions from this species. The accession *O. sp. 40*, an unplaced species from Uganda listed in FTEA, is sister to the rest of *O. puberula* with low support (LPP = 0.6). The rest of *O. puberula* is divided into two clades, with accessions from Tanzania in the first clade and accessions from Tanzania, Mozambique, Malawi, and Zambia in the second clade. The third, or "afzelioides", clade comprises samples of *O. afzelioides* resolved as a monophyletic species with moderate support (LPP = 0.88). The accessions of this species are split into two clades: (1) the first clade is composed of two accessions from Zambia; and (2) the second clade includes accessions from Tanzania and Rwanda. Next is a single accession of *O. maguirei* from South Africa with moderate support (LPP = 0.7), and then a strongly supported "polyneura" clade (LPP = 0.99). Sister to all other *O. polyneura* accessions is an accession listed as *O. sp. 42* in FTEA. The sampled *O. polyneura* accessions form a monophyletic "polyneura" clade with relationships between accessions receiving moderate to low support.

The final main clade represents the *O. holstii* complex, which is composed of *O. holstii*, *O. stolzii*, and *O. oxyphylla*. Together, these three taxa are the most recently diverging group of the section, with strong support (LPP = 0.99). Within this clade, *O. holstii* is currently defined as paraphyletic, with *O. holstii* I sister to *O. stolzii* with low support (LPP = 0.58), and together they are sister to *O. holstii* II + *O. oxyphylla* with strong support (LPP = 0.99). The sampling of *O. holstii* s.l. is broad, covering the range of its distribution from South Sudan to South Africa. The *O. holstii* I clade comprises 11 accessions, divided into two clades. The *O. holstii* II clade includes two accessions from Tanzania. *Ochna oxyphylla* is represented by three accessions, all from Tanzania, including *O. sp.*

47, an unplaced taxon from FTEA. A summary of these relationships is illustrated in Fig. 1B.

The concatenated ML analysis (Supplementary material 3) resolved similar relationships to the MSC results. Relationships of individual accessions within clades were largely congruent with the MSC results. The strongly supported (BS = 100) "mchanga" clade is again sister to the rest of *O.* sect. *Schizanthera* Clade I and includes accessions identified as *O. polyneura*. However, they clearly separate from the true *O. polyneura* accessions in the "polyneura" clade. Next is *O. puberula*, followed by *O. afzelioides*, both forming monophyletic groups with strong (BS = 100) and moderate (BS = 77) support, respectively. Next is a strongly supported "polyneura" clade (BS = 100), followed by a single accession of *O. maguirei* with strong support (BS = 100). The clade representing the *O. holstii* complex is composed of a clade consisting of *O. stolzii*, sister to both *O. holstii* and *O. oxyphylla*, both of which are retrieved as paraphyletic. *Ochna holstii* I is sister to a clade consisting of a paraphyletic *O. oxyphylla* with *O.*

holstii II nested within. A summary of these relationships is illustrated in Fig. 1C.

Phylogenetic discordance

High levels of gene tree conflict are found for relationships between species at different nodes in the MSC topology. Four nodes are identified to have the highest level of gene tree conflict (Fig. 1D–G). Node number four shows high levels of alternative topologies. However, in all circumstances, *O. oxyphylla* and *O. holstii* II are consistently resolved as sister species. Still, the placement of *O. holstii* I and *O. stolzii* in relation to these sister species is conflicting. For node 14, the core *holstii* clade labelled "holstii complex" was consistently resolved as sister to *O. polyneura* with competing topologies for relationships to the "holstii complex" + *O. polyneura* clade between *O. maguirei*, *O. afzelioides*, and *O. puberula*. Node 15 shows similar levels of topological gene tree conflict as node 14, with alternative topologies for the same species relationships. Finally, node 16 shows high levels
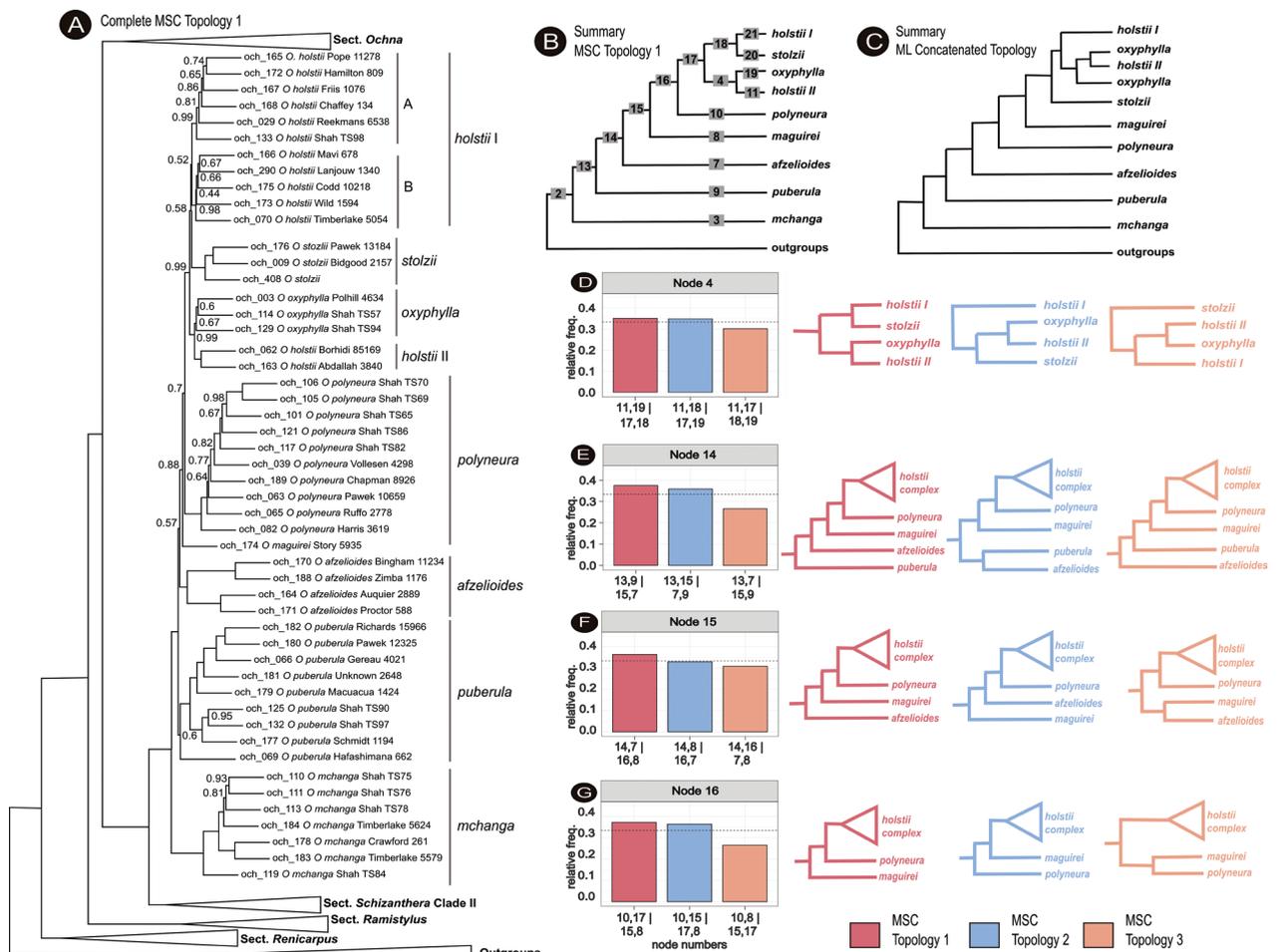
Figure 1. A. Well-sampled multi-species coalescent (MSC) tree of *Ochna* species within the *holstii* complex. The support values indicated above branches are local posterior probability (LPP) support values. Values not indicated = 1.0. **B**. Summary topology for species relationships through MSC analysis. **C**. Summary topology species relationships through concatenated maximum likelihood (ML) analysis. **D–G**. Gene-tree conflict and alternative topologies based on the MSC analysis for four nodes of interest. Bar graphs indicate quarter frequencies, with red bars representing the main topology and blue and orange bars representing the proportion of alternative topologies. Dotted lines indicate the threshold for equal possibilities for alternative topologies.

of discordance, with an alternative sister relationship for the "holstii complex" clade between *O. polyneura* and *O. maguirei*.

Morphology

All *Ochna* species are trees, shrubs, or geophytic shrublets, with alternate, simple leaves with serrate margins and a gynobasic style, often with the number of carpels visible. Species of *O.* sect. *Schizanthera* Clade I are generally shrubs or small trees, differentiating them from species in *O.* sect. *Schizanthera* Clade II, which are usually suffrutescent in habit in fire-prone habitats, except for *O. stolzii* which is mostly a suffrutex occurring in montane grassland of Tanzania and Malawi. The leaf shape of species within *O.* sect. *Schizanthera* Clade I is notably variable and largely influenced by environmental conditions. *Ochna holstii* is most easily separated by having large leaves up to 12 cm long, with clearly attenuate leaf apices. Other species within this section are easily recognized by having leaves that dry blue-black or green-black, most notably *O. polyneura*, *O. puberula*, and *O. maguirei*. Additional vegetative characters useful for species identification are the morphology of the young branchlets with indumentum differentiated from that of older growth and some species with lenticels. For instance, *O. afzelioides* has
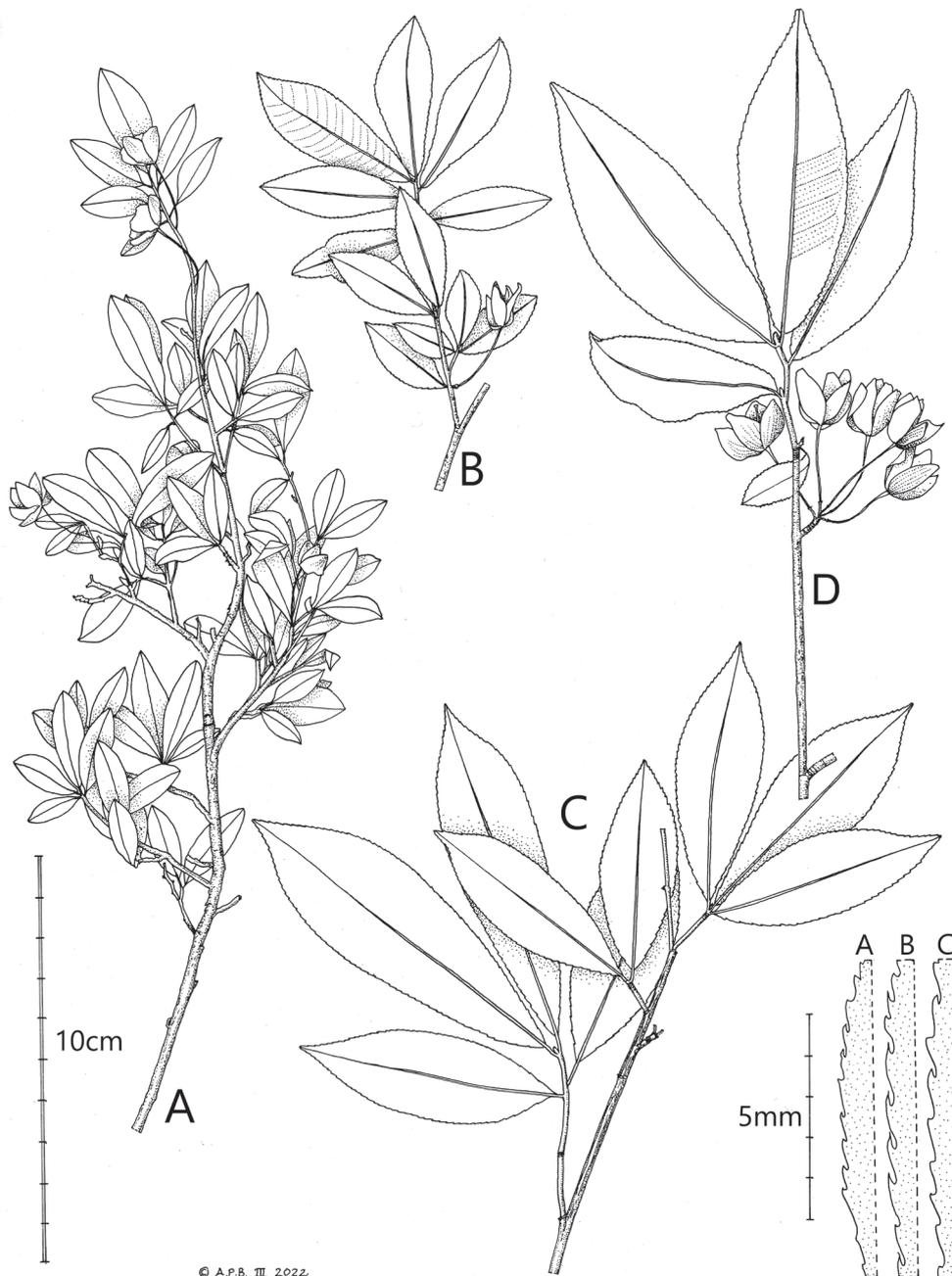
Figure 2. Species of *Ochna*, habit and leaf margin. **A**. *Ochna stolzii* (from *Richards 22529*). **B**. *Ochna oxyphylla* (from *Carmichael 354*). **C–D**. *Ochna holstii* (C from *Maas Geesteranus 4971*, D from *Pierlot 1731*). Drawn by Andrew Brown.

new growth densely lenticellate and puberulous with stiff pale brown hairs, while *O. maguirei* has olive-green new growth with brown-orange hairs.

Most species within the *O.* sect. *Schizanthera* clade I have exactly five carpels except *O. puberula* and *O. afzelioides*, which have 5–9 and 5–7 carpels, respectively. Figures 2 and 3 summarise inflorescence and leaf arrangement for all species in the revision. Species within the *O.* sect. *Schizanthera* Clade I are united by having longitudinal dehiscing anthers and a style united at the apex.

Inflorescence arrangement is predominately racemose (Fig. 5) with a varying number of flowers for different

species, although *O. stolzii* and *O. oxyphylla* usually have solitary flowers or racemes with few flowers. Pedicel length and articulation is another useful character and can help with species identification, although the measurements are variable within species and should be used in combination with additional characters or geography.

