

Numerical phenetic analysis of *Olinia rochetiana sensu lato* (Oliniaceae)

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Summary. Previous circumscriptions of *Olinia rochetiana* A. Juss. (Oliniaceae) presented a taxonomically variable and widespread species complex in central and tropical East Africa. Results of numerical phenetic analyses of morphological variation within *O. rochetiana sensu lato* indicate the existence of four taxa which are recognisable at specific rank corresponding to *O. huillensis* Welw. ex A. & R. Fern., *O. ruandensis* Gilg, *O. rochetiana* A. Juss. *sensu stricto* and *O. usambarensis* Gilg ex Engl. The analyses also indicate that *O. huillensis*, hitherto reported to occur only in Angola, occurs widely in southern Africa and shows geographic segregates characterised as *O. huillensis* Welw. subsp. *huillensis*, *O. huillensis* subsp. *burttidavii* Sebola and *O. huillensis* subsp. *discolor* Sebola (Map 2). The major delimiting characters were found to be the shapes of petals and leaves, presence or absence of indumentum and the degree of hairiness on floral parts, and the form of inflorescence units (i.e. being either compact or spreading). Phenetic and ecological concepts of species are applied at the specific and subspecific ranks, respectively. Keys to distinguish between the species and infraspecific taxa are presented, and full descriptions and citations of examined specimens are provided.

Key Words. cluster, morphology, *Olinia*, *Olinia rochetiana*, phenetic, phenon, species, subspecies.

Introduction

Taxonomic circumscriptions within *Olinia rochetiana sensu lato* remain unsatisfactory and species limits are blurred despite Verdcourt's (1975, 1978) and Verdcourt & Fernandes' (1986) pioneering work on *Olinia* for the Floras of tropical East Africa, Zambesiaca and Mozambique. Examination of a large number of herbarium specimens of *O. rochetiana sensu lato* during a study visit to the herbaria of the Royal Botanic Gardens, Kew and the British Natural History Museum, London (by R. J. Sebola) established that *O. rochetiana sensu lato* is heterogeneous and that taxa bear a close, yet superficial resemblance to each other with respect to leaf, inflorescence and floral morphology. This precipitated a need for a focussed study on the taxonomy of *O. rochetiana sensu lato* over its known range of distribution. *O. rochetiana sensu lato* comprises mainly shrubs and small to medium-sized trees and is diagnosed from other taxa in *Olinia* by possession of a leaf lamina with midrib impressed above; the secondary veins forming more than one loop before or at the margins; the petiole, which is reddish, puberulous and ranging from 1.5 – 10 mm long; the petals, which are

oblong to spatulate or distinctly spatulate; and the scales, which are highly puberulous and often seal the hypanthium throat. The inflorescence architecture in *Olinia* is generally uniform, regarded as a 'primitive monotelic' type (Weberling 1988), and without exception the main inflorescence axis ends with a terminal flower (Fig. 1). The secondary inflorescence axes branch off the main inflorescence axis and lead to inflorescence units, each comprising a triad of flowers (Sebola & Balkwill 1999). Within each triad the terminal flower is usually the oldest and largest compared to the lateral flowers (Figs. 1B – D). In other species of *Olinia* (*O. capensis* Klotzsch, *O. micrantha* Decne. and *O. radiata* Hofmeyr & E. Phillips) the axes of inflorescence units are reduced and the pedicels are minute, making the triad compact and tight (Fig. 1D).

The interpretation of floral whorls in *Olinia* has generated divergent views of the relative positions of the sepals and petals (Rao & Dahlgren 1969; Cronquist 1981; Dahlgren & Van Wyk 1988; Sebola & Balkwill 1999; Schönenberger & Conti 2003; Von Balthazar & Schönenberger 2006). Anatomical data

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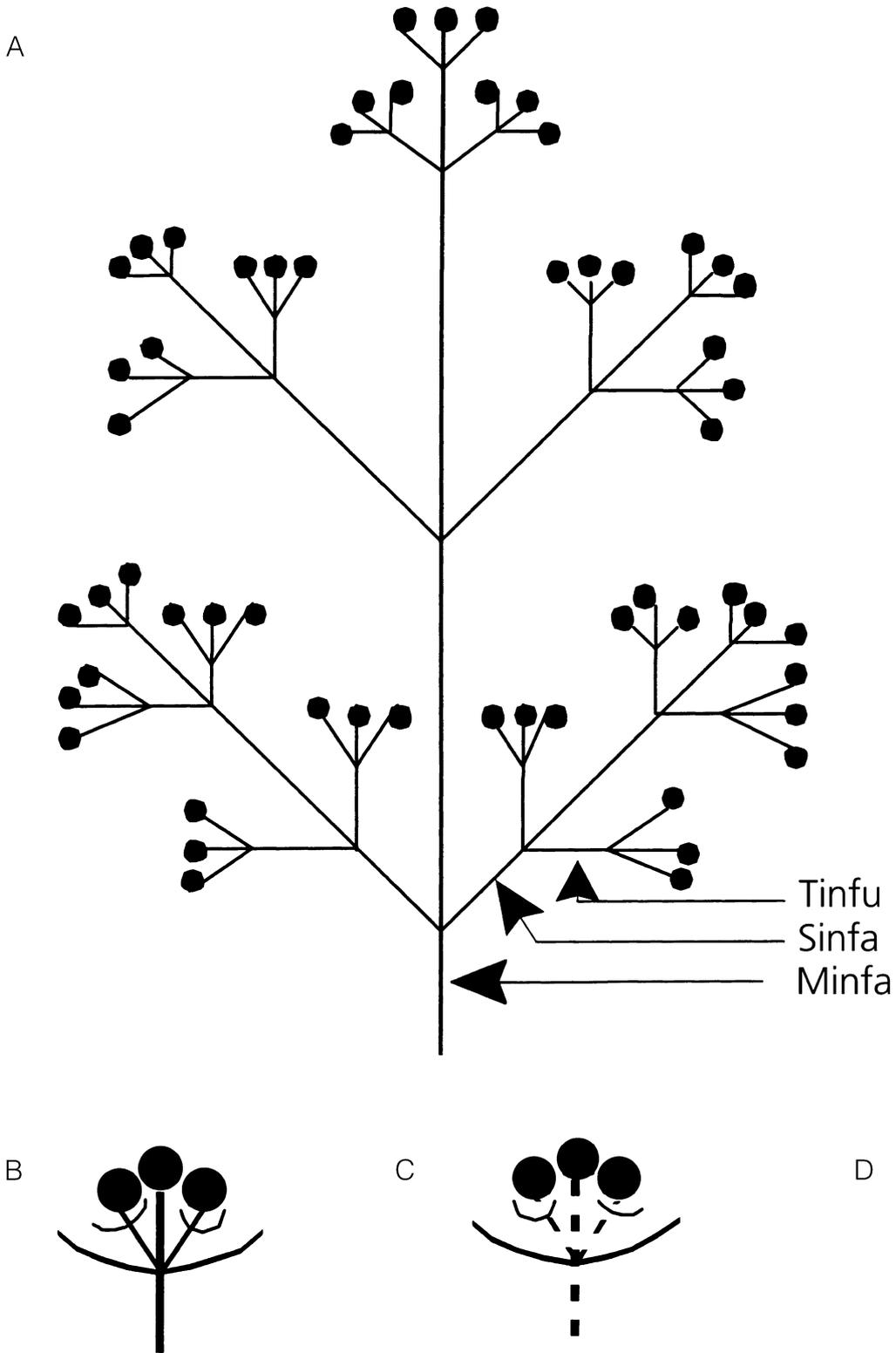