Molecular results placed *O. holstii* in two separate clades, with typical morphological characters proving indifferentiable between the clades. Embryo morphology was investigated to see if micromorphological characters such as position, size, and shape of the embryo would provide any additional characters for separating the two
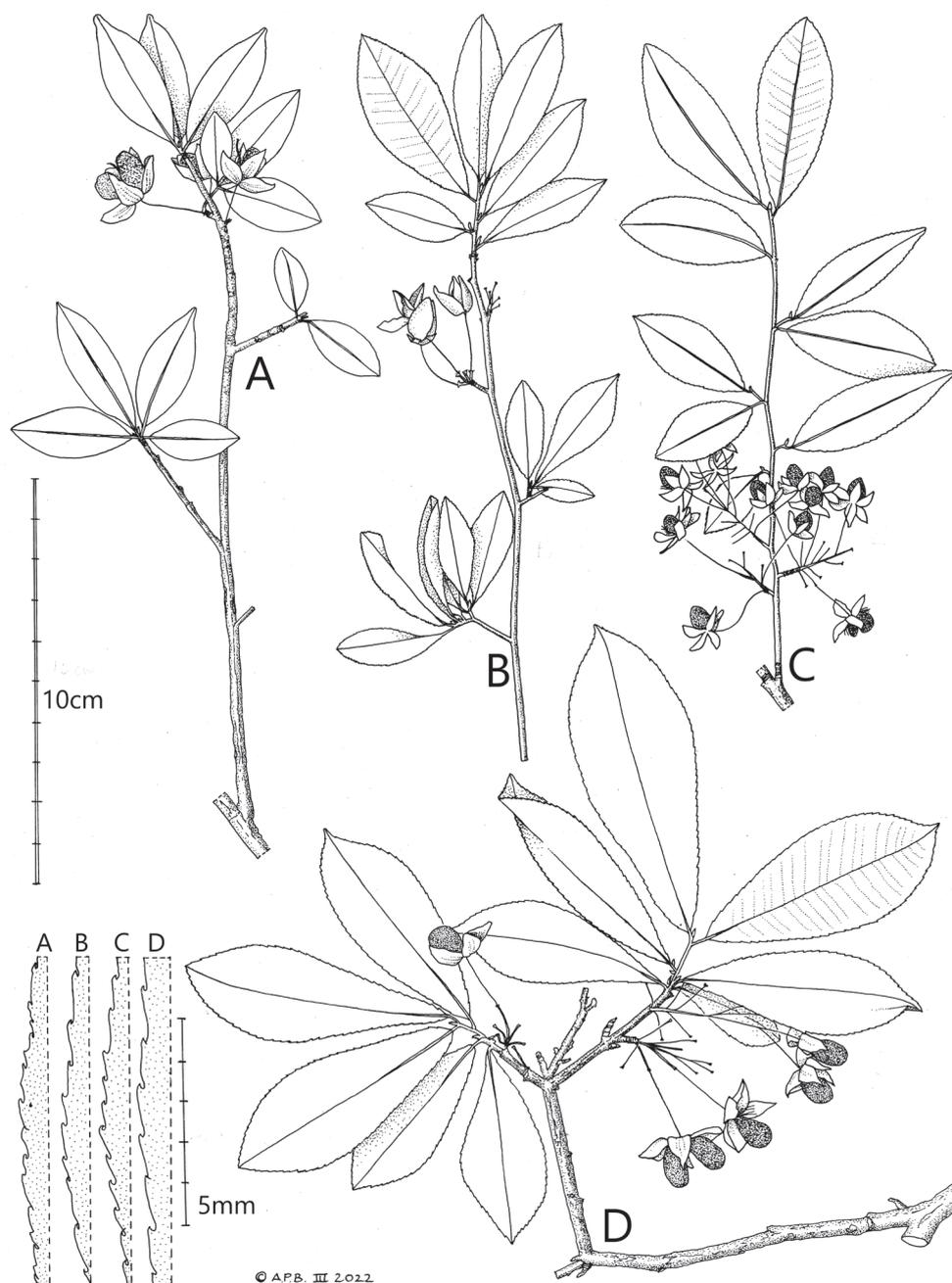
Figure 3. Species of *Ochna*, habit and leaf margin. **A.** *Ochna maguirei* (from *Story 5935*). **B.** *Ochna puberula* (from *Fanshawe 2648*). **C.** *Ochna afzelioides* (from *Richards 13726*). **D.** *Ochna polyneura* (from *Vollesen 4298*). Drawn by Andrew Brown.
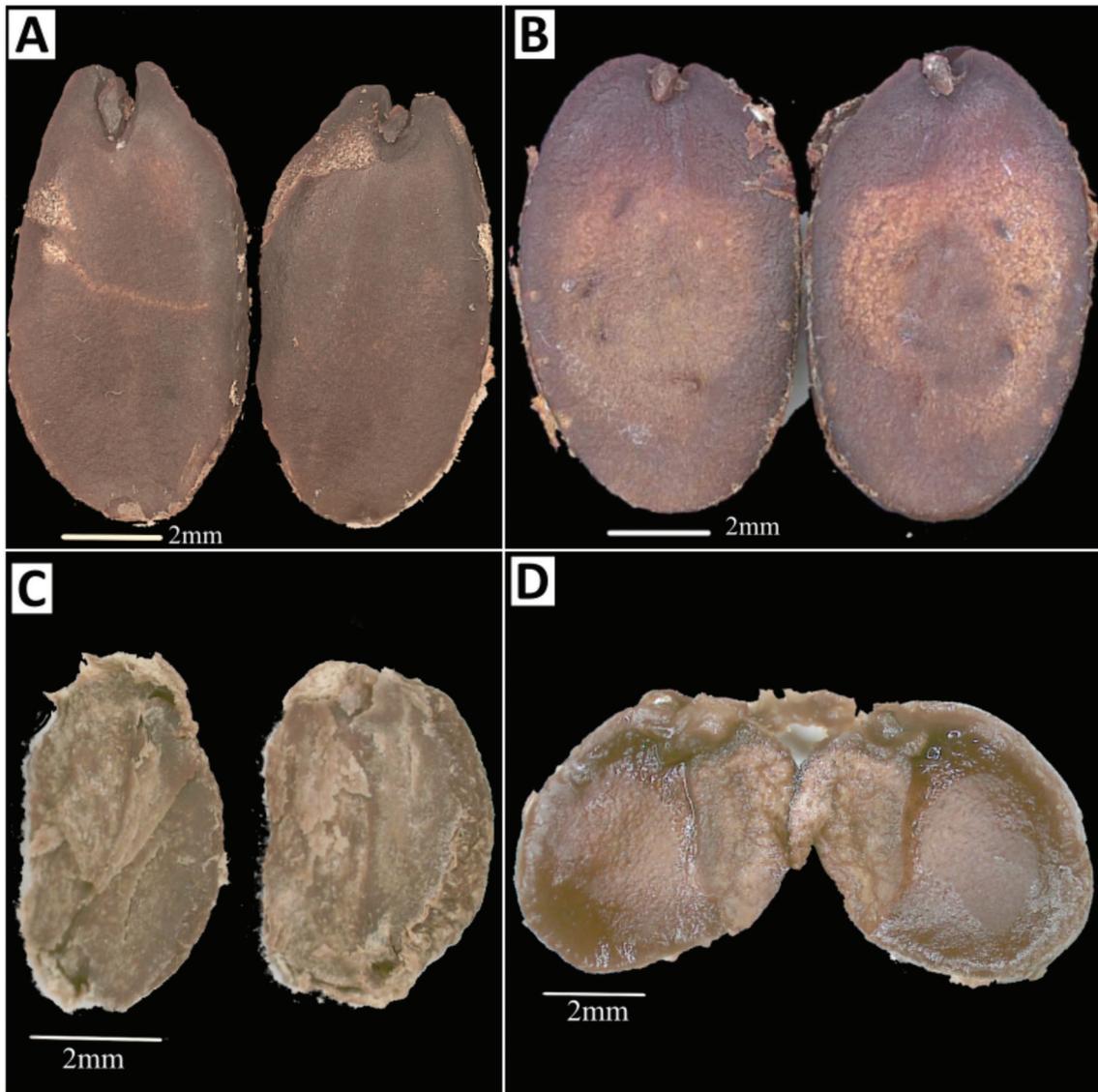
Figure 4. Dissection of rehydrated drupelets shows that there are no distinguishing morphological characters in the embryo of any of the mentioned taxa, particularly separating *Ochna holstii* I and II. **A**. *Ochna holstii* II. **B**. *Ochna holstii* I. **C**. *Ochna stolzii*. **D**. *Ochna oxyphylla*.
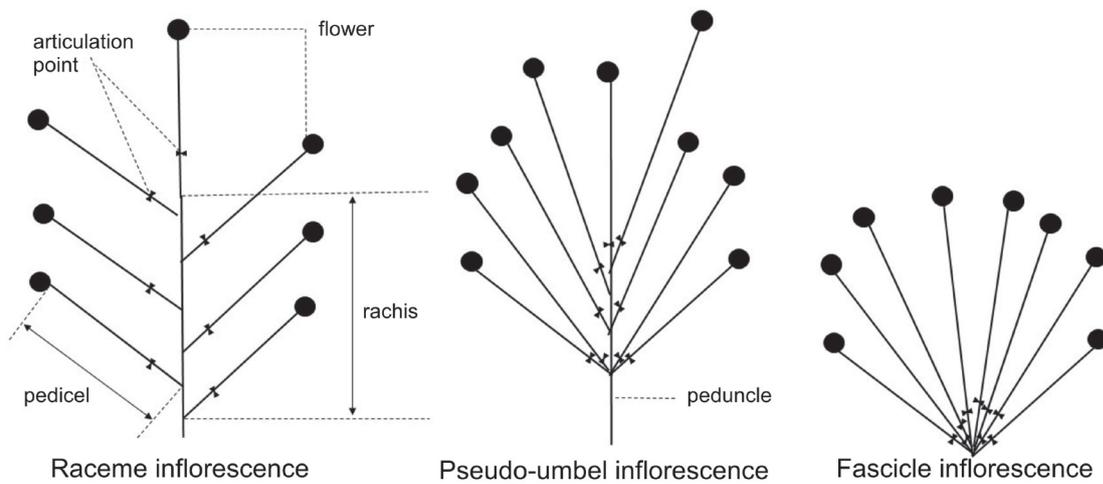
Figure 5. Diagram of inflorescence types for *Ochna* species showing three variations of inflorescence arrangements, including the position of the rachis, peduncle, pedicel, and articulation point.

clades of *O. holstii* and related species. Figure 4 shows drupelet dissections for *O. holstii* I and II, *O. oxyphylla*, and *O. stolzii*; however, no taxonomic discrimination could be made between the embryo of each specimen except for drupelet size and maturity. For detailed morphological results see the taxonomic treatment below.

DISCUSSION

Species relationships

Our densely sampled phylogenetic trees were essential to unravelling the relationships of *O. holstii* and closely related species using molecular and morphological data. Despite having several nodes with low support, the topologies of both analyses (MSC and concatenated ML) were largely congruent in addition to the morphological characters (see taxonomic treatment below) and ecological similarities within each group. This supports our decision to accept the monophyly of each species except for *O. holstii* (discussed below). The monophyly of *O. afzelioides* has been confirmed through our study, and its position in the phylogeny is consistent in both analyses. Previously, *O. polyneura* and *O. puberula* have often been confused with each other due to the similarity in leaves being oblanceolate to lanceolate, drying blue-black, an overlapping geographic distribution and both occurring in miombo woodland (i.e. seasonally dry, fire-prone woodland, usually dominated by detarioid legume genera, most notably *Brachystegia* Benth. and *Julbernardia* Pellegr.). Molecular evidence has confirmed the separation of the two species with supporting morphological criteria: *O. polyneura* has larger leaves, pedicels articulated farther from the base, and exactly 5 carpels vs *O. puberula* with smaller leaves, pedicels consistently puberulous and articulated closer to the base, and 5–9 carpels. The position of *O. puberula* is more or less consistent in all the topologies. However, the placement of *O. polyneura* is not confirmed with confidence, although both nodes receive strong alternative topologies (Fig. 1E–F). Furthermore, a group of specimens, previously misidentified as *O. polyneura* but clearly separable from the true *O. polyneura*, has been revealed through phylogenetic inference and supported by morphological and ecological differences (see taxonomic treatment below). This included the following specimens; *Shah TS75*, *Shah TS76*, *Shah TS78*, *Shah TS84*, *Timberlake 5624*, *Timberlake 5579*, and *Crawford 261*. This new species to science is consistently resolved as sister to the rest of *O.* sect. *Schizanthera* Clade I. Similarly to *O. puberula*, this species has been mistakenly identified as *O. polyneura* due to the leaves drying green-black, but the notable difference is that the species only occurs in dry sand-forest habitats along the coast of southeastern Tanzania and north-eastern Mozambique. This distribution follows the Rovuma Centre of Endemism, which is notable for its high numbers of endemic species (Darbyshire et al.

2019, 2020a), with several other newly discovered species from this area, such as *Casearia rovumensis* I.Darbysh. & J.E.Burrows, *Convolvulus goyderi* J.R.I.Wood, and *Vitex francesiana* I.Darbysh. & Goyder.

A further finding of our study is the placement of *O. maguirei*, a species recently described from South Africa by Balkwill (2020) that had erroneously been placed together with *O. holstii* in herbaria in the past. The species differ in that *O. maguirei* is a smaller tree with corky bark and leaves congested at apex, growing in more open habitats, whereas *O. holstii* is a larger tree, upright with a smooth to slightly rough bark, growing in forest habitats. Through our study, the position of *O. maguirei* within *O.* sect. *Schizanthera* Clade I has been corroborated with molecular evidence; however, its relationship to *O. holstii* and related species is still unstable with conflicting topological placement between the MSC and concatenation analyses and high levels of gene tree conflict (Fig. 1E–G). This may be due to having just a single sample representing the species and could be elucidated with denser sampling in future studies.

Molecular results for *O. oxyphylla* provided conflicting topologies between the MSC and concatenated analysis. In the former, *O. oxyphylla* was resolved as monophyletic with low support (LPP = 0.67), but paraphyletic in the latter method. This incongruence may be linked to the unstable status of *O. holstii* (discussed below), through which a widespread species has given rise to a range-restricted species with continued gene flow between them. Despite the conflicting topologies, we chose to follow the results of the MSC analysis as it can better account for alternative gene histories which may result from incomplete lineage sorting (Maddison 1997). The MSC results were further supported by morphological evidence uniting all the accessions of *O. oxyphylla* in this study.

Paraphyly of *Ochna holstii*

Regional flora accounts (Robson 1963; Verdcourt 2005) for *O. holstii* have stated the difficulty of specimen identification and species delimitation due to high morphological variability, where separation of infraspecific taxa has failed. The inclusion of a large number of samples in a phylogenetic framework has demonstrated the complexity of the group and revealed the non-monophyly of *O. holstii*.