Fig. 1. Diagram of *Olinia* inflorescence (adapted from Sebola & Balkwill 1999) showing: A typical inflorescence structure; B inflorescence unit with three flowers; C inflorescence unit with reduced axes; and D inflorescence unit with three compact and tightly held flowers — ‘Tinfu’ = tertiary inflorescence unit, ‘Sinfa’ = secondary inflorescence axis, and ‘Minfa’ = main inflorescence axis.

have influenced Schöenberger & Conti's (2003) interpretation that promotes an obhaplostemonous condition in *Olinia*. Accordingly, three floral whorls are recognised and the 'outermost' whorl is regarded as the epicalyx or as being made of teeth of an unspecified nature, the 'middle' whorl of coloured lobes is regarded as calyx, and the 'innermost' whorl as the corolla. In this definition the 'outermost' whorl lacks vascularisation unlike the other whorls, is only discernible late during floral development, and does not seem to have any taxonomic value (Von Balthazar & Schöenberger 2006). It is apparent that our current state of knowledge and understanding of the perianth organs and morphology in *Olinia* is insufficient, and further studies are required to determine with certainty the nature of perianth whorls in *Olinia* since the ontological and anatomical data (Rao & Dahlgren 1969; Tobe & Raven 1984; Schöenberger & Conti 2003; Von Balthazar & Schöenberger 2006) have proved inconclusive. In this study, the outermost whorl is considered to be a reduced calyx, the middle whorl of coloured lobes to be the corolla, and the innermost whorl to be scales, which is consistent with the interpretation of Sebola & Balkwill (1999). Although Schöenberger & Conti's (2003) interpretation of perianth whorls in *Olinia* seems convincing, the 'outermost' whorl is however considered here to be a true calyx, rather than an epicalyx until all the species of *Olinia* have been investigated.

Within *Olinia*, specific morphological features such as shape and size of leaves and bracts, size of petals and floral tubes, inflorescence architecture, and habit have been extensively used in the delimitation and recognition of taxa (Klotzsch 1836; Sonder 1862; Decaisne 1877; Gilg 1894; Sim 1907; Hofmeyr & Phillips 1922; Burt Davy 1926; Cufodontis 1960; Fernandes & Fernandes 1962; Verdcourt & Fernandes 1986; Sebola & Balkwill 1999, 2006) while anatomy (Rao & Dahlgren 1969; Mujica & Cutler 1974), embryology (Tobe & Raven 1984) and palynology (Patel *et al.* 1983) have been of limited use in the infrageneric taxonomy of *Olinia*. The foregoing provides the basis, in this paper, for focusing on analyses of morphological variation rather than anatomical, embryological or palynological features. The taxonomic concepts applied within *Olinia* to date have been mainly morphological.

The name *Olinia rochetiana*, based on Rochet d'Héricourt's specimen no. 18 collected during his voyages to Abyssinia (1842, 1843 & 1844), was published (de Jussieu 1846) when the only specimens of *Olinia* known to science had been collected from the Cape of Good Hope (Thunberg 1799). Noting the similarities between his diagnosis of Rochet's specimen no. 18 and those provided for *Olinia* by Thunberg, Jussieu was faced with a decision to either create a new genus, *Rochetia*, or recognise a new species

rochetiana under *Olinia*, and opted for the latter. It appears that Delile (1846) ignored Jussieu's taxon and instead proposed the name *Tephea aequipetala* for the same specimen (Rochet no. 18). Information from herbarium sheets suggests that *O. cymosa sensu* Hiern (1871) was based on material in flower and fruit collected by Roth, probably from the same locality as Rochet 18 (i.e. Choa, near Ankober in Abyssinia, nowadays Ethiopia) since Hiern's taxon is definitely not the same as Thunberg's. Decaisne (1877), in his attempt to characterise the Oliniaceae and establish their affinities, recognised de Jussieu's (1846) *O. rochetiana* from tropical Africa as distinct from four other species from southern Africa (*O. cymosa* Thunb., *O. capensis*, *O. acuminata* Klotzsch and *O. micrantha*). Since the collections of *Olinia* made by both Roth and Rochet, other botanical exploration in central and tropical East Africa (notable collections include those by Welwitsch in Angola; Holst, Schlieben and Volkens in Usambara, Tanzania; Mildbraed in Zaire (nowadays Democratic Republic of the Congo); Angus and White in Zambia; Richards in Malawi; Chase in Zimbabwe; and Mooney in Ethiopia) expanded the collections of *Olinia* known to science (Appendix 1), which led to a proliferation of new species names (i.e. *O. discolor* Mildbr., *O. macrophylla* Gilg, *O. ruandensis* Gilg, *O. ternata* Gilg ex Engl., *O. usambarensis* Gilg ex Engl., *O. vanguardoides* Baker f., *O. volkensii* Gilg ex Engl.). However, the tropical African material of *Olinia* has never been comprehensively reviewed, although there were attempts at the regional level (Fernandes & Fernandes 1962; Verdcourt 1975, 1978; Verdcourt & Fernandes 1986).

On the basis of *Olinia* material collected in tropical East Africa, Cufodontis (1960) recognised only two species, *O. aequipetala* (Delile) Cufod. and *O. usambarensis* on the basis of floral features, and also noted the possible confusion that could arise by misinterpreting floral changes due to infection by hemipteran larvae. This condition has long been acknowledged (Decaisne 1877; Hofmeyr & Phillips 1922; Phillips 1926) as affecting the size and shape of flowers in *Olinia*, and it has also been confirmed lately (Verdcourt 1975, 1978; Verdcourt & Fernandes 1986; Sebola & Balkwill 1999). Infected or galled flowers are either narrow with elongate tubercles or swollen (Fig. 2B, C). In a comparative analysis of *Olinia* material collected from Angola and elsewhere, Fernandes & Fernandes (1962) established that the Angolan plants are clearly distinct from *O. ventosa* (L.) Cufod. on the basis of floral and fruit features, but only superficially different from material from tropical Africa. On this basis the Angolan material was included in *O. rochetiana sensu lato* and recognised as a regional subspecies *O. rochetiana* subsp. *huillensis* Welw. (using the epithet *huillensis* proposed by the collector, Welwitsch) distinguishing it from other subspecies (i.e. subsp. *rochetiana*, subsp. *usambarensis* and subsp. *discolor*). The overlap of morphological



Fig. 2. Flowers in *Olinia* showing: **A** normal uninfected flower, *Bogdan* 4762 (K); **B** galled flowers showing elongate tubercles, *Goldsmith* 7 – 71 (K); and **C** galled flowers showing swollen tube, *Howard* IM81 (K). Scale bars **A** and **C** = 1 mm; **B** = 0.5 mm.

variation among OTUs from these regions prompted questions about their taxonomic status as species or infraspecific taxa. This observation led to an investigation and analysis of morphological variation of the populations of *O. rochetiana sensu lato* occurring in South Africa (Limpopo and Mpumalanga Provinces) (Sebola & Balkwill 2006). The use of anatomical features (i.e. the number of girders in the leaf) by Mujica & Cutler (1974) led to segregation of three South African species of *Olinia* (*O. emarginata* Burt Davy, *O. radiata* and *O. ventosa*) from the species of *Olinia* occurring in central and tropical East Africa (*O. aequipetala*, *O. usambarensis*, *O. volkensii*, *O. macrophylla*, *O. ruandensis*, *O. discolor* and *O. huillensis*) all of which were later subsumed under *O. rochetiana sensu lato* (Verdcourt 1975, 1978; Verdcourt & Fernandes 1986). The taxonomic history of *Olinia rochetiana sensu lato* is summarised in Table 1.

The subsuming of a number of species into *Olinia rochetiana sensu lato* by Verdcourt (1975, 1978) and Verdcourt & Fernandes (1986) presents a broader species concept, which has proved problematic when conducting comparative analyses of species to test hypotheses on the phylogeny of *Olinia* (Sebola & Balkwill, 2009b). It appears that more than one species can be recognised among the synonyms cited under *O. rochetiana sensu lato*, an observation reinforced by examining a large number of herbarium specimens on loan from B, BM, BOL, ETH, K, J, PRE, and SAM

(Appendix 1), the majority of which were not referred to by previous authors. This makes it possible to study and analyse the morphological variation within *O. rochetiana sensu lato* with the objective of assessing the species limits using numerical phenetic methods. The lack of a single, all encompassing definition of the term “species” remains a challenge for taxonomists, and this is exacerbated by the use of the term in several different senses (White 1962b; Sneath 1976; Van Valen 1976; Jonsell 1984; Raven 1986; Kornet 1993; Kornet & McAllister 1993; Mayden 1997). The biological species concept requires that entities or species be treated as groups of natural populations capable of interbreeding, and are reproductively isolated from other such groups of populations (Raven 1986). According to Stace (1989) the emphasis is on genetic isolation rather than on morphological limits, which is unattractive for plant taxonomists because in plants the morphological and genetic limits do not always coincide. The limited number of field observations and consequent reliance on herbarium specimens as the main source of data in this study prohibited a thorough assessment of the applicability of the biological concept of species in *O. rochetiana sensu lato*. The analyses of the available data allowed for an assessment of the applicability of the phenetic concept of species, which considers the species level as that at which distinct phenetic clusters can be observed (Sneath 1976). The ecological concept of species on

Table 1. Survey of historical accounts of taxa within *Olinia rochetiana sensu lato*.

Date	Author(s)	Taxa recognised
1846	Adrian Henri Laurent de Jussieu	<i>O. rochetiana</i> A. Juss.
1894	Engler	<i>O. usambarensis</i> Gilg ex Engl.
1895	Gilg	<i>O. macrantha</i> Engl.
1895	Gilg	<i>O. volkensii</i> Gilg ex Engl.
1911	Baker	<i>O. vanguardoides</i> Baker f.
1914	Gilg	<i>O. macrophylla</i> Gilg, <i>O. ruandensis</i> Gilg
1921	Engler	<i>O. ternata</i> Gilg ex Engl., <i>O. abyssinica</i> Engl.
1932	Mildbraed	<i>O. discolor</i> Mildbr.
1959	Cufodontis	<i>O. aequipetala</i> (Del.) Cufod.
1962	Fernandes & Fernandes	<i>O. huillensis</i> Welw. ex A. & R. Fern.

the other hand relates to a lineage or closely related set of lineages, which occupy an adaptive zone minimally different from that of any other lineage in its range (Van Valen 1976).

In this study, all available morphological characters of systematic relevance to *Olinia rochetiana sensu lato* are analysed and summarised by multivariate methods in order to gain new insights into the taxonomy of the group. The aim of this paper is to provide an improved understanding of the taxonomic circumscriptions within *O. rochetiana sensu lato*. Resolving the species limits within *O. rochetiana sensu lato*, which occurs predominantly in tropical Africa, would also contribute significantly to the knowledge and understanding of *Olinia* over its full geographic range, now that the status of southern African species of *Olinia* has been clarified (Sebola & Balkwill 1999).

Materials and Methods

Study Material and Measurements

This study was based entirely on herbarium material of *Olinia* from tropical Africa. A representative collection of herbarium specimens was loaned from B, BM, BOL, ETH, K, NBG (incorporating the South African Museum Herbarium, SAM, and Stellenbosch Herbarium, STE) and PRE to supplement those at J (abbreviations according to Holmgren *et al.* 1990) to cover the entire range of known distribution of *O. rochetiana sensu lato* (see Appendix 1 for list). The specimens were studied and sorted *a priori* into hypothetical groups, without regard to names on labels, and based solely on the similarity of a few macro- and micro-morphological characters previously used in *Olinia* to define taxonomic groups. Considering that previous studies of *Olinia* in the *Flora Zambesiaca* and tropical East African regions have consistently separated *O. vanguerioides* from *O. rochetiana sensu lato* (Verdcourt 1975, 1978; Verdcourt & Fernandes 1986), it became logical in this study to include specimens belonging to *O. vanguerioides* and use the levels of similarity at which they group together on phenograms as a yard stick for recognising taxonomic groups within *O. rochetiana sensu lato*. A total of 100 fertile (either flowering or fruiting) specimens was studied. These included specimens labelled as types (either holotype or syntype) for the species names *O. usambarensis*, *O. volkensii*, *O. macrophylla*, *O. huillensis*, *O. discolor* and *O. aequipetala*. A total of 60 characters, 11 of which are quantitative continuous (obtained by measurement), 2 quantitative discontinuous (obtained by counting) and 47 qualitative discontinuous (obtained by scoring each specimen into states) was measured per specimen (Table 2). A minimum of five measurements was made for all the quantitative continuous characters per specimen and

statistical means were calculated. Measurements of larger parts such as lengths and widths of leaves and lengths of inflorescence units were made to the nearest 0.5 mm. An ocular micrometer was used to measure smaller structures such as the lengths of petioles, pedicels, hypanthia, and lengths and widths of sepal lobes at 6× to 31× magnifications to the nearest 0.1 mm.

Methods of Analysis

The *a priori* groups (i.e. groups of specimens formed on the basis of similarities and/or dissimilarities of leaf shapes, inflorescence structure and floral features without regard to labels on herbarium sheets) were tested using the numerical methods of analysis available in the program, NTSYS-PC Version 2.02j (Rohlf 1998). The full data matrix was standardised using the STAND option to render the characters dimensionless and to reduce all characters to a scale of comparable range with a mean of zero and a standard deviation of unity. Both ordination and cluster analyses were performed on the standardised data matrix.

Since the data set contained a mixture of quantitative and qualitative characters, the principal coordinate analysis (PCoA) was preferred over the principal component analysis (PCA) because the latter is applicable on the quantitative continuous characters and not suitable for discrete qualitative characters (Sneath & Sokal 1973; Schilling & Heiser 1976; Kent & Coker 1992). PCoA is applicable to datasets containing both quantitative continuous and qualitative discontinuous characters (Small & Brookes 1990; Small *et al.* 1999; Sebola & Balkwill 2009a). In this study PCoA was applied on the full dataset containing both quantitative continuous and qualitative discrete characters since the method does not have the same constraints on the data set nor the same assumptions as the principal components analysis (Austin 1985). Principal coordinate analysis was performed from the correlation matrix on standardised data using the procedure SIMINT, DCENTER, EIGEN, and MOD3D available in the program NTSYS-PC Version 2.02j (Rohlf 1998).