The samples of *O. holstii* are grouped in two major clades, namely "holstii I" and "holstii II" (Fig. 1A). In the "holstii I" group, the samples are split into two groups, with samples from the "holstii I A" from South Sudan, Ethiopia, Burundi, Kenya, Tanzania, and Zimbabwe, largely north of the equator. While "holstii I B" consists of samples largely south of the equator, from Tanzania, Mozambique, Zimbabwe, and South Africa, all from high-altitude moist forests. The second clade, "holstii II", consists only of two samples from Tanzania, specifically from the West Usambara Mountains, in Tanga Region. However, the two clades (holstii I and II)

are indifferentiable by morphology, united by usually being large trees (up to 27 m tall) with long-attenuate leaves, often arranged in clusters and with long fruiting pedicels, characters that are diagnostic for *O. holstii*. It is not unlikely that "holstii II" may represent a single cryptic species from the Usambara Mountains as the mountains are part of the ancient Eastern Arc Mountain chain, comprising 13 montane blocks in Kenya and Tanzania and renowned for their large numbers of endemic species (Burgess et al. 2007; Platts et al. 2011). Therefore, it would not be surprising for this area to reveal a further range-restricted taxon. Nevertheless, recognising a cryptic species here would require significant nomenclatural changes; the type specimen of *O. holstii* is from the West Usambaras, and so the holstii II clade is likely to represent *O. holstii* s.s. (although we did not sample the type specimen due to lack of material and consciousness of destructive sampling of a type specimen). Therefore, splitting *O. holstii* into two species would require the larger clade (holstii I) to be renamed (using one of the available names currently in synonymy, most likely *Ochna prunifolia* Engl.) and a clade with only two specimens from the Usambara Mountains to retain the name *O. holstii*. Without substantial morphological synapomorphies, complications in specimen identification, collection, and most importantly, conservation action of this characteristic Afromontane tree species will likely arise. Therefore, we favour the recognition of *O. holstii* in its current sense as a paraphyletic species under the separately evolving metapopulation concept of De Queiroz (2007). Future studies with more samples from the Usambara Mountains and the wider Eastern Arc Mountains may allow the recognition of both clades at the species level. Additional data based on the chemistry or characteristics of living plants (e.g. bark and slash characters) may also prove useful for separating the groups. Nested in the two holstii clades are monophyletic groups of *O. oxyphylla* and *O. stolzii,* here recognised and maintained at species level. We have chosen not to reduce these species to synonymy or any infraspecific rank due to notable and characteristic morphological and ecological features. *Ochna oxyphylla* is a small to medium tree species found in upland moist forest in the Eastern Arc Mountains and the Lake Nyasa Highlands of Tanzania. It is easily differentiated from *O. holstii* by having much smaller leaves and reduced inflorescence with usually 1–2 flowers but sometimes up to 6. Similarly, *O. stolzii* is uniquely different from *O. holstii* and *O. oxyphylla* by being mostly a dwarf shrub or geoxylic suffrutex, with small leaves and is often characteristic of montane grassland in south-western Tanzania and north-eastern Malawi.

Resolving relationships of rapid radiations is known to be a challenge in plant systematics (Cooper et al. 2022; Lagomarsino et al. 2022). Preliminary data from Shah et al. (unpubl. data) estimate that section *Schizanthera* Clade I (holstii complex) originated recently, with 95% HPD interval between 5 and 16 Ma, yet dispersed widely across Africa, suggesting a recent rapid adaptation. In the process, it is possible that a large, widespread ancestral species could have colonised East Africa and given rise to more range-restricted daughter species in nearby mountain areas, namely *O. oxyphylla* and *O. stolzii*. This type of non-monophyly has been shown to occur in other groups, particularly in the South American rainforests and savannas, such as species of *Inga* Mill. (Dexter et al. 2010); species of *Protium* Burm.f. (Fine et al. 2014) and *Ficus insipida* Willd. (Honorio Coronado et al. 2014), as highlighted and summarised by Pennington and Lavin (2016). Our study corroborates the predictions of Pennington and Lavin (2016) that using well-sampled phylogenies for widespread woody rainforest species, such as *O. holstii*, is likely to reveal groups with young stem ages with genes that do not coalesce. Our study is one of the first empirical studies using genomic-scale data to show this pattern for a woody tree species of Africa.

Future work using plastome data in conjunction with nuclear data may provide additional insights to decipher species relationships. Plastome data are known to have a relatively conserved rate of evolution (Li et al. 2021) and could elucidate gene tree conflict or highlight any hybridization events, providing more evidence to test our current findings.

TAXONOMIC TREATMENT

Identification key to the species within the *Ochna holstii* complex

Before using this key, the authors advise consulting the relevant flora to ensure that species outside this species complex are correctly excluded.

1. Large tree, usually above 10 m and up to 27 m tall but sometimes 6–10 m, very rarely shrubby forms between 1.5–3 m; leaves 40–120(–165) mm long, lanceolate to oblanceolate, leaf apex attenuate to markedly so; flowers 6–16, arranged in racemes with rachis up to 20 mm long; pedicels 15–40 mm long, articulated at or near the base, or up to 3 mm from the base; upland to montane evergreen forest, 1000–4600 m elevation; South Sudan to South Africa ....1. *O. holstii*
– Smaller trees, shrubs or suffrutices, up to 10 m tall; other characters not in the above combination **2**
2. Flowers mostly solitary or sometimes arranged in fascicles or racemes with 2–5(–6) flowers; pedicels articulated at or near the base, never more than 5 mm above the base; upland grassland, rocky outcrops or upland forest, 1400–2400 m elevation **3**
– Flowers in racemes, fascicles or pseudo-umbels with (2–)4–11 flowers, never solitary; pedicels articulated at or near the base or up to 13 mm above the base; miombo woodland, coastal thicket or riverine forest, 20–1940 m elevation **5**

3.   Shrubs or suffrutex 0.4 –1.8(–2) m tall; leaves small 10–45 mm long, 5–20 mm wide; grasslands, rocky outcrops, forest patches or upland miombo woodland; 1524–2400 m elevation; S Tanzania, N Malawi... 2. **O. stolzii**

–   Shrubs or small trees (1.5–)2–8 m tall; leaves 20–80 mm long, 10–40 mm wide; savannas or upland, montane and riverine forests; E & S Tanzania and NE South Africa...**4**

4.   Flowers arranged in 2–4 racemes in short axillary shoots, sometimes several flowering shoots near the tip of the same branch, rachis 1.5–4.5 mm long; pedicels 8.5–13.5 mm long, articulated more than 1 mm above the base; leaf apex acute or narrowly rounded, margin coarsely toothed; bark grey-brown, corky; savanna amongst boulders; 1430–1490 m elevation; NE South Africa .... 4. **O. maguirei**

–   Flowers solitary or arranged in short 2–6 flowered racemes, rachis 0–2 mm long; pedicels 8–35 mm long, articulated up to 5 mm above the base; leaf apex sharply acute, margin finely toothed; bark dark brown, slightly fissured and lenticellate, not corky; upland, montane and riverine forest; 1400–2400 m elevation; E & S Tanzania ....3. **O. oxyphylla**

5.   Leaves drying green throughout during flowering and fruiting, sometimes black when young, margins densely serrate with teeth fine and prominent, leaves evenly distributed along branches; pedicel puberulous with stiff white hairs below articulation point, usually glabrous above articulation or sometimes glabrous throughout, drying brown-green; bark grey-white or grey-brown with pale white lenticels or white linear markings, rough; miombo woodland, evergreen and riverine forest; 1000–1450 m elevation; W Tanzania, Rwanda, Zambia ....7. **O. afzelioides**

–   Leaves drying blueish-black, green-blue, or green-black at least towards the apex, margins serrate but not densely so, most often appearing clustered at end of shoots; pedicel indumentum uniform above and below articulation; bark brown-green or grey-brown, appearing corky, fissured or slightly peeling **6**

6.   Flowers 4–8 in pseudo-umbels or racemes; sepals markedly accrescent, 3.5–5.5 mm long in flower, extending to 10–20 mm long and 8–12 mm wide in fruit, usually enclosing the drupelets; carpels 5–9; cross-section of young stem growth quadrangular; bark grey-white or grey-brown, sometimes with peeling bark; miombo woodland, rocky ground; 740–1940 m elevation; Uganda, Tanzania, Malawi, DRC, Mozambique, Zambia, Zimbabwe .... 6. **O. puberula**

–   Flowers 6–11 in racemes or up to 7 in fascicles; sepals not markedly accrescent, not enclosing the fruit; carpels 5; cross-section of young stem growth rounded or ribbed, not quadrangular; bark grey–brown, corky and fissured, sometimes peeling **7**

7.   Flowers 7–10 in racemes or 2–5 in fascicles, rachis 3–30 mm long, sepals during flowering 7.5–10 mm long, 3.5–6 mm wide; young growth drying brown-green, glabrous or sometimes puberulous, often with pale and sparse lenticels; bark grey–brown, or sandy-brown, corky and fissured; miombo woodland and wooded grasslands; 23–1880 m elevation; Tanzania, Malawi, Zimbabwe.......... .... 5. **O. polyneura**

–   Flowers 6–11 in racemes or 5–7 in fascicles, rachis 6–15 mm long, sepals during flowering 5.5–7 mm long, 3–3.5 mm wide; young growth dusty brown, puberulous; bark grey-brown or sometimes whitish, rough, fissured and slightly peeling; coastal thicket and dry/deciduous forest, on sandy soil; 65–830 m elevation; SE Tanzania, NE Mozambique .... 8. **O. mchanga**

1. ***Ochna holstii*** Engl. (Engler 1894: 69)

Figs 2C–D, 4A–B, 6

Diporidium holstii (Engl.) Tiegh. (Tieghem 1902: 356) – Type: same as for *Ochna holstii*.

Biramella holstii (Engl.) Tiegh. (Tieghem 1903: 97) – Type: same as for *Ochna holstii*.

Ochna prunifolia Engl. (Engler 1895: 273; Gilg 1903: 236; Brenan and Greenway 1949: 384) – Type: TANZANIA • Rombo Mku; 1894; *Volkens 1960*; lectotype (**designated here**): E! [E00200459]; syntype: B† • KENYA • Kitui; *Hildebrandt 2825*; syntype: B† • TANZANIA • Mkulia; *Volkens s.n.*; syntype: B†.

Diporidium prunifolium (Engl.) Tiegh. (Tieghem 1902: 356) – Type: same as for *Ochna prunifolia*.

Ochna longipes Baker (Baker 1897: 247; Brenan 1953: 234; White 1962: 251) – Type: MALAWI • Mt Malosa near Zomba; 1896: *Whyte 429*; holotype: K! [K000431165].

Ochna shirensis Baker (Baker 1897: 247) – Type: MALAWI • Mt Zomba & Mt Malosa; 1896: *Whyte 430*; holotype: K! [K000431163].

Ochna acutifolia Engl. (Engler 1900: 433) – Type: TANZANIA • West Usambaras; *Buchwald 350*; lectotype (**designated here**): K! [K000431145]; isolectotype: BM; syntype: B† • TANZANIA • Uluguru, near Nghweme; *Stuhlmann 8852*; syntype: B†.

Diporidium acutifolium (Engl.) Tiegh. (Tieghem 1902: 356) – Type: same as for *Ochna acutifolia*.

Ochna densicoma Engl. & Gilg (Gilg 1903: 241; Brenan and Greenway 1949: 382) – Type: TANZANIA • East Usambaras, Nderema; 1901; *Scheffler 169*; holotype: B†; lectotype (**designated here**): EA! [EA000002025]; isolectotypes: BM [BM000798536], BR [BR0000006266356], E! [E00200461], K! [K000431144].

Ochnella densicoma (Engl. & Gilg) Tiegh. (Tieghem 1903: 40) – Type: same as for *Ochna densicoma*.

Ochna chirindica Baker f. (Rendle et al. 1911: 37) – Type: ZIMBABWE • Melsetter District, Chirinda Forest; 1905; *Swynnerton 106*; holotype: K! [K000431166]; isotype BM [BM000798543].

Ochna keniensis Sleumer (Sleumer 1934: 69; Dale and Greenway 1961: 338; Beentje 1994: 121) – Type: KENYA • Mt Rupingazi River; 1922; *Fries & Fries 2031*; holotype: UPS [fide Verdcourt 2005]; isotype: S [S-G-4319].

Type. TANZANIA • West Usambaras, Mbalu; 1893; *Holst 2601*; holotype: B†; lectotype (**designated here**): K!

[K000431146]; isolectotypes: BR [BR0000006265694], HBG [HBG509293].

Description. Small to large <u>tree</u> 4–27 m tall, usually over 10 m tall, rarely with shrubby forms 1.5–3 m tall. <u>Bark</u> grey-brown. <u>Stems</u> dark grey, sometimes peeling, with white lenticels, these sometimes sparse; young stems dark brown, with white lenticels, glabrous. <u>Stipules</u> brown, linear, sometimes persistent to deciduous, 2–15 mm long. <u>Leaves</u> green, often drying brown or rarely blue-black, chartaceous, glabrous, lanceolate to oblanceolate, 4–12(–16.5) cm long, 1–5(–5.5) cm wide; leaf base attenuate-cuneate (rarely rounded), leaf apex attenuate, margins serrate; lateral veins 20–28, appearing at right angles to midrib, tertiary vernation reticulate; petiole 0.5–3.5 mm long; buds brown, large, up to 7.5(–9) mm long. <u>Flowers</u> in racemes with 6–16 flowers; rachis 0.5–2 cm long, glabrous; pedicels 1.5–4 cm long, articulated at or near the base, or up to 3(–10) mm above the base, glabrous throughout. <u>Sepals</u> green to brown in flower, oblong to elliptic, 8–10 mm long, 4–6 mm wide in flower, turning red in fruit, then 11–14 mm long, 4–8(–10) mm wide. <u>Petals</u> yellow, often pale, obovate, 8.5–10.5 mm long, 3.5–4 mm wide. <u>Anthers</u> dehiscing by longitudinal slits, 1.5–2 mm long; filaments 2–3.5 mm long. <u>Carpels</u> 5; styles united to apex, 4–7 mm long <u>Drupelets</u> black, ellipsoid, 8–13 mm long, 4–6 cm wide, attached at the base.

Distribution. Widespread in montane regions of eastern Africa: South Sudan, Ethiopia, Democratic Republic of the Congo (DRC), Uganda, Kenya, Tanzania, Burundi, Rwanda, Mozambique, Malawi, Zambia, Zimbabwe, South Africa (Fig. 6).

Habitat. Usually found in upland and montane (Afromontane) moist forests as a medium- to large-sized tree; occasionally recorded in more open habitats including montane grassland and amongst rocky boulders. Altitude: 1000–4600 m.

Phenology. Most flowering and fruiting specimens are collected from October to March. This corresponds to the shorter rainfall season in East Africa (October to December) and the longer rainfall season in southern Africa (November to March).

Preliminary IUCN conservation assessment. *Ochna holstii* is a medium- to large-sized tree (rarely in shrubby form), widespread across montane forests in East and Southern Africa. The estimated extent of occurrence (EOO) is 3,888.294 km², and the area of occupancy (AOO) is 548 km². Forest loss due to agricultural expansion and wood harvesting, particularly at its lower altitudinal limit, may have an impact on some subpopulations. Although the species falls within the range of values for the vulnerable category due to its AOO for criteria B2, the species is known from substantially more than 10 threat-defined locations, it is assessed as Least Concern (LC).

Additional material examined. SOUTH SUDAN – **Equatoria Province** • Mt Lotuke, Didina Mts; 6500 ft; 20 Apr. 1939; fl.; *Myers 10959*; K [K001383230] • Imatong Mountains, Bushbuck Hill; 2300 m; 21 Feb. 1982; fl.; *Friis & Vollesen 982*; K [K001383227].

ETHIOPIA – **Oromia** • Mogada; 5°30'N, 38°20'E; 1700 m; Jun. 1976; fr.; *Haile 696*; K [K001271514].