Cluster analysis is known to impose a hierarchical structure on any data (Thorpe 1983); and often shows clusters that may not be recoverable in ordination analysis (Chandler & Crisp 1998). For these reasons, and also as a means to test the consistency of clusters obtained, cluster analysis was applied to the same data matrix on which principal coordinate analysis was performed. Therefore, cluster analysis was used to test whether groups similar to those obtained in principal coordinate analysis could be recovered; and also to visualise the level of morphological similarity/dissimilarity using appropriate coefficients between and within the *a priori* groups. It was performed by

Table 2. Descriptions of morphological characters and coding (in parenthesis) used in the numerical phenetic analyses of specimens of *Olinia rochetiana sensu lato*.

1	Mean leaf lamina length
2	Mean leaf lamina width
3	Ratio of leaf width : length
4	Mean petiole length
5	Mean hypanthium length
6	Mean fruit length (taken from point of attachment with pedicel to the hypanthium rim)
7	Mean petal lobe length
8	Mean petal lobe width
9	Ratio petal width : length
10	Mean inflorescence axis length
11	Mean inflorescence unit length
12	Mean peduncle length
13	Mean pedicel length
14	Number of units per inflorescence axis
15	Mean bract lamina length
16	Mean bract lamina width
17	Ratio bract width : length
18	Petiole surface glabrous (0), sparsely pubescent (1), markedly pubescent (2)
19	Surface of inflorescence axis, glabrous (0), sparsely pubescent (1), markedly pubescent (2)
20	Inflorescence unit glabrous (0), sparsely pubescent (1), markedly pubescent (2)
21	Hypanthium surface glabrous (0), sparsely pubescent (1), markedly pubescent (2)
22	Peduncle surface glabrous (0), sparsely pubescent (1), markedly pubescent (2)
23	Pedicel surface glabrous (0), sparsely pubescent (1), markedly pubescent (2)
24	Inflorescence organisation loose /sparse (0) or dense/compact (1)
25	Internodes along inflorescence axis shorter than inflorescence units (0) or longer (1)
26	Flowers respond to galling by swelling up (0) or elongating to narrow tubercles (1)
27	Leaf texture glossy, soft & smooth (0), stiff to leathery (1) or thin to papery (2)
28	Leaves clustered at base of inflorescence axes and units (0) or present at every internode (1)
29	Secondary veins curving (0) or parallel each other (1)
30	Abaxial surface of petal glabrous (0), sparsely pubescent (1), markedly pubescent (2)
31	Adaxial surface of petal glabrous (0), sparsely pubescent (1), markedly pubescent (2)
32	Style surface glabrous (0), sparsely pubescent (1), markedly pubescent (2)
33	Adaxial surface of bract glabrous (0), sparsely pubescent (1), markedly pubescent (2)
34	Abaxial surface of bract glabrous (0), sparsely pubescent (1), markedly pubescent (2)
35	Leaf discoloured (0) or concolorous (1)
36	Secondary veins visible (0) or invisible (1) on adaxial surface of leaf lamina
37	Secondary veins visible (0) or invisible (1) on abaxial surface of leaf lamina
38	Leaf margin flat (1) or sparsely in-rolled (0)
39	Bract coloration light to yellow (1) or green (0)
40	Bract texture papery (0) or leathery (1)
41	Bract caducuous (0) or persistent through anthesis (1)
42	Leaf shape elliptic (0) or not (1)
43	Leaf shape oblong (0) or not (1)
44	Leaf shape obovate (0) or not (1)
45	Leaf apex emarginated (0) or not (1)
46	Leaf apex mucronate (0) or not (1)
47	Petal shape oblong (0) or not (1)
48	Petal shape obovate (0) or not (1)
49	Petal shape spatulate (0) or not (1)
50	Petal apex truncate (0) or not (1)
51	Petal apex shortly mucronate (0) or blunt (1)
52	^a Leaf shape index
53	^a Number of secondary veins counted on both sides of midrib
54	^a Angle of branching of secondary veins
55	^a Mean areole length measured on adaxial surface
56	^a Mean areole width measured on adaxial surface
57	^a Mean number of veinlets per areole counted on adaxial surface
58	^a Mean number of branches per veinlet measured on adaxial surface
59	^a Angle of leaf apex measured on adaxial surface
60	^a Angle of leaf base measured on adaxial surface

Quantitative continuous characters are represented by the mean values per individual specimen measured in millimeters (mm) while quantitative discontinuous characters represent maximum values.

^a Characters defined as in Hickey (1973), Hill (1980) and Herman *et al.* (1987)

calculating the similarity matrix between OTUs using the average taxonomic distance coefficient from the standardised matrix, clustering the OTUs by using the unpaired group method of arithmetic averages (UPGMA), computing the cophenetic values and the cophenetic correlation using COPH and MXCOMP, respectively, to measure the distortion between the original distance matrix and the resultant phenogram (Crisci *et al.* 1979; McDade 1997; Sebola & Balkwill 2009a). Each taxon recognised was evaluated against the categories and criteria (Version 3.1) set out by the IUCN (2001) and where possible all criteria met at the highest threat category were listed.

Results and Discussion

Ordination

The two dimensional PCoA plot of the full data set separated the specimens into six groups (Fig. 3). Principal coordinate 1 accounted for 38.9% of the variation, principal coordinate 2 accounted for 17.8% of the variation while principal coordinate 3 (not shown) accounted for 8.7% of the variation. The characters most strongly correlated with the first PCO axis with high values (>0.5) were leaf texture, leaf

shape, pattern of venation on lamina, size of floral tubes, shape of petals and bracts and persistence of bracteoles after anthesis. Specimens determined as *Olinia vanguerioides* and marked *a priori* into group VG are all grouped together on the left side along the first axis. The specimens of *O. rochetiana sensu lato* form five groups, three of which are formed by specimens belonging to different *a priori* groups (i.e. marked AA&AB, LL&LP, and ML&NE), showing a considerable degree of overlap. The group characterised by OTUs marked BR is clearly separable from the other groups, and occupies the far right side of the first axis whilst the group marked by MP occupies the centre of the plot (see Appendix 2 for list of OTU codes).

The formation of clusters comprising OTUs of AA&AB and ML&NE that share similar phenetic space reflects some pattern of geographical distribution. The OTUs comprising cluster AB are mainly from south western Zambia and eastern and southern Angola, while OTUs in clusters AA, ML&NE are from Angola (Huambo and Lubango Districts), South Africa (Limpopo and Mpumalanga provinces), Zimbabwe (Chimanimani District) and south western Malawi (Mt Mlanje and the environs). The prevalence of short and robust inflorescence units and thick textured floral tubes among the OTUs of *a priori*

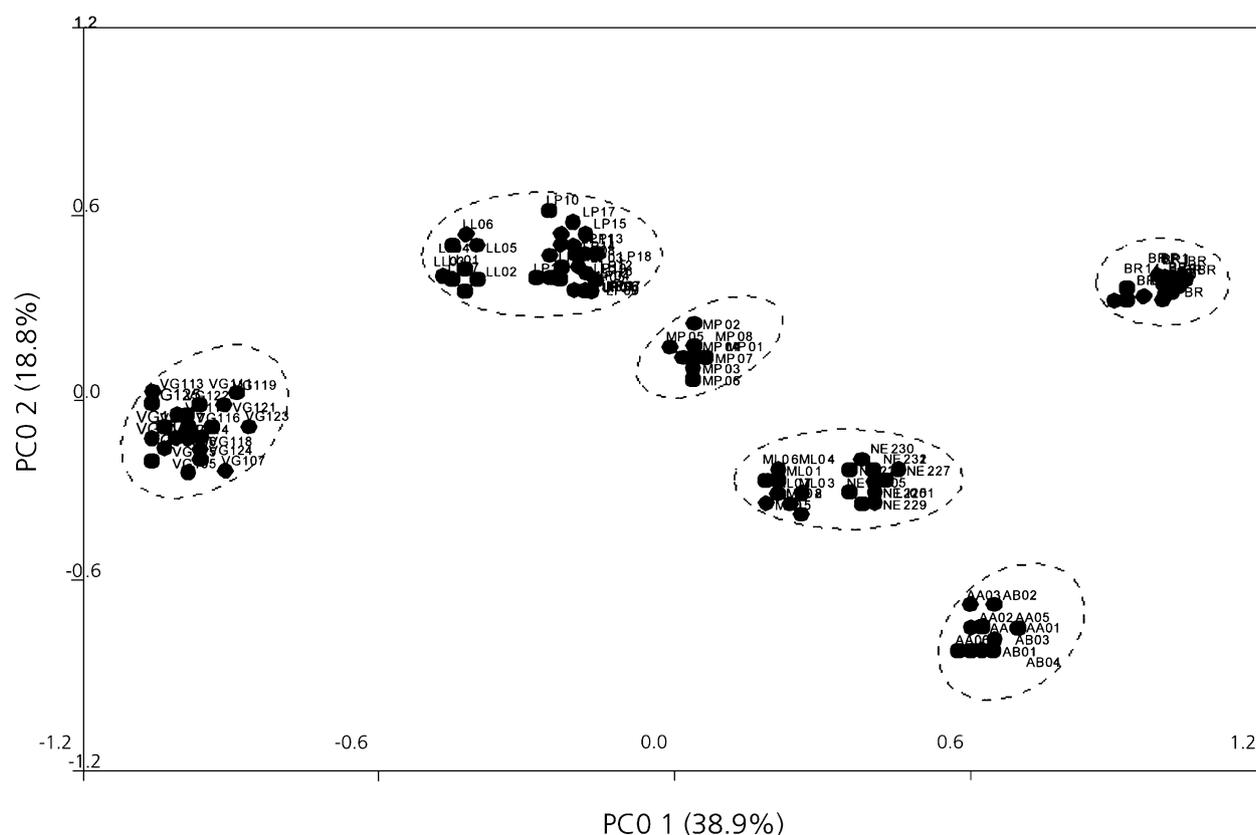


Fig. 3. Plot of the first two principal coordinate analysis obtained from analysing morphological data from specimens of the *Olinia rochetiana sensu lato*. The first and second PCO axes explain 38.9% and 17.8% of the total variation, respectively.

groups ML&NE, in contrast to the slender, spreading inflorescence units and thin textured floral tubes among OTUs of *a priori* groups AA&AB make these useful differentiating characters. Although there is clear separation of specimens belonging to a *a priori* group ML from those of a *a priori* group NE along the first axis, this distinction is blurred and not recognisable along the second axis and the third axis (not shown). However, both the first and second axes separate the OTUs in a *a priori* groups AA&AB from those in a *a priori* groups ML&NE.

Clustering

The UPGMA cluster analysis of the entire data set separates five clusters (1 – 5) at a dissimilarity level of 0.89 (Fig. 4), corresponding largely to those obtained in the PCoA analysis. The cophenetic correlation coefficient value of $r = 0.944$ obtained in the analysis indicates a very good fit between the triangular distance matrix and the phenogram (Sneath & Sokal 1973; Rohlf 1998). In Fig. 4 the phenon line is used at three different similarity levels (**a**, **b** and **c**) to recognise taxa at different taxonomic hierarchies. The *a priori* groups were recognised as distinct taxa at different hierarchies if all their OTUs did not mix between clusters, and also considering the level of phenetic distance at which OTUs cluster together. The occurrence of the type specimens within the clusters on the phenogram (indicated by arrows) was used to apply the names to clusters. In this analysis, the OTUs comprising the *a priori* VG were easily recognisable and could not be confused with any other group(s) within *Olinia rochetiana sensu lato*. The *a priori* group VG represents *O. vanguardoides*, and therefore the level of similarity at which all the OTUs of the *a priori* group VG unite were used as a yardstick to establish the most acceptable level of unity among members of other taxa at the specific rank.

Phenon line **a** is placed at the mid-point (i.e. 0.89) along the dissimilarity scale, and delimits a total of five clusters. In all but one cluster (i.e. cluster 5) the constituent OTUs are from different *a priori* groups (i.e. AA, AB, ML&NE). The mixing of *a priori* groups in cluster 5 is also supported by the results of principal coordinate analysis (Fig. 3), where there is some overlap in the phenetic space among specimens of the AA&AB *a priori* groups and between those of ML&NE *a priori* groups. Adoption of phenon line **a**, which segregates the *a priori* group VG at the level from which all its OTUs unite, calls for a broad taxonomic concept comprising *a priori* groups AA, AB, ML&NE which correspond to *Olinia huillensis*, the geographic distribution of which covers southern Angola, southwestern Zambia, northeastern South Africa, southern Zimbabwe and Malawi.

The cluster denoted by a *a priori* group BR is the first to branch off from all other clusters and comprises

specimens characterised by compact inflorescence units and with larger and showier persistent bracts and bracteoles that are puberulent on both surfaces. This cluster includes the specimen Holst 9115 (indicated by arrow), and is therefore determined as *Olinia usambarensis*. The two clusters denoted by a *a priori* groups MP and LL&LP also appear as distinct from each other in the ordination analysis (Fig. 3) along the PCO 1. These clusters are recognised in this analysis as representing the *O. discolor-volkensii* and *O. macrophylla-ruandensis* groups, respectively by the presence of specimens Volkens 1816 & 2000 (for *O. volkensii*), Schlieben 20 (for *O. discolor*) and the presence of specimens Mildbraed 1027 & 2541 (for *O. macrophylla*).

At a higher dissimilarity of 0.73 cluster 5 comprising the *a priori* groups AA, AB, ML, LJ&NE, and referred to *Olinia huillensis* is split into two distinct sub-clusters (**a** & **b**) formed by the *a priori* groups AA&AB and ML, LJ, PN&NE, respectively. At this high level of dissimilarity (0.73) a total of six taxa (excluding *O. vanguardoides*) is recognised within *O. rochetiana sensu lato*. These clusters would correspond to *O. usambarensis* (for *a priori* group BR), *O. ruandensis* (for *a priori* group MP), *O. rochetiana sensu stricto* (for *a priori* groups LL&LP), *O. huillensis* subsp. *huillensis* (for *a priori* groups AA&AB), *O. huillensis* subsp. *burttdavii* (for *a priori* group NE, LJ&PN) and *O. huillensis* subsp. *discolor* (for *a priori* group ML) at the specific and subspecific rank.