KENYA • **Baringo** • Eldama Ravine and Mau; 7500 ft; May 1900; fr.; *Whyte 1898*; K. – **Narok** • Nguruman Range, Lebetero Hills; Jan 1961; fr.; *van Someren EA12286*; K [K001082543]. – **Kericho** • Londiani District, Tinderet Forest Reserve, between Camp 4 and Tinderet Triangulation Point; 0°05'00"S, 35°21'30"E; 2300 m; 1 Jul. 1949; fr.; *Maas Geesteranus 5311*; K [K001082539]. – **Samburu** • Lorogi forest; 1°04'N, 36°52'E; 2170 m; 26 Mar. 1967; fr.; *Gillett 18095*; EA, K [K001082519] • Elgon; 7500 ft; 23 Apr. 1968; fr.; *Hamilton 809*; K [K001082523]. – **Meru** • Mount Kenya Forest Reserve between Naro-Moro and Nyeri; 21 Feb. 1973; fr.; *Lawton 1751*; K [K001082534].

UGANDA – **Eastern** • N.E. Mt Elgon; 6500 ft; May 1933; fr.; *Dale 3121*; K [K001082516; K001082517] • Imatong Mountains; 7800 ft; Apr. 1938; fr.; *Eggeling E3539*; K [K001082514]. – **Northern** • Dodoth, Kidepo National Park; 1800 m; 16 May 1972; fr.; *Synnott 984*; EA, K [K001082512].

TANZANIA – **Korogwe District** • Shume, Korogwe, in the Shume valley bottom, about 0.5 miles from the Forest House; 7 Jan. 1947; fr.; *Hughes 16*; EA, K [K001082587]. – **Lushoto District** East Usambaras, Derema; 3200 ft; 29 Dec. 1932; fl.; *Greenway 3308*; EA, K[K001082578] • W. Usambaras; 6200 ft; 16 Jan. 1952; fr.; *Parry 105*; EA, K [K001082589] • Near Lushoto water supply; 20 Feb. 1962; fl.; *Mgaza 452*; EA, K [K001082591]. – **Njombe District** • Ruhuji Waterfalls; 9°14'12.48"S, 34°45'44.46"E; 1823 m; 26 Jan. 2020; fr.; *Shah TS98*; K [K001271562].
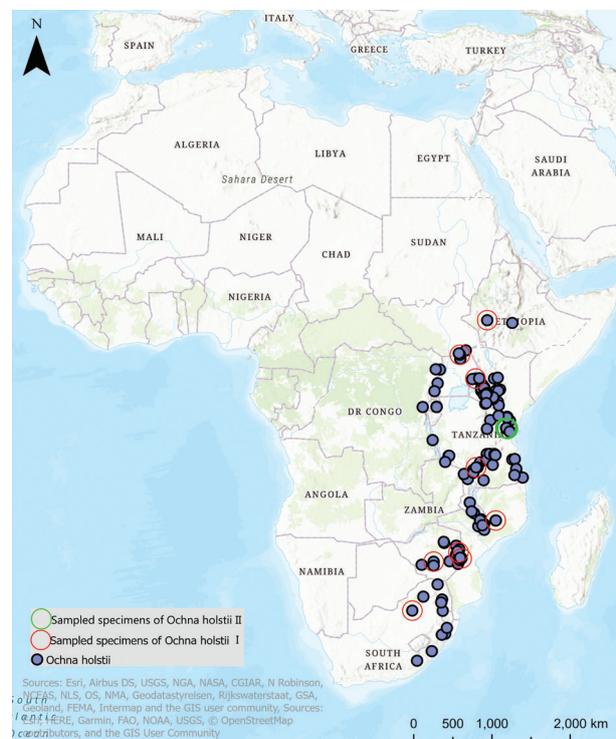
Figure 6. Distribution map of *Ochna holstii* from georeferenced herbarium specimens in Africa.

DEMOCRATIC REPUBLIC OF THE CONGO – **South Kivu** • Kalehe, Mikouzi, vallée de la Tshinganda; 1950 m; 10 Dec. 1957; fr.; *Pierlot 1731*; K [K001391607]. – **Haut Katanga** • Plateau des Kundelungu; 1960 m; 28 Nov. 1968; fr.; *Malaisse 6122*; K [K001391606].

MALAWI – **Thyolo District** • Cholo Mt; 1400 m; 20 Sep. 1946; fl.; *Brass 17668*; BM, K [K001387307]. – **Chitipa District** • Lundazi, upper slopes of Kangampande Mt, Nyika Plateau; 7000 ft; 8 May 1952; *White 2793*; K [K001271529] • Mulanje Mt forest; 8 Oct. 1957; fl.; *Chapman 454*; BM, K [K001387304] • Nyika Plateau, Luselo Evergreen Forest patch; *Salubeni 356*; K [K001387298]. – **Mulanje District** • Mt Mulanje, close to the site of the old Boma hut; 1840 m; 3 Nov. 1986; *Chapman & Chapman 8186*; E [E01123512], K [K001387295].

MOZAMBIQUE – **Zambezia Province** • Chiperone Mountain; 29 Nov. 2006; *Patel & Bayliss HP 7183*; K [K000545146] • Namuli Mountain, Naconha Plateau; 15°22'40"S, 37°01'09.2"E; 1977 m; 21 Nov. 2007; fr.; *Timberlake et al. 5267*; K [K000613996] • Namuli Mountain, Muretha Plateau-Mukocha forest; 15°23'57.4"S, 37°02'29.9"E; 1730 m; 28 May 2007; *Timberlake et al. 5054*; K [K000613434].

ZIMBABWE – **Mutare District** • Umtali; 8 Nov. 1948; fl.; *Chase 1256*; BM, K [K001387323]. – **Chipinge District** • Chirinda Forest; 4 Jan. 1948; fr.; *Chase 433*; BM, K [K001387316] • Old Bikita, on edge of forest plateau; 4300 ft; 16 Dec. 1953; fr.; *Wild 4407*; K [K001387315] • Gwasha, on the first range; 4500 ft; 22 Sep. 1960; fr.; *Rutherford-Smith 168*; K [K001387335]. – **Chimanimani District** • Chimanimani Mountain, Martin Forest Reserve; 17 Nov. 1967; fl.; *Mavi 678*; K [K001387313]. – **Mberengwa District** • Bukwa Mt, main ridge; 1700 m; 30 Oct. 1973; fl.; *Pope et al. 1126*; K [K001387336].

SOUTH AFRICA – **KwaZulu-Natal** • Ingeli Forest Reserve; 18 Dec. 1915; fr.; *Chilvers 1946*; K [K001271523]. – **Mpumalanga** • Barberton; 22 Jan. 1957; *Story 5993*; K [K001271517]. – **Limpopo** • Mariepskop; 3 Dec. 1959; fr.; *Schiff 4754*; K [K001271518]. – **Eastern Cape** • Engcobo Forest; 18 Jan. 1996; fr.; *Flanagan 2696*; K [K001271522].

Bibliography. Engler (1895: 273); Gilg (1903: 234, 241); Brenan and Greenway (1949: 382); Eggeling and Dale (1952: 279); Dale and Greenway (1961: 337); Robson (1963: 240); Bamps and Farron (1967: 8); du Toit and Obermeyer (1976: 5); Blundell (1987: 62); Beentje (1994: 121); Vollesen (1995: 66); Verdcourt (2005: 2).

Notes. Morphological work on this species has proved challenging. Like taxonomists in the past (Robson 1963; Verdcourt 2005), we note significant variation in habit, leaf size and arrangement of leaves along the branches, and inflorescence structure. This widespread species is generally recognizable by being a medium- to large-sized tree, occurring in upland moist forest with leaves variable in size (4–12 cm long and 1–5 cm wide) with a distinct attenuate leaf apex, and 6–16 flowers with long pedicles arranged in a distinct raceme. Difficulty arises with specimens that are sterile, shrubbier in habit, and/or with smaller leaves occurring in more open and drier habitats.

These individuals may be confused with *O. stolzii* and *O. oxyphylla*; however, they differ by the latter two species generally having smaller leaves (1–4.5 cm long, 0.5–2 cm wide and 2–8 cm long, 1–4 cm wide respectively) without prominent attenuate leaf apices, and fewer flowers per inflorescence, often solitary but sometimes up to six flowers.

2. *Ochna stolzii* Gilg ex Engl. (Engler 1921: 480)

Figs 2A, 4C, 7

Type. TANZANIA • Station Kyimbila; 1913; *Stolz 2212*; holotype: B†; lectotype (**designated here**): M [M0109480]; isolectotypes: G [00341181], JE [JE00002320], S [S08-21470], U [U0283523], WAG [WAG0002472].

Description. <u>Shrub</u> or <u>suffrutex</u> 0.4–1.8(–2) m tall. <u>Bark</u> smooth grey to brown. <u>Stems</u> brown to purple, glabrous, sometimes with white lenticels and often flaking off; young new growth brown and densely puberulous. <u>Stipules</u> brown, linear, semi-persistent, 3.5–4 cm long. <u>Leaves</u> green, drying blue-black above and brown below or brown throughout, slightly coriaceous, glabrous, small, elliptic to obovate or sometimes lanceolate, 1–4.5 cm long, 0.5–2 cm wide; leaf base cuneate, acute to rounded or sometimes attenuate at the apex, margins spinulose–serrate; lateral veins 15–20, ± prominent on both sides, tertiary vernation reticulate above and below, midrib raised on both sides; petiole obsolete or up to 1.5 mm long; buds small brown, glabrous, bud scales deciduous, up to 4.5 mm long; annual shoot scales deciduous, 3.5–4 mm long sometimes up to 1.5 cm long. <u>Flowers</u> solitary or arranged in fascicles with up to 4 flowers, or in racemes with 3–6 flowers; rachis 0.5–2.5 mm long, often puberulous; pedicels 1–2.5 cm long, articulated at or near the base, or up to 2.5 mm, glabrous or slightly puberulous. <u>Sepals</u> green to brown, elliptic, 7–9 mm long, 5–7 mm wide in flower, turning carmine red in fruit, 7–19 mm long, 6.5–10 mm wide. <u>Petals</u> yellow, obovate, 9–11.5 mm long, 5.5–8.5 mm wide. <u>Anthers</u> dehiscing by longitudinal slits, 1.5–1.8 mm long; filaments longer than anthers, 2–3 mm long. <u>Carpels</u> 5; styles united at apex, 5–7 mm long. <u>Drupelets</u> black, ellipsoid, 10–13 mm long, up to 1 cm wide, attached at the base.

Distribution. Tanzania and Malawi (Fig. 7).

Habitat. Upland and montane grassland, rocky outcrops, and upland *Brachystegia* woodlands. Altitude: 1525–2400 m.

Phenology. Mostly flowering and fruiting from November to February, which corresponds to the short rainfall season (November and mid-January) in Tanzania and the hot and rainy season occurring (November and April) in Malawi.

Preliminary IUCN conservation assessment. *Ochna stolzii* has an estimated EOO of 58,579 km^2 and an AOO of 80 km^2. The species faces threats of habitat destruction in parts of its range. For example, many of the montane grasslands of the Njombe area have been converted to rangeland or extensive timber plantations.

This is a growing threat to the Sao Hill occurrence in the Mufundi area as well. With its restricted range and only being known from 10 locations, with the ongoing threat of habitat destruction, the species is therefore assessed as Vulnerable: VU B2ab(ii,iii).

Additional material examined. TANZANIA – **Njombe District** • Stromgebiet des oberen Ruhudje; 1931; fr.; *Schlieben 1140A*; K [K001383210] • Njombe; Oct. 1931; fl.; *Staples 190*; K [K001383206] • Njombe; 10 Dec. 1931; fr.; *Lynes DK93*; K [K001383204] • Msima Stock Farm; 1932; fr.; *Emson 387*; EA, K [K001082550] • Msima Stock Farm; 1932; fr.; *Emson 241*; EA, K [K001082553] • Rugauga, south, Highlands club; 19 Jan. 1952; fr.; *Wigg 999*; K [K001383201] • Idunduge; Nov. 1953; fr.; *Carmichael 314*; EA, K [K001383203] • Njombe-Milo Rd.; 1950 m; 28 Jan. 1961; fr.; *Richards 14019*; K [K001383208]. – **Iringa District** • Dabaga; 7 Feb. 1932; fr.; *Lynes 12*; K [K001383157]. – **Mufindi District** • Sao Hill; Dec. 1963; fr.; *Proctor 2466*; K [K001383199] • Mufindi tea estates, near Ngwazi lake; 1850 m; 20 Nov. 1986; fr.; *Brummit & Mwasumbi 18072*; K [K001383198] • Lake Ngwazi; 8°31'S, 35°09'E; 1850 m; 28 Mar. 1991; fr.; *Bidgood & Vollesen 2157*; K [K001271359] • Mafinga-Mufindi 23 km; 8°24'0.00"S, 35°28'40.08"E; 1900 m; 9 Nov. 2008 fr.; *Luke 12770*; K [K001383197].
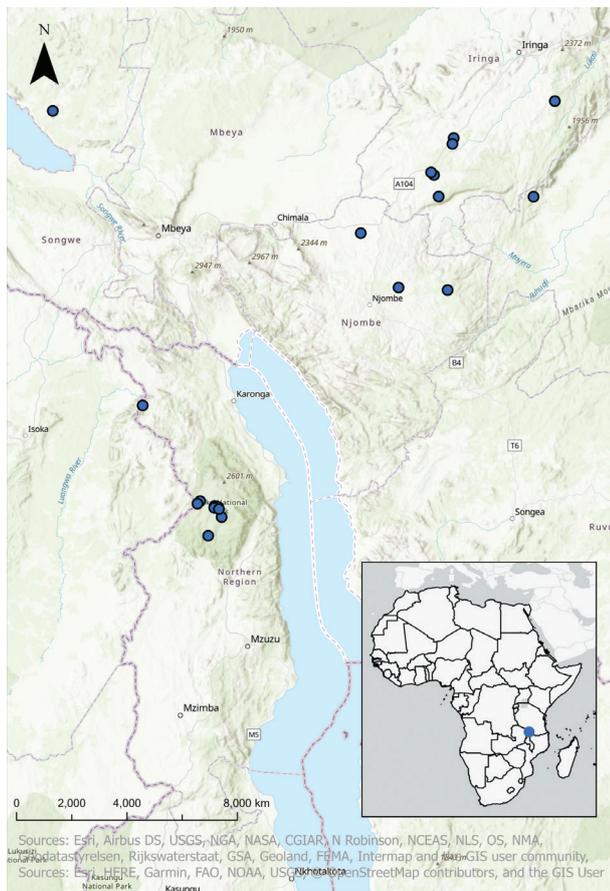
Figure 7. Distribution map of *Ochna stolzii* in Tanzania and northern Malawi.