Sub-cluster **5a** comprises mainly Angolan material and includes the specimen Welwitsch 991. The unity of some Angolan material at this similarity level (0.73) supports Cufodontis's (1960) concept of *Olinia huillensis* as being largely restricted to Angola. Sub-cluster **5b** is, however, a heterogeneous group comprising specimens collected in Malawi (Northern Province, Mt Mlanje, Mafingi Hills), Zambia (Isoka district, Mafingi Mts), Zimbabwe (Chimanimani Mts), Mozambique (Manica and Tete Provinces), South Africa (Limpopo and Mpumalanga Provinces) and some specimens from Angola (Huilla district where Welwitsch 991 was collected). This suggests that *O. huillensis* as described by Cufodontis is perhaps more widespread than reported because the non-Angolan materials studied show continuous and overlapping morphological variation with those from Angola (Fig. 5). Similar clusters as in Fig. 4 were also obtained from cluster analysis based only on quantitative characters (results not shown).

At a lower level of dissimilarity (0.65) cluster **5b** is split into two sub-clusters, **5b(i)** and **5b(ii)**. Further examination of these sub-clusters revealed that they correspond to the taxa recognised in an appraisal of *Olinia rochetiana* in South Africa (Sebola & Balkwill 2006). Comparative morphological studies of specimens of these sub-clusters show that these taxa are distinct both at a local scale in northeastern South

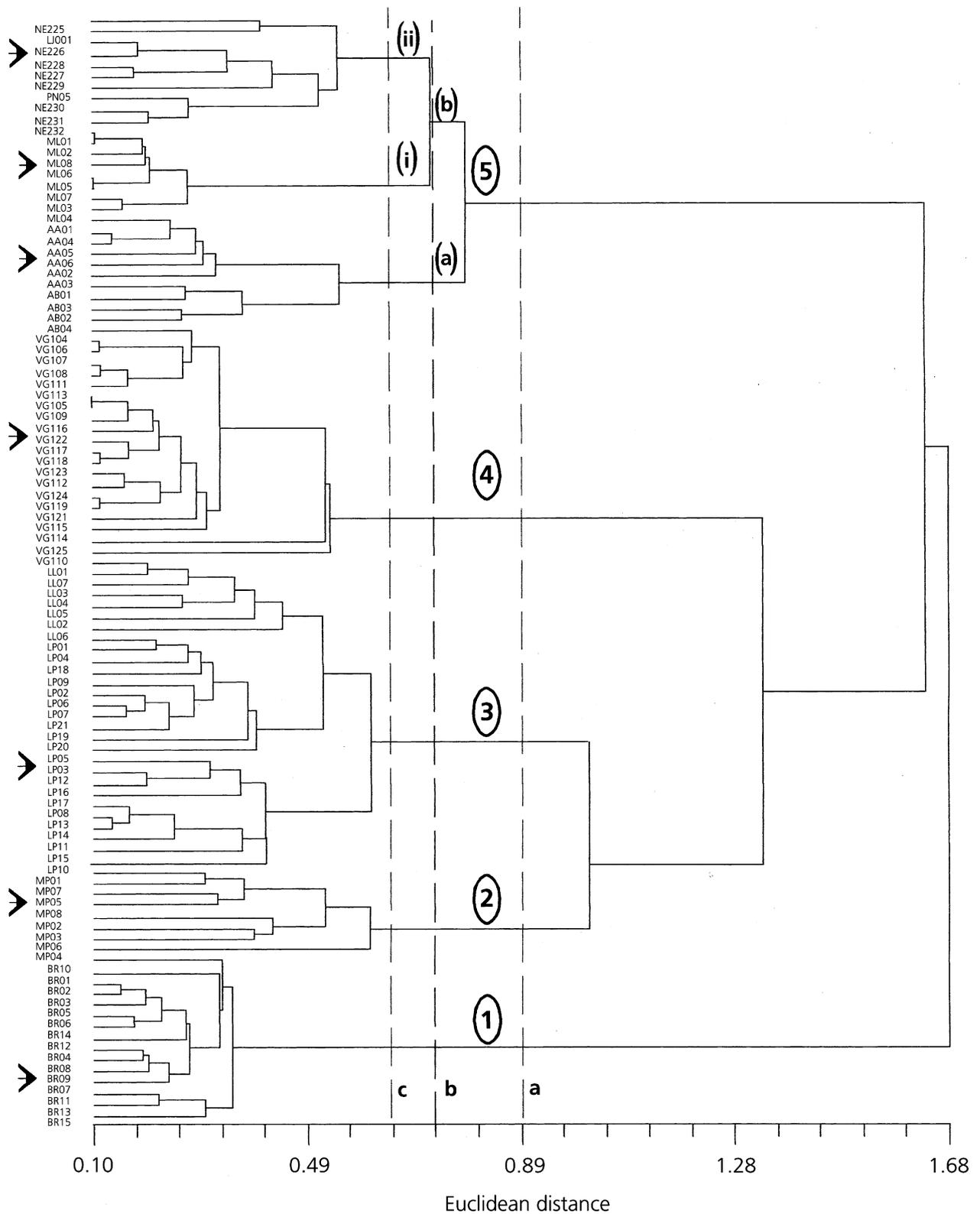


Fig. 4. UPGMA phenogram resulting from cluster analysis of the full data matrix of *Olinia rochetiana sensu lato*. Co-phenetic correlation ($r = 0.944$). Vertical dotted lines **a**, **b** and **c** indicate phenon lines. The numbers **1**, **2**, **3**, **4**, and **5** indicate distinct clusters recognisable at species level, and correspond to *O. usambarensis*, *O. rochetiana*, *O. ruandensis*, *O. vangerioides* and *O. huillensis*, respectively. The OTUs are listed in Appendix 2 (Table 3).