MALAWI – **Chitipa District** • Near the top of the Mafinga Mts, above Chisenga; 22 Nov. 1952; *Angus 839*; K [K001387712]. – **Rumphi District** • Nyika Plateau, 2 miles from Zambia Rest House; 2250m; 14 Nov. 1967; *Richards 22529*; K [K001387711] • Nyika Plateau, Chelenda Bridge and River; 21 Nov. 1967; fr.; *Richards 22670*; K [K001387786] • Nyika Plateau, Chowo grassland; 27 Dec. 1975; fr.; *Phillips 745*; K [K001387714] • Nyika Plateau, edge Fingira Rock; 5 Nov. 1977; fr.; *Pawek 13177*; K [K001387713] • Nyika Plateau; 5 Nov. 1977; fr.; *Pawek 13184*; K [K001387783] • Nyika Plateau; 3 Jan. 1977; fr.; *Pawek 12240*; K [K001387785] • Nyika Plateau, Chowo Rocks; 2200 m; 11 Jan. 1983; fr.; *Dowsett-Lemaire 561*; K [K001387784] • Nyika national park, near Chirinda falls, between Chelinda and Chirinda; 10°37'S, 33°50'E; 2400 m; 13 Dec. 1983; fr.; *Kruif 1330*; K [K001271505].

Bibliography. Gilg (1925: 68); Sleumer (1934: 69); Robson (1963: 241); Verdcourt (2005: 25).

Notes. By its leaf shape and inflorescence arrangement, *O. stolzii* most closely resembles *O. oxyphylla*, differing by its suffrutescent habit (0.4–1.8 m tall) and small leaves, being a small or dwarf shrub 0.4–1.8 m tall. It also differs in habitat, with *O. stolzii* found on grasslands, woodlands and rocky outcrops, whereas *O. oxyphylla* is only found in forests. *Banda 764* and *White 2806* from Nikya Plateau, Malawi, could be *O. stolzii* although the plants are slightly larger, up to 3.5 m tall, and the young stems are glabrous.

3. *Ochna oxyphylla* N.Robson (Robson 1962: 21)

Figs 2B, 4D, 8

Ochna sp. 47 of FTEA (Verdcourt 2005: 39).

Type. TANZANIA – **Morogoro District** • Uluguru Mts, Bondwa Hill; 1953: *Drummond & Hemsley 1764*; holotype: K! [K000431154], isotypes: BR [BR0000009861305], EA! [EA000002038], K! [K000431155], SRGH [SRGH0106493-0].

Description. Shrub or small tree, 2–8(–10) m tall. Bark rough or smooth, red to pale brown. Stems purple to brown, slightly ribbed with numerous, prominent lenticels; young new growth often with prominent white lenticels, brown, puberulous, often densely so, with rusty brown hairs or sometimes glabrous. Stipules orange-brown, narrowly oblong-lanceolate, up to 1 cm, deciduous. Leaves green to brown, often drying brown or rarely blue-green, thin, glabrous, narrowly elliptic to oblanceolate or lanceolate, 2–8 cm long, 1–4 cm wide; leaf base rounded to cuneate, acute at apex, sometimes very acute to acuminate, margins densely serrate or spinulose-serrate with teeth curving inwards; lateral veins numerous, ± 20–25, tertiary vernation reticulate above and below, midrib raised above and below; petiole obsolete or 0.5–3 mm long; buds small, brown, deciduous, annual shoot buds larger, pale brown, bud scales deciduous, up to 9.5 mm long. Flowers solitary, or arranged in short racemes 2–5 flowered, or pseudo-umbellate with up to 10 flowers; rachis 0–2 mm long; pedicels 1.5–3.5 cm long, articulated at or near the base, or up to 5 mm above base, red brown-pink, puberulous,

sometimes densely so or glabrous. <u>Sepals</u> green-brown, elliptic-oblong, 6–13 mm long, 3–6 mm wide in flower, turning red in fruit, 9–15 mm long, 5–9 mm wide. <u>Petals</u> yellow, narrowly obovate, 6.5–10 mm long, 3–6 mm wide. <u>Anthers</u> dehiscing by longitudinal slits, 1.5–2.5 mm long, filaments 1.5–3.5 mm long. <u>Carpels</u> 5 (6); style capitate at apex with lobes, 4–7 mm long. <u>Drupelets</u> black, ellipsoid, 8–10 mm long, attached at the base.

Distribution. Tanzania, Eastern Arc Mountains and Lake Nyasa Highlands (Fig. 8).

Habitat. Upland rain forest, montane forest, grassland/montane forest boundary, riverine forest. Altitude: 1400–2400 m.

Phenology. Mostly flowering and fruiting from September to March during the short rainfall season (October to December), but before the long rainfall season (April to June).

Preliminary IUCN conservation assessment. *Ochna oxyphylla* is restricted to the Eastern Arc Mountains and Lake Nyasa Highlands of Tanzania, with an estimated EOO of 90,440 km² and an AOO of 116 km². The species is threatened by encroachment, small-scale logging, and fuel wood collection in the montane forests (Toral Shah pers. obs. 2018). For these reasons, the species is assessed as Near Threatened (NT) as it nearly meets the B2 criteria for Vulnerable; however, it is present in more than 10 locations, up to 16 locations, therefore is assessed as NT.

Additional material examined. TANZANIA – **Lushoto District** • Tanga, West Usambara Mts, Mtumbi F.R.; 10 Feb. 1985; fr.; *Borhidi, Iversen, Mziray & Temu 85657*; K [K001082588] • Shume Nature Forest Reserve NE of Lushoto; 21 Feb. 1982; fr., *Borhidi, Hall, Hedberg & Mahoo 82062*; K [K001082590]. – **Morogoro District** • Uluguru Mts, Mgeta R. above Bunduki; 7°02'S, 37°38'E; 1 Jan. 1975; fr.; *Pollhill & Wingfield 4634*; K [K001271348, K001383146] • Uluguru South Catchment Forest Reserve, W-slopes of the forest on the path from N'gungulu village to Lukwangule plateau; 2400 m; 5 Feb. 2001; *Jannerup & Mhoro 405*; K [K001271445] • Uluguru-Gebirge, Lukwangule Plateau; 23 Feb. 1933; fl.; *Schlieben 3564*; BM, EA, K [K001383147] • Below Lukwanguli, Uluguru Mountains; 3 Jan. 1934; fl.; *Michelmore 900*; EA, K [K001383148] • Nguru Mts 3km S of Maskati Mission; 1750 m; 11 Feb. 1991; fr.; *Manktelow & Swenson 91296*; EA, K [K001383149]. – **Kilolo District** • Udzungwa NP, Mt Luhomero; 7°47'S, 36°33'E; 1800 m; 30 Sep. 2000; fl.; *Luke et al. 6789*; EA, K [K001383165] • Udzungwa Mountains NP, pt 48; 7°41'S, 36°52'E; 1880 m; 31 Oct. 2005; *Luke et al. 11337*; EA, K [K001383155] • Udzungwa Mountains; 7°52'S, 36°22'E; 1460 m; 28 Nov. 1999; fr.; *Price & Mhoro WK263*; K [K001082568] • Ndundulu FR, pt 604; 7°47'S, 36°30'E; 1800 m; 11 Sep. 2004; *Luke et al. 10448*; EA, K [K001383150] • Mt Selegu; 7°30'S, 36°10'E; 2100-2400 m; 28 Dec. 1986; fr.; *Lovett & Congdon 1232*; K [K001383202] • Mt Selegu; 7°30'S, 36°10'E; 2100–2400 m; 28 Dec. 1986; fr.; *Lovett & Congdon 1244*; K [K001383151] • Mt Image, Selegu Peak; 7°30'S, 36°10'E; 2100 m; 13 April 1986; fr.; *Lovett & Lovett 639*; K [K001271506] • Kidabaga village,

New-Dabaga Forest Reserve; 8°06'45.07"S, 35°55'45.73"E; 1873 m; 24 Jan. 2020; *Shah TS94*; K • Dabaga forest; 18 Oct. 1937; fr.; *Pitt 576;* EA, K [K001383156]. – **Ledewa District** • Mdando Forest Reserve; 15 Nov. 1966; fr.; *Gillett 17866*; K [K001383209] • Livingstone Mountains, on ridge top ca 1.5 km S of Msalaba Mountain above Luana; 10°00'S, 34°35'E; 2150 m; 23 Nov. 1992; *Gereau et al. 5126*; EA, K [K001383164] • Livingstone Mountains, at and near the summit of Ligala Mountain along foot trail from mission at Madunda; 9°51'S, 34°27'E; 2320 m; 12 Feb. 1991; fr.; *Gereau & Kayombo 3982*; EA, K [K001383166] • Luhega Forest Reserve; 8°21'S, 35°58'E; 1650 m; 20 Jan. 1997; fl.; *Frimodt-Møller et al. TZ122*; K [K001383163]. – **Kinondoni District** • Kigogo; fr.; Dec. 1953; *Carmichael 329*; EA, K [K001383158] • Kigogo; fr.; Feb. 1954; *Carmichael 354*; EA, K [K001383169] • Kigogo fr; 8°40'S, 35°15'E; 1800 m; 12 Nov. 2008; *Luke & Luke 12805*; EA, K [K001383154] • Mafinga Club; 31 Jan. 1955; fr.; *Sangiwe 64;* K [K001383200]. – **Mbeya District** • Poroto Mts, Ikuyu, about 8 km N of Irambo; 1825 m; 10 Feb. 1979; fr.; *Cribb et al. 11380*; K [K001383161, K001383162] • N. slopes of Poroto Mts, below Mporoto sawmill; 8 Mar. 1932; *Clair-Thompson 725*; EA, K [K001383167]. – **Wanging'ombe District** • Nyumbanitu; 22 Sep. 1958; fl.; *Ede 42*; EA, K [K001383168]. – **Ileje District** • Bundali Mts, pts 292; 9°43'S, 33°50E; 2070 m; 20 Nov. 2008; *Luke & Luke 12841*; K [K001383153]. – **Njombe District** • Between Lisitu and Lugalawa; 9°48'S, 34°43'E; 2000 m; 23 Sep. 1970; fl.; *Thulin & Mhoro 1120*; EA, K [K001383160].
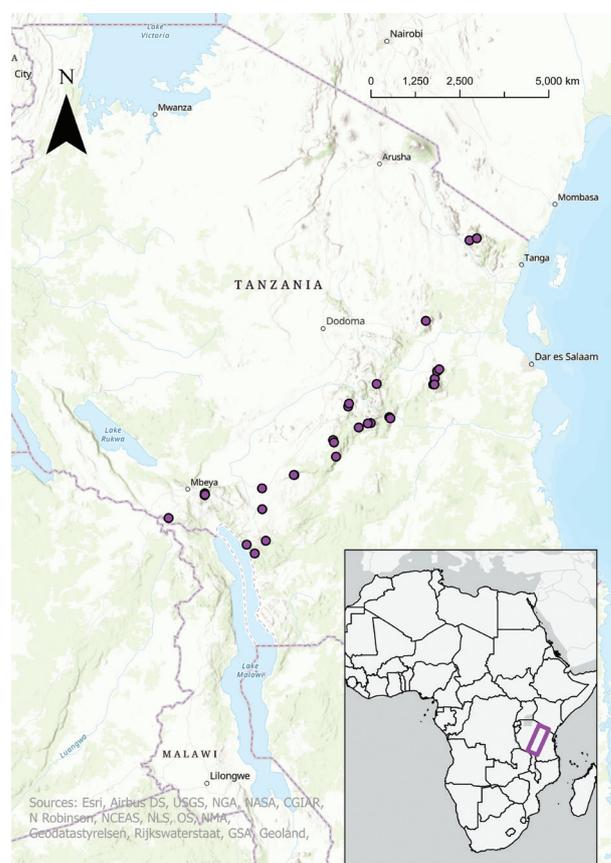
Figure 8. Distribution map of *Ochna oxyphylla* in Tanzania.

– **Rufiji District** • Idunduge; Nov. 1953; fl.; *Carmichael 310;* EA, K [K001383152].

Bibliography. Robson (1963: 241); Verdcourt (2005: 24).

Notes. *Ochna oxyphylla* is most often confused with *O. stolzii*, as both species have few-flowered inflorescences (1–5 flowers), but is distinguished by being a small tree up to 8 m tall, whereas *O. stolzii* is mostly a suffrutex up to 2 m tall. The specimen *Jannerup & Mhoro 405* from the moist forest before Lukwangule Plateau, Uluguru Mountains, Tanzania, is listed as *O. sp. 47* in the FTEA (Verdcourt 2005). Molecular results from a more recent specimen, *Shah TS57*, collected from the same locality, have confidently placed it within *O. oxyphylla,* which is further corroborated by morphological characters (having leaf apex sharply acute, leaf margin finely toothed; bark dark brown, slightly fissured and lenticellate, not corky; upland) and found in montane and riverine forest, between 1400–2400 m elevation. Verdcourt (2005) separated this specimen as it had been previously determined as *O. holstii*; however, it has solitary flowers rather than several-flowered racemes as in *O. holstii.* The specimen cited in FTEA states that the plant as up to 20 m tall, which is likely erroneous as the maximum height recorded for this species is 10 m.

4. *Ochna maguirei* K.Balkwill (Balkwill 2020: 299)

Figs 3A, 9

Type. SOUTH AFRICA • Limpopo Province, 2329 (Pietersburg): Lajuma Research Centre, between Lajuma Peak and the farmhouse; *Balkwill et al. 13658*; holotype: J; isotypes: BM, K, MO, PRE.

Description. (adapted from Balkwill 2020) Small tree 2–3.4(–7) m tall, usually single-stemmed from the base with branches forming a crowded canopy. Bark grey-brown, deeply fissured, corky, not peeling; young new growth olive green with brown-orange hairs. Stipules spathulate, sharply acute (3.5–)5.3–7.5(–8.0) mm long. Leaves bright green when young, becoming darker with age, drying dark green or blue-black, slightly leathery, glabrous, narrowly obovate to obovate, (23–)37–56(–63) mm long, (8–)15–24(–28) mm wide; leaf base narrowly rounded to round, broadly acute to rounded at apex, margins coarsely serrate along entire length; lateral veins (19–)21–28(–36), tertiary vernation raised above and below on dried specimens of mature leaves; petiole (1.0–)1.20–2.0(–2.4) mm long, u-shaped in cross-section, with a ridge or wing down each side. Flowers in condensed racemes often produced amongst the leaves, (1–)2–4(–6) on short axillary shoots; pedicels (7.0–)8.7–13.8(–18.0) mm long, articulated at or near the base or up to 1 mm from the base, red-brown, glabrous to puberulous. Sepals brown to yellow-brown, narrowly to broadly elliptic with rounded tip (6.5–)7.3–9.0(–9.5) mm long, (3.0–)3.7–5.3(–6.0) mm wide in flower, turning red-brown in fruit, (8.0–)8.8–10.0(–10.5) mm long, (4.5–)4.8–6.8(–8.5) mm wide. Petals pale yellow, spathulate, (9.0–)9.2–10.8(–11.0) mm long, (5.0–)5.1–6.2 mm wide. Anthers dehiscing by

longitudinal slits, (1.2–)1.25–1.5(–1.7) mm; filaments 3.0–3.8(–4.5) mm long. Carpels unknown; styles fused. Drupelets black, slightly oblate and slightly laterally compressed, (5.5–)5.6–6.6(–7.5) mm long, attached at the base.

Distribution. NE South Africa, known from three mountain ranges (the Soutpansberg, Waterberg, and Magaliesberg) and from a mountain near Loskop Dam (Fig. 9).

Habitat. Savanna amongst boulders. Altitude: approximately 1200–1700 m (estimated from Google Earth).

Phenology. This species has a short flowering period in the dry season, between September and November, and fruiting from October, but mostly from November through to January.

Preliminary IUCN conservation assessment. With an EOO of approximately 100,000 km^2 and an AOO likely above 20 km^2, the species is known to have over 1000 individuals from more than five locations. Furthermore, with populations appearing to be stable over the last 21 years and resilience to the major threat of fire, the species is assessed as Least Concern (LC) (Balkwill 2020).

Additional material examined. SOUTH AFRICA • Soutpansberg, above Louis Trichardt; 16 Dec. 1928; *Hutchinson 2025*; K • Bokpoort, in forest under cliffs; 2 Jan. 1936; fr.; *Smuts & Gillett 3357*; EA • Above Punchbowl

Figure 9. Distribution map of *Ochna maguirei* in South Africa.

Hotel, Soutpansberg; 16 Oct. 1956; fr.; *Story 5935*; K [K001271443].

5. ***Ochna polyneura*** Gilg (Gilg 1903: 240)

Figs 3D, 10

Polyochnella polyneura (Gilg) Tiegh. (Tieghem 1903: 18) – Type: same as for *Ochna polyneura*.

Ochna hylophila Gilg (Gilg 1903: 242; Brenan and Greenway 1949: 383) – Type: TANZANIA • Mampyui road on E Ungoni border; 1900–1901; *Busse 732*; holotype: B†; lectotype (**designated here**): G [G00341215], K! photo; isolectotype: EA.

Polyochnella hylophila (Gilg) Tiegh. (Tieghem 1903: 40) – Type: same as for *Ochna hylophila*.

Ochna sp. 42 of Flora of Tropical East Africa (Verdcourt 2005: 37) – Type: TANZANIA • Uzaramo District, Pande Hill.

Type. TANZANIA • Mbarangandu region; *Busse 681;* lectotype (**designated here**): EA [EA000002036]; syntype: B† • TANZANIA • Mbarangandu region; *Busse 671*; syntype: B†; isosyntype: EA [EA000002037].

Description. Shrub or small tree, 2–8 m tall. Bark whitish-grey or brown, corky and sometimes appearing fissured. Stems rusty brown, sometimes grey, more prominently fissured, sometimes with sparse pale lenticels, glabrous; young new growth brown-green, glabrous or sometimes puberulous, often with pale sparse lenticels. Stipules brown, linear, narrow, 1.8–4.5 mm long, deciduous. Leaves green, often drying blue-black; young leaves often rusty brown with a yellow midrib; mostly thin but sometimes slightly coriaceous, glabrous, oblanceolate-lanceolate or sometimes ovate, 5–11.5 cm long, 1.5–4.5 cm wide; leaf base cuneate-attenuate, rounded or rarely acute at apex, margins serrate; lateral veins numerous, ± 20, tertiary vernation reticulate above and below, midrib raised below and above; petiole 1–3 mm; buds brown, up to 1 cm long, bud scales deciduous, up to 9 mm long. Flowers arranged in racemes with 7–10(–13) flowers or in fascicles with 2–5 flowers; rachis up to 3 cm long; pedicel 2–3.5 cm long, articulated at or near the base, or up to 13 mm, brown-green, sometimes drying blue-black, often puberulous below articulation or glabrous. Sepals green to red-brown, oblong-elliptic, 7.5–10 mm long, 3.5–6 mm wide in flower, turning red in fruit, 9–11 mm long, 5–6 mm wide. Petals yellow, orbicular, long-clawed, 6–15 mm long, 5–12 mm wide. Anthers dehiscing by longitudinal slits, 1.2–2 mm long; filaments 3–4.5 mm long. Carpels 5; style capitate at apex with lobes, 3–6 mm long. Drupelets black, ellipsoid, 6–9 mm long, 5–8.5 mm wide, attached at the base.

Distribution. Tanzania, Malawi, Zimbabwe, and Mozambique (Fig. 10).

Habitat. Miombo woodland, wooded grassland, open thicket. Altitude: 23–1880 m.

Phenology. Flowering and fruiting from October to January, which coincides with early rainfall.

Preliminary IUCN conservation assessment. *Ochna polyneura* occurs in miombo woodland across eastern and southern Africa and has an estimated EOO of 940,865 km² and AOO of 92 km². Even though the AOO falls within the threshold for the Endangered category under criterion B, the species occurs in 15 locations and 14 occurring within protected areas. Although there are some localised declines in individuals due to firewood harvesting, extensive areas are still intact within its large range. For this reason, the species is assessed as Least Concern (LC).

Additional material examined. TANZANIA – **Morogoro District** • 5 Jan. 1932; fr.; *Wallace 255*; K [K001082494] • Morogoro, 9 miles NE of Kingolwira station; 7 Jan. 1955; fr.; *Welch 266*; EA, K [K001082496] • Morogoro, Near Kingolwira Station; 17 Nov. 1956; fl.; *Welch 336*; EA, K [K001082497]. – **Songea District** • Forest near Songea on Songea-Tunduru road; Nov. 1951; fl.; *Eggeling 6360*; EA, K [K001082507] • About 12 km E of Songea by Nonganonga stream; 990 m; 27 Dec. 1955; *Milne-Redhead & Taylor 7915*; EA, K [K001082506, K001082505] • About 12 km E of Songea by Nonganonga stream; 990 m; 21 Jan. 1956; *Milne-Redhead & Taylor 7915a*; EA, K [K001082504]. – **Bagamoyo District** • Bana Forest Reserve; Dec. 1964; *Proctor 2804*; EA, K [K001082493] • Bana Forest Reserve; 28 Oct. 1965; fl.; *Mgaza 757*; K [K001082490]. – **Mbeya District** • Pande Hill; 6°42'S, 39°05'E; 22 Nov. 1969; *Harris*
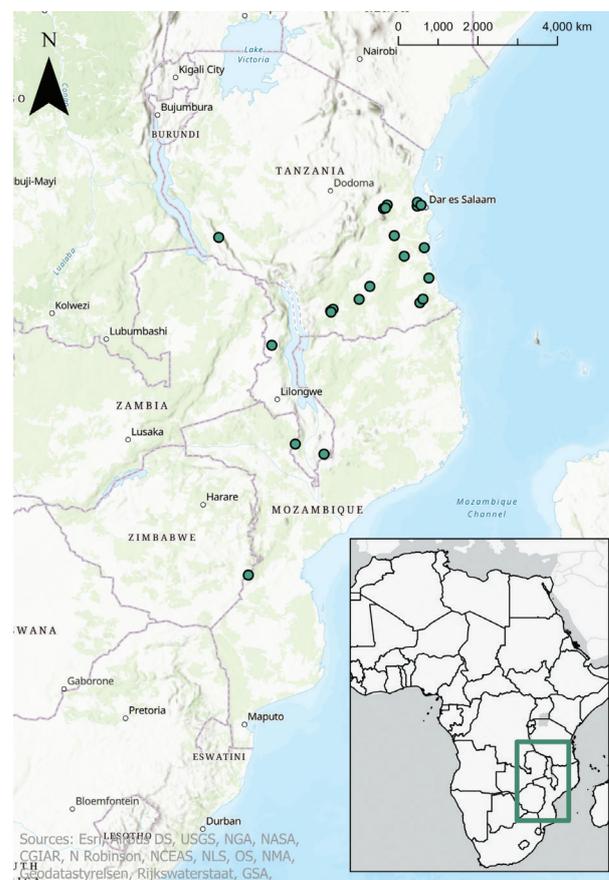
Figure 10. Distribution map of *Ochna polyneura* in Tanzania, Malawi, and Mozambique.

et al. BJH3619; K [K001271417]. – **Rufiji District** • Selous Game Reserve, ca 17 km SW of Kingupira; 8°36'S, 38°28'E; 175 m; 9 Jan. 1977; fr.; *Vollesen 4298*; K [K001271383] • Selous GR, Lodge-Kivuko Hill; 7°47'S, 38°08'E; 80 m; 13 Dec. 1989; fr.; *Luke & Luke 5609*; EA, K [K001082491]. – **Sumbawanga District** • Muva Mbizi FR; 1880 m; 21 Nov. 1987; fr.; *Ruffo & Kisena 2778*; K [K001082559]. – **Kisarawe District** • Tamburu Forest Reserve, off the main Dar es Salaam-Lindi Road, before reaching Somanga, near Kiwanga village; 8°16'47.42"S, 39°12'16.45"E; 23 m; 9 Jan. 2020; *Shah TS65*; K [K001271507]. – **Kilwa District** • Miruba/Mandawa, Ngarama Forest Reserve North; 9°24'32.69"S, 39°22'36.44"E; 281 m; 11 Jan. 2020; *Shah TS69*; K [K001271508] • Miruba/Mandawa, Ngarama Forest Reserve North; 9°24'32.69"S, 39°22'36.44"E; 281 m; 11 Jan. 2020; *Shah TS70*; K [K001271509]. – **Newala District** • Above Ndanda mission station, on dirt road close to the plateau of Makonde escarpment, near the village at the top; 10°19'39.76"S, 39°2'27.92"E; 880 m; 15 Jan. 2020; *Shah TS82*; K [K001271510]. – **Mtwara District** • Liganga, Rondo Plateau on general land/village land outside of the nature reserve boundaries; 10°11'33.83"S, 39°9'17.10"E; 676 m; 16 Jan. 2020; fr.; *Shah TS86*; K [K001271511].

MALAWI – **Mzimba District** • 4 mi. E of Mzambazi; 30 Dec. 1975; fr.; *Pawek 10659*; K [K001271408]. – **Chitipa District** • Mt Mulanje low down the Likhubula valley; 860 m; 7 Nov. 1987; fl.; *Chapman & Chapman 8926*; E [E01123514], K [K001387306].

Bibliography. Brenan and Greenway (1949: 383); Robson (1963: 242); Vollesen (1980: 25); Verdcourt (2005: 25).

Notes. *Ochna polyneura* is easily recognised by its leaves drying blue-black, racemose inflorescences, and somewhat exfoliating bark. It closely resembles *O. puberula* but it differs by having exactly 5 carpels, whereas the latter has 5–9 carpels, and a largely accrescent calyx in fruit. In general, *O. puberula* is a smaller plant with smaller leaves and flowers. Molecular results have placed the undescribed species *O. sp. 42* from FTEA (Verdcourt 2005) as sister to all samples *O. polyneura.* In this study, we have included the specimen within the delimitation of *O. polyneura*, given that it shares morphological similarities with other individuals of the species, such as having a corky fissured bark, similar leaf shape and size, drying blue-black. However, it is likely that Verdcourt (2005) kept this specimen separate as it has paired flowers, which differs from typical *O. polyneura*, which has 7–10 flowers in a raceme. Additional specimens from Pande Hill, Uzaramo District are required for a more thorough study as it may prove to be a distinct species or infraspecific taxon.

6. ***Ochna puberula*** N.Robson (Robson 1962: 25)

Figs 3B, 11

Ochna afzelioides sensu Bamps and Farron (1967) quoad *Schmitz 2653*, non Robson (1962: 36).

Ochna holstii sensu Bamps and Farron (1967) quoad *Schmitz 6548*, non Engler (1894: 69).

Ochna sp. 40 of Flora of Tropical East Africa (Verdcourt 2005: 37) – Type: UGANDA • Ankole District, Bushenyi, S Kasyoha – KitomiForest, Kamukaaga, between R. Kyambura and R. Nzozi.

Type. ZAMBIA • Abercorn [Mbala], Kawimbe; 1958; *Richards 10235*; holotype: K [K001387768 – Sheet 1, K001387769 – Sheet 2].

Description. Shrub or small tree, 0.5–6 m tall. Bark grey-white or grey-brown, rough, sometimes with white, peeling or exfoliating bark. Stems and young new growth rusty brown, sometimes with white lenticels, puberulous, often drying blue-black. Stipules pale brown, linear, semi-persistent, 2.5–6 mm long. Leaves green, drying blue-black, thin, glabrous, lanceolate–oblanceolate to elliptic, (1.5–)3–8 cm long, 1–3 cm wide, leaf base cuneate to attenuate, acute to obtuse at apex, margins serrate, often densely so with teeth curving inwards; lateral veins > 20, tertiary vernation reticulate on both sides, midrib raised above and below; petiole 0.5–2 mm long; buds brown, glabrous, bud scales linear, semi-persistent up to 1 cm long. Flowers almost always precocious, arranged in pseudo-umbels or racemes, (2–)4–8 flowers; rachis up to 1.5 cm; pedicels 1.5–3 cm long, articulated at or near the base or up to 7 mm above base, puberulous or rarely glabrous, often drying blue-black. Sepals green, elliptic to broadly elliptic, 3.5–5.5 mm long, 3–4 mm wide in flower, turning red in fruit 1.5–2 cm long, 0.8–1.2 cm wide. Petals yellow, obovate, 1.2–9.5 mm long, 0.7–4 mm wide. Anthers dehiscing by longitudinal slits, sometimes drying bluish, 0.8–1.5 mm long; filaments 2.5–3.5 mm long. Carpels 5–9; style capitate at apex with lobes, 3–6.5 mm long. Drupelets black, ellipsoid-subglobose, 6–13 mm long, 6–7 mm wide, attached at the base.

Distribution. Democratic Republic of the Congo (DRC), Uganda, Tanzania, Malawi, Mozambique, Zambia, and Zimbabwe (Fig. 11).

Habitat. Miombo woodland, on rocky ground. Altitude: 740–1940 m.

Phenology. Flowering and fruiting October to February. This corresponds to the short rainfall season in East Africa from October to December and the longer rainfall season in southern Africa from November to March.

Preliminary IUCN conservation assessment. *Ochna puberula* occurs in miombo woodland across east and southern Africa. The species has an estimated EOO of 1,695.266 km^2 and AOO of 200 km^2. Since the species has a large EOO, occurs in up to 29 locations with more than 10 in protected areas, and has no direct threats to its population size, number of mature individuals and distribution, the species is assessed as Least Concern (LC).

Additional material examined. DEMOCRATIC REPUBLIC OF THE CONGO – **Haut Katanga** • Katanga, Entre Pweto et Kapulo; 25 June 1957; *Duvignaud 3690*; BR • Katanga, Route Kipiri-Pweto-Mitwaba, km 88; 30 May 1957; *Duvignaud 3788*; BR • Luiswishi; 22 Nov. 1984;

fl.; 1208 m; *Malaisse 13386*; BR [BR0000017182324], K [K001271482].

UGANDA – **Western** • Ankole district; Bushenyi, S Kasyoha-Kitomi Forest; Oct 1998; fr.; *Hafashimana 0662*; K [K000545621, K000545622].