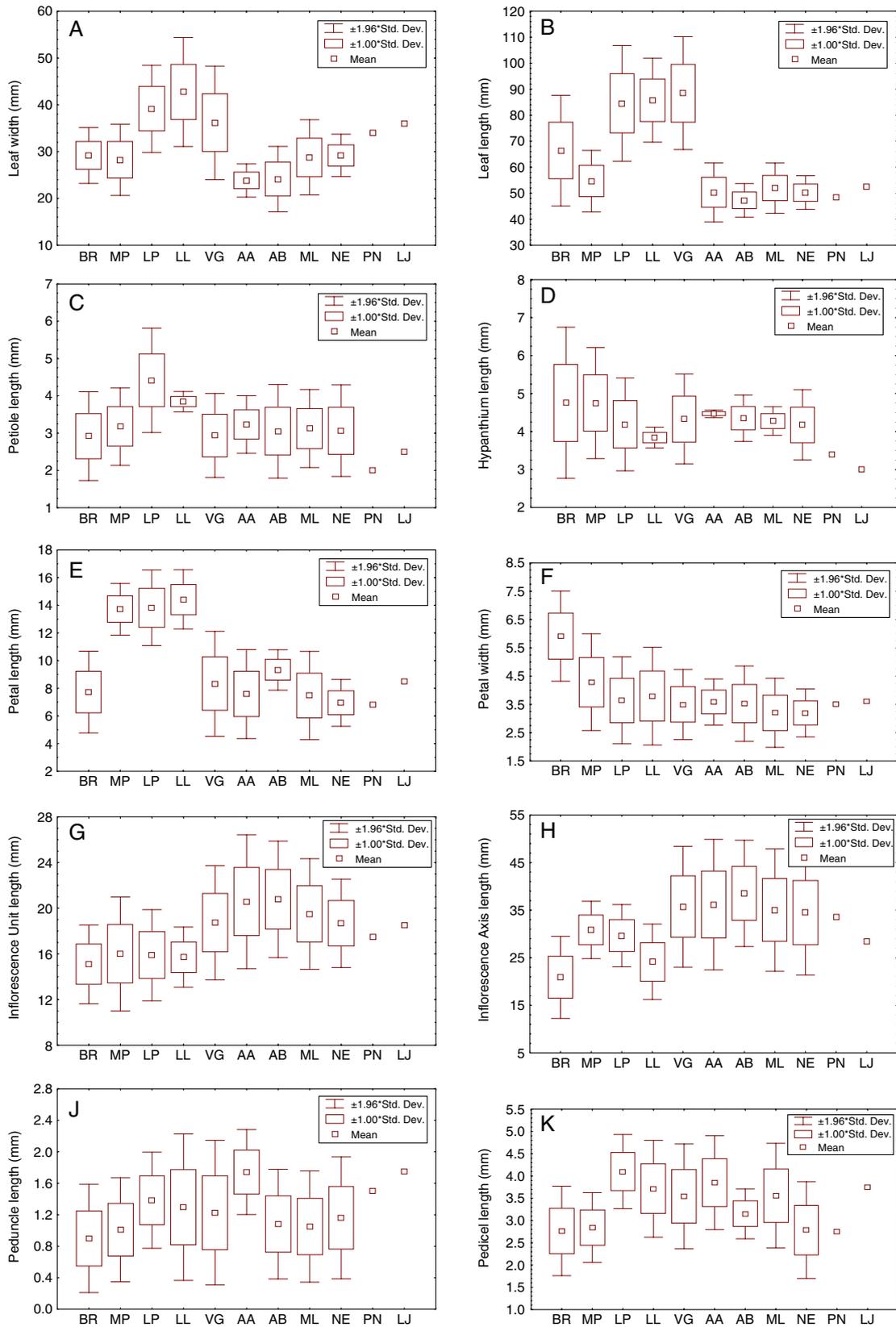


Fig. 5. *Olinia rochetiana sensu lato*. showing variation in: A leaf width; B leaf length; C petiole length; D hypanthium length; E petal length; F petal width; G inflorescence unit length; H inflorescence axis length; J peduncle length; and K pedicel length.

Africa (Sebola & Balkwill 2006) and a broader scale including material from as far north as Zambia, and to the east, in Mozambique and Malawi. The sub-cluster **i** comprises OTUs with very short petioles, leaves that are broadly elliptic to obovate and leathery; inflorescence axes with shorter internodes and clustered; walls of floral tubes are thickly textured, robust and have broad openings/throats; and correspond to the 'shrubby dwarf' form occurring in South Africa (Sebola & Balkwill 2006). This is in contrast to the main features of specimens in sub-cluster **ii**, which are characterised by slender terminal branches and branchlets; longer petioles; thin, glossy and papery leaves (fresh material); slender inflorescence axes with longer internodes, peduncles, pedicels and thinly textured walls of floral tubes; and corresponds to the 'slender tree-like' form in the reappraisal and identification of *O. rochetiana* in South Africa (Sebola & Balkwill 2006).

The three phenon lines (**a**, **b** and **c**) all delimit the same phenetic clusters (**1**, **2**, **3**, and **4**) except for cluster **5**, which comprises *a priori* groups AA, AB, ML&NE (Fig. 4) and is variously delimited. It is the interpretation of the morphological variation exhibited by these *a priori* groups which informs the concept of *Olinia huillensis* adopted in this study. The cluster representing *O. vanguerioides* is distinguishable even at the high dissimilarity level of 1.28, above which (i.e. at 1.44 dissimilarity) the gap in similarity between the clusters of OTUs is small and merged with clusters representing *O. ruandensis* and *O. rochetiana*. The shape of leaf lamina, the distinct venation pattern, and the shape of petals are decisive characters for keeping *O. vanguerioides* separate from *O. rochetiana sensu lato*. Flowers that are infected by insects form distinctive galls with tubercles along elongated ridges, which are different from the swollen flowers of *O. rochetiana sensu lato* when infected (Fig. 2). This feature was, however, not included in the analyses despite being consistent among infected flowers of *O. vanguerioides* and *O. rochetiana sensu lato* since not all specimens that had flowers included infected flowers. The nature and pattern of morphological variation analysed from a large number of specimens of *O. vanguerioides* on loan from BM, K and PRE in this study allowed the conclusion that supports the position of previous workers on *Olinia* that *O. vanguerioides* is a morphologically unique and distinct species from *O. rochetiana sensu lato* (Verdcourt 1975, 1978; Verdcourt & Fernandes 1986).

Trends in Character Variation

This morphological study, based on herbarium specimens, established that circumscription of taxa within *Olinia rochetiana sensu lato* is more problematic for the central and tropical East African taxa than those

occurring in southern temperate regions, mainly southern Africa. The analyses indicate that the discontinuities and gaps in morphological variation are mainly due to quantitative features and a few qualitative features relating to indumentum and shapes of floral parts. The overlapping pattern of morphological variation between taxa within *O. rochetiana sensu lato* (Fig. 5) suggests that these taxa once formed a continuum, which later differentiated into several forms adapted to particular ecological conditions. It is noteworthy that taxa of *Olinia* occurring in moist, tropical regions tend to have larger leaves (length and width), and thicker terminal branches compared to those occurring in drier, temperate regions.

The persistence and retention of bracts through and after anthesis versus the loss of bracts is an important feature that separates and distinguishes between two main groups of taxa. The *a priori* group BR (which has bracts retained through anthesis) is distinguishable from all other *a priori* groups that have caducous bracts and bracteoles. In this analysis, the apparent usefulness of the characters of the bract could be due to unintentional overweighting of the bract characters against other characters because there were eight features of the bracts and bracteoles coded only for those OTUs with persistent bracts and bracteoles. Lengths of inflorescence axes and units vary greatly within one specimen, and thus could not be used as reliable measures of differences between specimens. Equally unreliable as a useful taxonomic feature was the number of units along the axis of an inflorescence. This highlights the limitations of herbarium specimens as the only source of taxonomic data. Often there are no records of critical characters of living material, for example whether the specimens represent the most mature of the flowering branches found on the plant or not. It is inappropriate to assume that all the flowering branches and inflorescences on specimens are at the same stage of development. For this reason, measurements of the lengths of inflorescence axes and units were made only on fruiting specimens. This approach was also used to successfully separate *Olinia capensis* from *O. ventosa* and *O. micrantha* from *O. emarginata* (Sebola & Balkwill 1999). The analyses have, however, established that floral features (presence or absence of bracts and bracteoles after anthesis, shapes and sizes of petals, presence or absence of indumentum and degree of pubescence on floral parts) are the most reliable characters of high taxonomic value for segregating taxa within *O. rochetiana sensu lato*.