TANZANIA – **Kondoa District** • Near Mnenia on scarp; 13 Jan. 1928; fr.; *Burtt 1053*; BM, EA, K [K001383181, K001383180]. – **Kigoma District** • Simbo hills; 8 Jan. 1928; *Burtt 1027*; EA, K [K001383176, K001383175]. – **Same District** • Kinyassi Mt; 2 Jan. 1928; *Burtt 921*; K [K001383172] • 27 Jan. 1932; fr., *Lynes 33*; K [K001383178]. – **Sumbawanga District** • ca 2.0 km SW from junction with the Sumbawanga-Mbala (Zambia) Road on the road to Safu; 08°34'54"S, 31°29'27"E; 1790–1820 m; 14–15 Nov. 1933; *Schmidt 1194*; K [K001383191] • Muse Escarpment; 2 Dec. 1963; fl.; *Vesey-FitzGerald 4254*; K [K001383192] • Sumbawanga district, 1.0 km S of Moravian Mission at Tatanda (Livingstone Memorial Mission) on the Sumbawanga-Mbala (Zambia) Road; 08°30'07"S, 31°30'08"E; 1780 m; 13 Nov. 1993; fr.; *Schmidt et al. 1171*; K [K001383193]. – **Mkalama District** • Usule-Kiraminu, 15 Nov. 1933; fr.; *Michelmore 822*; EA, K [K001383177]. – **Biharamulo District** • Bukoba road; 13 Nov. 1948; *Ford 851*; K [K001383190]. – **Iringa District** • 4 mls from Iringa on Dodoma road; Feb. 1961; fr.; *Procter 1763*; K [K001383171] • Nyororo town, Idetero,

Figure 11. Distribution map for *Ochna puberula* in Tanzania, Uganda, Democratic Republic of the Congo, Malawi, Mozambique, Zambia, and Zimbabwe.

off main road after Nyororo town along Mbeya road; 08°32'44"S, 35°00'51.3"E; 1795 m; 26 Jan. 2020; fr.; *Shah TS97*; K [K001271512]. – **Ludewa District** • Livingstone Mountains, steep E-facing slope of Ligala Mountain along foot trail from mission at Madunda; 09°51'S, 34°27'E; 1940–2110 m; 13 Feb. 1991; fr.; *Gereau & Kayombo 4021*; K [K001082549]. – **Kilolo District** • Kihesa-Kilolo town, off main Iringa–Dodoma road, near Kihesa town near old dump site; 07°43'53.8"S, 35°43'43.3"E; 1634 m; 22 Jan. 2020; *Shah TS90*; K [K001271513]. – **Makete District** • Lower Ndumbi Valley; 08°55'S, 34°05'E; 1400–1800 m; 14 Dec. 1986; fr.; *Lovett & Congdon 1109*; K [K001383174, K001383179]. – **Manyoni District** • Madibira Hills; 1400 m; 9 Dec. 1990; fl.; *Congdon 303*; K [K001383183, K001383182].

MALAWI – **Chitipa District** • Misuku crossroads; 30 Dec. 1972; *Pawek 6257*; K [K001387718] • Mzimba district, 1 mi. S of Mzambazi Mission; 1380 m; 28 Dec. 1975; *Pawek 10598*; K [K001387720]. – **Rumphi District** • Vwaze Marsh Reserve, Bowe road; 5 Feb. 1977; fr.; *Pawek 12325*; K [K001387722]. – **Karonga District** • 10 mi. SW of Karonga, Chaminade Sec. School; 740 m; 5 Jan. 1978; *Pawek 13537*; K [K001387719].

MOZAMBIQUE – **Tete Province** • Angonia, Ulongue, dentro da pastagem da veterinaria; 11 Dec. 1980; fr.; *Macuácua 1424*; K [K001387717].

ZAMBIA – **Lusaka Province** • Mteshi woodland on top of scarp overlooking Mweru Wantipa, near Mpundu; 08°45'S, 29°50'E; 24 Oct. 1949; fl.; *Bullock 1377*; K [K001387765]. – **Southern Province** • Mazabuka, Siambo Forest Reserve, near Choma; 13 Dec. 1952; fr.; *Angus 939*; K [K001387741] • Mazabuka district, Siamambo Forest Reserve; 17 Jan. 1960; *White 6307*; K [K001387755] • Choma; 14 Jan. 1963; *van Rensburg 1208*; K [K001387753] • Chilongowelo, old Mplungo Road; 12 Jan. 1952; fr.; *Richards 360*; K [K001387764] • Firebreak Chilongowelo, right side path; fl.; *Richards 2296*; K [K001387745]. – **Northern Province** • On steep rocky slopes of Sunzu Hill; 18 Nov. 1952; *White 3706*; K [K001387762] • Kawimbe; 1680 m; 16 Nov. 1956; fl.; *Richards 7000*; K [K001387744] • Kambole Escarpment; 1500 m; 29 Jan. 1964; fr.; *Richards 18875*; K [K001387751] • Mbala district, in woodland, grass and rocks across the road from Ndundu; 1740 m; 30 Dec. 1967; *Richards 22836*; K [K001387756]. – **Copperbelt Province** • Ndola; 10 Dec. 1953; fl.; *Fanshawe 565*; K [K001387736] • Ndola; Feb. 1954; *Fanshawe 840*; K [K001387742] • Sunzu Kalambo Farm; 8 Jan. 1955; *Richards 3952*; K [K001387763] • Kitwe; 11 Dec. 1955; *Fanshawe 2648*; K [K001387757] • Kitwe; 13 Dec. 1959; fl.; *Fanshawe 5316*; K [K001387767] • Kitwe; 16 Nov. 1955; fl.; *Fanshawe 2610*; K [K001387746] • Mufulira; 3 Jan. 1956; fr.; *Fanshawe 2686*; K [K001387740]. – **Eastern Province** • Nsadzu Br.; 900 m; 27 Nov. 1958; fl.; *Robson 745*; K [K001271504] • Nsadzu Br.; 900 m; 27 Nov. 1958; fl.; *Robson 745*; K [K001271504] • Hillside above Ndundu; 1740 m; 28 Jan. 1962; *Richards 15966*; K [K001387759] • Slope of Nakatari Hill; 1650 m; 4 Nov. 1965; fl.; *Richards 20666*; K [K001271503]. – **North-Western Province** •
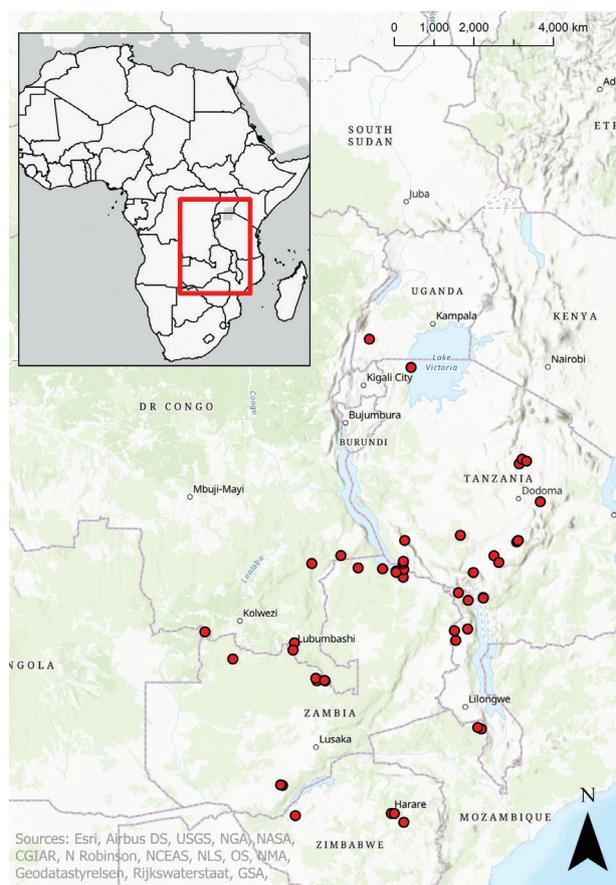
Mwinilunga district, Zambesi River Rapids, 4 miles from Kalene Mission; 1500 m; 5. Nov. 1962; fr.; *Richards 17227*; K [K001387761] • Mwinilunga district, Kabompo Gorge; 1200 m; 22 Nov. 1962; fl.; *Richards 17471*; K [K001387760]. ZIMBABWE – **Harare District** • Salisbury; 13 Nov. 1921; *Eyles 3216*; K [K001387732] • Salisbury, Bishops Mount; 6 Feb. 1933; *Mundy 7907*; K [K001387728]. – **Chimanimani District** • Melsetter, Rocklands, near "The View"; 7 Oct. 1950; *Sturgeon 30492*; K [K001387730, K00138773]. – **Binga District** • Sebungwe district; 20 Nov. 1951; *Lovemore 35082*; K [K001387729]. – **Mashonaland District** • Marandellas, Grasslands Research Station; 6 Dec. 1965; *West 6994*; K [K001387735].

Bibliography. Robson (1963: 244); (Verdcourt 2005: 26).

Notes. For differences to the closely similar species *O. polyneura,* see the note under that species. The distribution for *O. puberula* extends into south-eastern Democratic Republic of the Congo (DRC). It is noteworthy that Robson (1962) and Verdcourt (2005) did not acknowledge this range extension as it is possible that they only saw material of *O. puberula* from cultivated areas of DRC. Robson (1962) included the non-cultivated DRC specimens under *O. afzelioides.* Later work, however, by Bamps and Farron (1967) revised the material from Lubumbashi (Elisabethville), Katanga province, DRC and placed it under *O. puberula*, listing *O. afzelioides* as a synonym. In this study, we clearly distinguish between the two species and can confirm the distribution of each. Moreover, an undescribed species, *Ochna sp. 40* listed in FTEA (Verdcourt 2005), is placed under *O. puberula* in this study based on molecular evidence supported by the morphology. The inclusion of the specimen *Hafashimana 0662* here has extended the species' range into Uganda. The specimen has an accrescent calyx that encloses the drupelets and has leaves drying blue-black, similar to other specimens of *O. puberula*. However, flowering material of this species from S Kasyoha-Kitomi forest, Ankole district, Uganda, has not been seen, and more material from this region would be ideal to place it confidently within *O. puberula*. As the specimen is sister to the rest of *O. puberula,* additional fertile material may reveal differences between specimens from this region and true *O. puberula*.

7. *Ochna afzelioides* N.Robson (Robson 1962: 23)

Figs 3C, 12

Type. TANZANIA • Kasulu, Kigoma province; Oct. 1930; *Rounce B3*; holotype: K! [K000431153]; isotype: EA! [EA000002033].

Description. <u>Shrub</u> or <u>small tree</u>, 4–5 m tall. <u>Bark</u> grey-white or grey-brown with pale white lenticels or linear markings. <u>Stems</u> brown or purple with prominent white lenticels and sometimes with white peeling bark; young new growth green-brown densely lenticellate and densely puberulous with stiff pale brown hairs, or green-brown without lenticels and glabrous, usually later or in fruit. <u>Stipules</u> brown–pale brown, tapering with wide base or

linear, deciduous, 1–2.5 mm. <u>Leaves</u> green, thin, glabrous, ovate to lanceolate-oblanceolate, 2–9 cm long, 2–4 cm wide; leaf base cuneate to rounded, acute to obtuse or sometimes retuse at apex, margins densely spinulose-serrate, teeth prominently curving inwards, sometimes teeth up to 0.7 mm long; lateral veins numerous > 20, tertiary vernation reticulate on both sides, midrib prominent above and below; petiole 0.8–2.5 mm long; buds small green-brown, glabrous. <u>Flowers</u> arranged in racemes 8–10 flowered, or fascicles 6–8 flowered; rachis 2–11 mm long; pedicels 1.3–4 cm long, articulated 1–5(–8) mm from base, puberulous with stiff white hairs, usually glabrous above articulation or sometimes glabrous throughout, brown-green. <u>Sepals</u> green, elliptic to oblong, 5.5–9 mm long, 1.4–3 mm wide, turning red in fruit 6–9 mm long, 2.5–3.5 mm wide. <u>Petals</u> yellow, obovate to oblanceolate, 8–20 mm long, 4–7 mm wide. <u>Anthers</u> dehiscing by longitudinal slits, 1–1.8 mm long; filaments 2.5–5 mm long. <u>Carpels</u> 5–7; style capitate at apex, 4.5–6 mm long. <u>Drupelets</u> black, ellipsoid, 4–5.5 mm long, up to 3 mm wide, attached at the base.

Distribution. Tanzania, Rwanda, and Zambia (Fig. 12).

Habitat. Miombo woodlands and riverine forests. Altitude: 1000–1450 m.

Phenology. Flowering and fruiting from October to March.
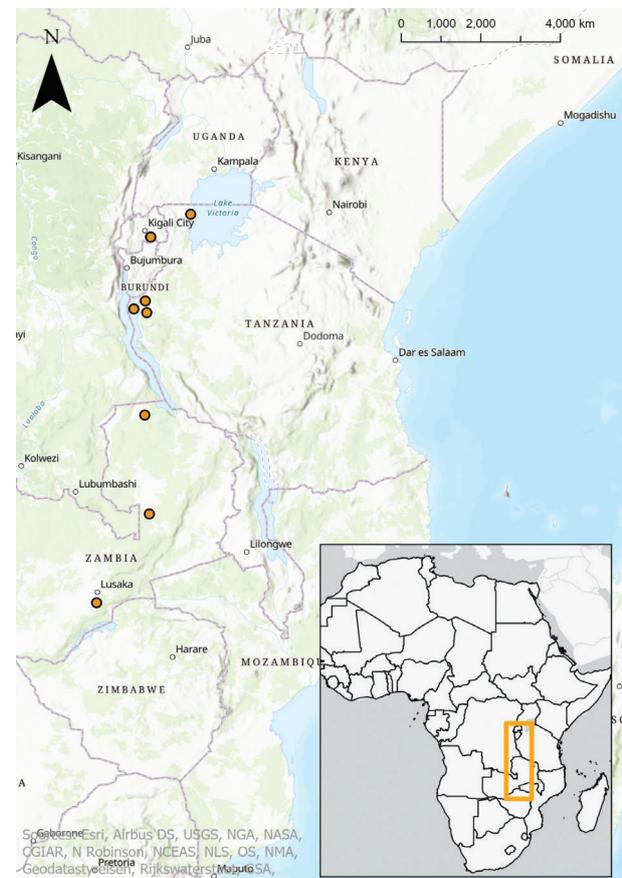
Figure 12. Distribution map for *Ochna afzelioides* in Tanzania, Rwanda, and Zambia.

Preliminary IUCN conservation assessment. *Ochna afzelioides* is found in woodland and forest habitats in Tanzania, Rwanda, and Zambia, with an estimated EOO of 44,725 km² and AOO of 36 km², which falls within the limits of EN under criterion B2. Furthermore, only known seven locations are known, with at least four locations outside of protected areas. Species occurring in north-western Tanzania and Rwanda are particularly prone to habitat destruction. Therefore, with the limited AOO and fewer than 10 locations, with observed decline in the quality of the habitat, the species is assessed as Vulnerable: VU B2ab(iii).

Additional material examined. TANZANIA – **Bukoba District** • Kiamawa; Sep.–Oct. 1935; fl.; *Gillman 458*; EA, K [K001383044]. – **Kigoma District** • near Tubila Railway station; Nov. 1956; fl.; *Procter 588*; EA, K [K001383042]. ZAMBIA – **Northern Province** • Mporokoso district, Choma, Mweru-Wantipa; 1000 m; 16 Dec. 1960; fr.;
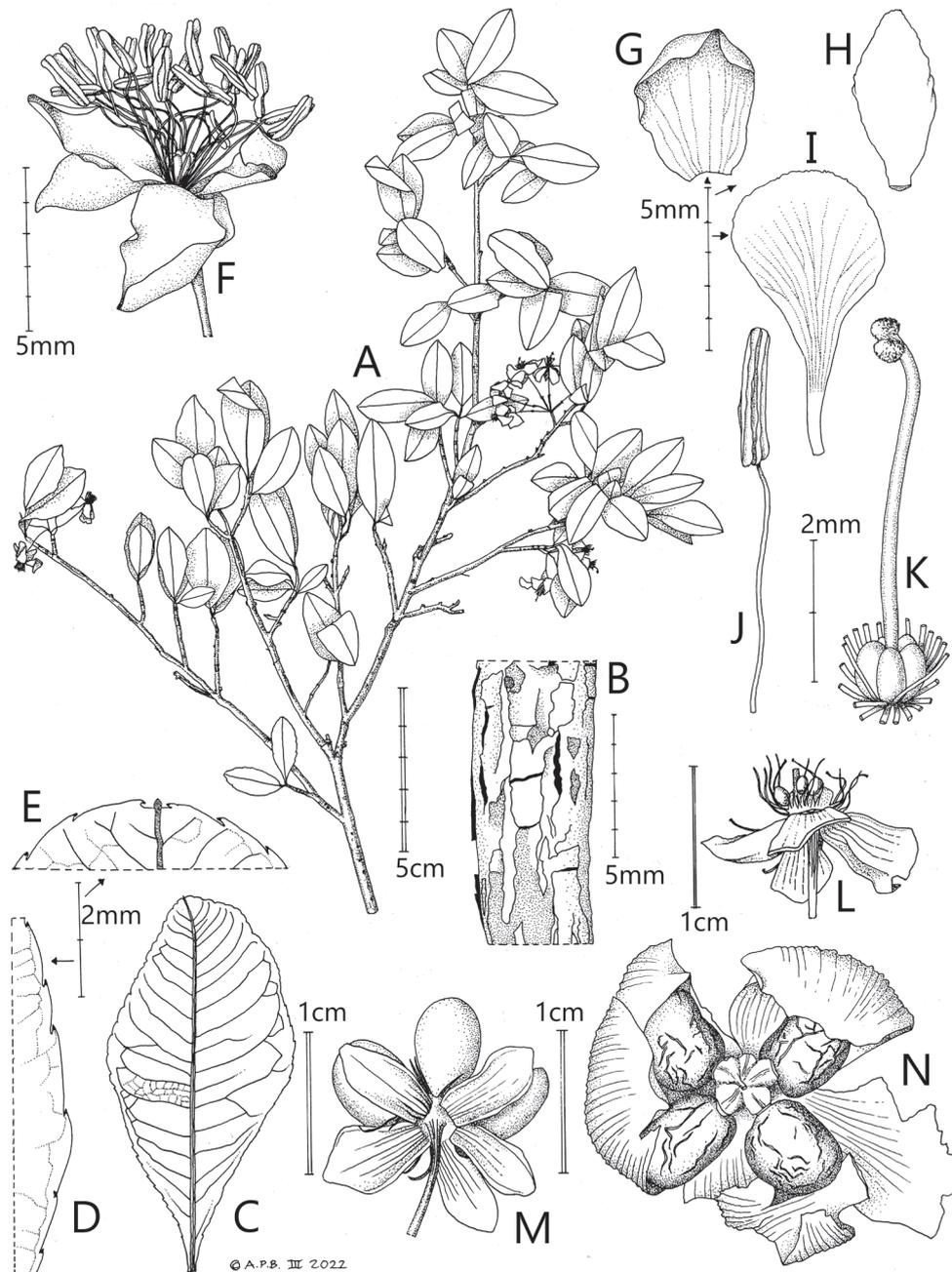
Figure 13. Illustration of *Ochna mchanga*. **A**. Habit. **B**. Bark on mature stem. **C**. Adaxial of a medium-sized leaf. **D**. Serration of leaf margin, adaxial. **E**. Leaf apex, adaxial. **F**. Flower after loss of petals (style absent). **G–H**. Inner surface of sepals. **I**. Inner surface of the petal. **J**. Stamen. **K**. Ovaries, style, and stigma. **L**. Side view of flower post pollination showing immature drupelets. **M**. Underside of flower with three developing drupelets and a few persistent filaments. **N**. Upper side of flower with four mature drupelets. A, C, D, E from *Luke et al. 13822* (K); B, N from *Timberlake et al. 5579* (K); F–K from *Vollesen 4309* (K); L, M from *Timberlake 5624* (K). Drawn by Andrew Brown.

Richards 13726; K [K001387605] • Grassy top near Kambole Escarpment; *Richards 10835*; K [K001387606]. – **Lusaka Province** • Lusaka Waterworks, Iolanda, Muchuto River gorge; 15°47.6'S, 28°14.9'E; 1000 m; 4 Dec. 1996; fl.; *Bingham 11234*; K [K000073089, K000073088]. – **Central Province** • Serenje district in Kasanka National Park; 12°29'47"S, 30°11'41"E; 1250 m; 13 Jan. 2000; fr.; *Zimba, Smith, Fisher NBZ 1176*; K [K001387607].
RWANDA – **Bugesera Ditstrict** • Gashora; 1450 m; Sep. 1972; fl.; *Auquier 2889*; BM, K [K001391608].
Bibliography. Robson (1963: 242); Verdcourt (2005: 28).

8. *Ochna mchanga* T.Shah, **sp. nov.**

urn:lsid:ipni.org:names:77318379-1
Figs 13, 14

Type. MOZAMBIQUE • Cabo Delgado, Ntukwe to Kisongore, pt 441; 10°36'24.84"S, 40°19'40.44"E; 95 m; 15 Nov. 2009; fl.; *Luke 13822*; holotype: K! [K000787156]; isotypes: EA!, LMA, P, MO.

Diagnosis. This species resembles *O. polyneura* Gilg in its leaf shape and in the foliage generally drying blue-black, but it differs by having generally smaller leaves 2–8 cm long and 1–3.5 wide (vs 5–11.5 cm long and 1.5–4.5 cm wide in *O. polyneura*), smaller petals 6–7 mm long (vs 6–15 mm long in *O. polyneura*), a shorter inflorescence rachis of 6–15 mm long (vs 3–30 mm long in *O. polyneura*) and by having grey-brown or sometimes whitish, rough, fissured and slightly peeling bark (vs grey-brown, or sandy-brown, corky and fissured bark in *O. polyneura*). *Ochna mchanga* is only recorded from coastal forests of south-eastern Tanzania and north-eastern Mozambique, whilst *O. polyneura* is widespread in miombo woodlands of Tanzania, Malawi, and Zimbabwe.

Description. Shrub or small tree, 1–9 m tall. Bark grey-brown sometimes appearing whitish, rough, often fissured and slightly peeling. Stems grey-white or brown; new young growth dusty brown, puberulous. Stipules pale brown, linear, deciduous 1–1.5 mm long. Leaves green, drying dark blue-black, thin, glabrous, oblanceolate to oblong or elliptic, 2–8 cm long, 1–3.5(–4) cm wide, leaf base cuneate to attenuate, obtuse to acute or sometimes attenuate at apex, margins densely but shallowly serrate; lateral veins 10–14, almost at right angles to midrib then curving upwards, tertiary vernation reticulate prominent on both sides, midrib raised above, flat below; petiole 0.5–4.5 mm long; leaf buds brown, imbricate, pubescent, 1–6 mm long. Flowers precocious, arranged in racemes with 6–11 flowers, or in fascicles with 5–7 flowers; rachis 6–15(–20) mm long; pedicels 1–3 cm long, articulated 1–5 m from base, puberulous when flowering, seemingly glabrous in fruit, drying blue–black. Sepals green, often drying blue-black, oblong, 5.5–7 mm long, 3–3.5 mm wide, turning red in fruit 5–10(–20) mm long, 4–5.5 mm wide. Petals yellow, obovate–round, clawed, 6–7 mm long, 5.5 mm wide. Anthers dehiscing by longitudinal slits, 1.5–2 mm long; filaments 2.5–5 mm long. Carpels 5; style capitate at apex, 4–6.5 mm long. Drupelets black, ovate–round, 5–8 mm long, 5–6 mm wide.

Distribution. South-eastern Tanzania, north-eastern Mozambique (Fig. 14).

Habitat. Coastal thicket, coastal dry forest, woodland, on sandy soil. Altitude: 65–828 m.

Phenology. Flowering and fruiting November to February, which corresponds to the rainy season occurring between November and March.

Etymology. The specific epithet is the Swahili word for sand. This is because this species is most often found growing on sand in thickets and dry forests along the coast.

Preliminary IUCN conservation assessment. *Ochna mchanga* is known only from south-eastern Tanzania and north-eastern Mozambique, with an estimated EOO of 83,998 km² and an AOO of 52 km². Timberlake et al. (2011) and Darbyshire et al. (2020a) noted significant threats to the dry forests and thickets of the Rovuma centre of endemism, including the increasing threat of land clearance for agriculture and settlements. As the species has a restricted distribution, with an AOO less than 2000 km², and is known from approximately seven locations and with a continuing decline in the area and extent of habitat, the species is assessed as Vulnerable under criterion B: VU B2ab(iii).

Figure 14. Distribution map for *Ochna mchanga* in Tanzania and Mozambique.

Additional material examined. TANZANIA • Luwangino; fl.; 1953; *Crosse-Upcott 21A*; K [K001082503]. – **Rufiji District** • Selous Game Reserve; fl.; 4 Oct. 1970; *Rogers 1157*; K [K001082501] • Selous Game Reserve, N of Nakilala Thicket; 8°41'S, 38°20'E; 350 m; fr.; 14 Dec. 1975; *Vollesen 3082*; EA, K [K001082498] • Selous Game Reserve, Malemba Thicket; 8°40'S, 38°25'E; 400 m; fl.; 11 Jan. 1977; *Vollesen 4309*; EA, K [K001082500]. – **Mtwara District** • Naliendele Forest Reserve; 10°25'17"S, 40°08'04"E; 145 m; st.; 13 Jan. 2020; *Shah TS75*; K [K001561915] • Naliendele Forest Reserve; 10°25'23"S, 40°08'07"E; 151 m; st.; 13 Jan. 2020; *Shah TS76*; K [K001561914]• Mtiniko/Mneveta Forest Reserve; 10°35'46"S, 39°55'06"E; 210 m; st.; 13 Jan. 2020; *Shah TS78*; K [K001567194]. – **Lindi District** • Rondo plateau, Mchinjidi [Mchinjiri], Rondo Nature Reserve; 10°08'31"S, 39°11'48"E; 828 m; st.; 16 Jan. 2020; *Shah TS84*; K [K001561916].

MOZAMBIQUE – **Nampula Province** • Districto de Mossuril, Reserva Florestal da Mecrusso de Matibare; fr.; 17 Feb. 1984; *Groenendijk 1145*; K [K000072636, K001387771]. – **Cabo Delgado Province** • Macomia district, Quiterajo; 11°49'39.9"S, 40°20'27.9"E; 100 m; fr.; 29 Nov. 2008; *Timberlake 5579*; K [K000738316] • Palma district, 10 km NW of Palma; 10°40'27.3"S, 40°25'55.3"E; 65 m; fr.; 6 Dec. 2008; *Timberlake 5624*; K [K000738319] • Palma district, intersection of oil cutline 34 with the Palma to Quissungule road; 10°41'23"S, 40°19'32"E; 115 m; fl., 19 Nov. 2009; *Clarke 135*; K [K000787149] • Quiterajo, within Majambo Forest; 11°52'05.2"S, 40°19'40.5"E; 90 m; fr.; 27 Nov. 2008; *Crawford FC261*; K [K000738317] • Quiterajo, S edge of forest block; 11°45'56"S, 40°22'04"E; fr.; 27 Nov. 2008; *Müller 4091*; K [K000738313].

Notes. *Ochna mchanga*, previously mistaken as *O. polyneura*, is elucidated as a cryptic species based on molecular and morphological evidence. The species is notably different by having smaller leaves and smaller inflorescences, including shorter rachis, shorter length of the pedicels below the articulation point and smaller petals. Furthermore, its bark is greyish-brown and fissured, compared to the brown corky bark of *O. polyneura*. Additionally, the two species differ in their habitat and ecology. *Ochna mchanga* occurs in coastal dry forests of south-eastern Tanzania and north-eastern Mozambique (also known as the Rovuma centre of endemism) that are not fire-prone or arguably fire-intolerant, whereas *O. polyneura* occurs in miombo woodlands of east and southern Africa that undergo regular burning.

CONCLUSION

This research is the first comprehensive study using both molecular and morphological evidence to delimit the relationships of *Ochna holstii* and related species. Previous taxonomic revisions highlighted the need for a better understanding of the group due to extreme morphological variation of the widespread species. We revealed that *O. holstii* is not monophyletic, with a clade (holstii I) represented by 11 specimens spanning the Afromontane highlands from South Sudan to South Africa, whilst a second clade (holstii II) was represented by two specimens from the Usambara Mountains in Tanzania. As no morphological evidence from herbarium specimens supported the separation of these clades, the species has been left as paraphyletic in its current circumscription, although we recognize that further evidence based on chemistry, morphological characters of living material and more fertile material with flowers may elucidate the non-monophyly of *O. holstii* in the future. In our study, a cryptic species is recognized as a new species, separate from *O. polyneura*, based on subtle morphological characters and supported by notable ecological differences.

Additionally, three undescribed taxa listed in FTEA (*O. sp 40, O. sp. 42*, and *O. sp. 47*) have now been placed within the species *O. puberula*, *O. polyneura*, and *O. oxyphylla*, respectively. Finally, we conclude that integrated taxonomic revision is integral to species delimitation of difficult groups such as *Ochna*, wherein morphological features are often lacking or difficult to detect in herbarium material. The use of molecular data in species delimitation is growing, and it is likely that as more population-level DNA sequencing is carried out, further species, particularly those that are widespread and common, will be revealed as non-monophyletic. It is also likely that similarly dense sampling will continue to reveal new species with cryptic morphological characters overlooked in traditional taxonomic methods. If widespread species lack gene flow, then it is possible that they will give rise to more restricted daughter species whilst being resolved as non-monophyletic. Using molecular data in combination with traditional morphological species delimitation is key for elucidating cryptic species, and molecular data should not be seen as a replacement for morphology but rather as an integrated method that can resolve difficult taxonomic groups.

ACKNOWLEDGEMENTS

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SUPPLEMENTARY MATERIAL

Supplementary material 1

Table showing voucher information and capture success for each sample and gene.
Link: https://doi.org/10.5091/plecevo.85589.suppl1

Supplementary material 2

Table summarizing gene recovery for each sample.
Link: https://doi.org/10.5091/plecevo.85589.suppl2

Supplementary material 3

Well-sampled phylogenetic concatenation maximum-likelihood tree of *Ochna* species in the *holstii* complex. The support values indicated above branches are bootstrap support values. Values not indicated = 100.
Link: https://doi.org/10.5091/plecevo.85589.suppl3