Taxonomic Concepts

The applicability and suitability of species concepts such as the phenetic, ecological, and the biological species concepts for defining and recognising taxa

within *Olinia rochetiana sensu lato* was considered in the context of the pattern of morphological variation, and also evaluated against Stace's (1989) three main criteria (i. e. that (1) individuals should bear a close resemblance to one another such that they are always readily recognisable as members of that group; that (2) there should be gaps between the spectra of variation exhibited by related species, and if there are no such gaps then there is a case for amalgamating the taxa as a single species; and that (3) each species occupies a definable geographical area and is demonstrably suited to the environmental conditions which it encounters). Field studies and breeding experiments are, however, required among *O. rochetiana sensu lato* populations to assess the applicability of Stace's (1989) criterion of fertility, i.e. that the individuals should be capable of interbreeding with little or no loss of fertility, and there should be some reduction in the level or success of crossing with other species.

Given the operational limitation of the 'biological species concept' compared to the phenetic species concept, especially in the field (Sokal & Crovello 1970) and consideration of the objective of this study being to provide a practical taxonomy of *Olinia rochetiana sensu lato*, taxa were defined as species according to Sneath's (1976) concept of "...distinct phenetic clusters" and the infra-specific taxa were recognised for distinct sub-clusters that correspond with the ecological concept of species (Van Valen 1976). Some taxa, notably *O. rochetiana sensu stricto* and *O. ruandensis*, are widespread in distribution but show morphological variation with a consistent suite of characters, thus fitting Sneath's concept of a distinct phenetic cluster that is not limited to geographical or ecological conditions. The pattern of variation in other taxa is easily correlated with geographical or ecological factors, thus yielding distinct geographical entities to which Van Valen's (1976) concept of species is applied. The distinctiveness of taxa in this category dissolves when more material representative of a wide geographical area is examined. The morphological similarity or dissimilarity between organisms is often considered to infer underlying genetic differences (Stace 1989). Thus, morphological discontinuity is considered to indicate a discontinuity in genetic flow, suggesting some interrelationships between the morphological species concept, which is equivalent to the traditional phenetic species concept (Sneath & Sokal 1973) and the biological species concept (Mayr 1982; Jonsell 1984; Raven 1986), which is based on interbreeding ability and specific mate recognition systems (Paterson 1978, 1985) to discriminate between species. The phylogenetic species concept (Cracraft 1983; Nixon & Wheeler 1990; Baum 1992; Davis & Nixon 1992; Baum & Donoghue 1995) calls for advanced unique characters (synapomorphies) and considers species to have unique sets or combinations of

characters distinguishing them, and this links to the composite species concept, which also calls for unique combinations of character states to diagnose species. Within *O. huillensis* there are major sub-clusters with discernible differences in floral structures that possibly serve as pre-pollination isolation barriers, and occur in different ecological zones. The three sub-clusters comply with the ecological concept, and are thus accorded a subspecific rank. White (1962a) referred to species that show high geographical variation as 'ochlo-species' to denote 'troublesome' species which are not easily delimited by ordinary means. The pattern of morphological variation within *O. rochetiana sensu lato* can be described according to the 'ochlo-species' concept. However, the application of both the phenetic and ecological concepts to the specific and subspecific ranks, respectively, does not imply the inapplicability of other taxonomic concepts such as the biological species concept to *O. rochetiana sensu lato* or throughout *Olinia*. As more knowledge (i.e. genetic and/or molecular) accumulates about taxa in *Olinia*, it might be necessary to re-consider and adjust these taxonomic concepts.

Conclusion

Maintaining the notions that species should be distinct phenetic clusters/entities, possessing unique character states for floral features; and that subspecies should be the smallest recognisable entities with specific habitat and ecological preferences, four species (*Olinia huillensis*, *O. ruandensis*, *O. rochetiana* and *O. usambarangensis*) and three subspecies (*O. huillensis* subsp. *huillensis*, *O. huillensis* subsp. *burttdavii*, and *O. huillensis* subsp. *discolor*) are recognised within *O. rochetiana sensu lato*. The interpretation of the clustering pattern in this study was influenced by the objective to seek a functional and purposeful taxonomy of *O. rochetiana sensu lato* that would provide the basis for further studies on the phylogeny of *Olinia*. The present study indicates that *O. vanguardoides* is easily distinguishable from *O. rochetiana sensu lato* on the basis of a range of floral and vegetative features. Verdcourt's (1975, 1978) taxonomic interpretation of *O. rochetiana* that it is "...one very variable species..." is not supported by this study, because on the basis of numerical phenetic analysis of the morphological variation, a narrower circumscription of *O. rochetiana* is proposed with formal recognition of four additional taxa at the specific rank. Furthermore, intra-specific variation is formally recognised within *O. huillensis*.

The circumscription of *Olinia huillensis* in this study indicates a widely distributed species (Map 2) that shows regional and geographic variations, contrary to Cufodontis' (1960) concept of a localised species. The large number of specimens available for this study were obviously not referred to by Cufodontis (1960),

but some were studied by Verdcourt (1975, 1978) in his floristic accounts of *Olinia* in *Flora Zambesiaca* and *Flora of Tropical East Africa* where he preferred to lump *O. huillensis* under *O. rochetiana sensu lato* pending further analysis. Within *O. huillensis* it is possible to recognise three subspecies, the typical subsp. *huillensis*, which occurs in Angola, Democratic Republic of the Congo, Zambia and South Africa (far northern region); *O. huillensis* subsp. *burttdavii*, which is confined to South Africa (north eastern region); and *O. huillensis* subsp. *discolor* which occurs from western Malawi (North and Western Provinces), southern Zambia, and southwestern Tanzania (Map 2). The predominant vegetation in the region between the Limpopo and the Zambezi watershed is mainly miombo woodland dominated by species of *Brachystegia*, *Jubbernardia* and *Ochna* for which White (1962a) alluded to an occurrence of excessively variable species that are difficult to delimit. *O. huillensis* appears to fit the definition of an ‘ochlo-species’ (White 1962a), given its morphological variation that

integrates and overlaps over a wide geographic area within the miombo woodland. In this study, the variation within *O. huillensis* is conveniently categorised into subspecies until further evidence suggests otherwise. The main distinctions between the subspecies of *O. huillensis* are, however, based on habit and on dimensions and shapes of leaves and floral parts.

The analyses in this study and Sebola & Balkwill (2006) established that the use of single diagnostic characters to differentiate between taxa within *Olinia rochetiana sensu lato* is limiting; instead a combination of characters adequately differentiates among the taxa. The most reliable characters for delimiting taxa of *O. rochetiana sensu lato* can be obtained from flowers as well as inflorescences. A detailed account of the morphological variation within *Olinia*, based on analytical descriptions of both vegetative and reproductive characters, is presented in a monographic study of *Oliniaceae* (Sebola & Balkwill 2009c). The circumscription of the four species within *O. rochetiana sensu lato* allows for an assessment of phylogenetic relationships within *Olinia*.

Taxonomic Treatment

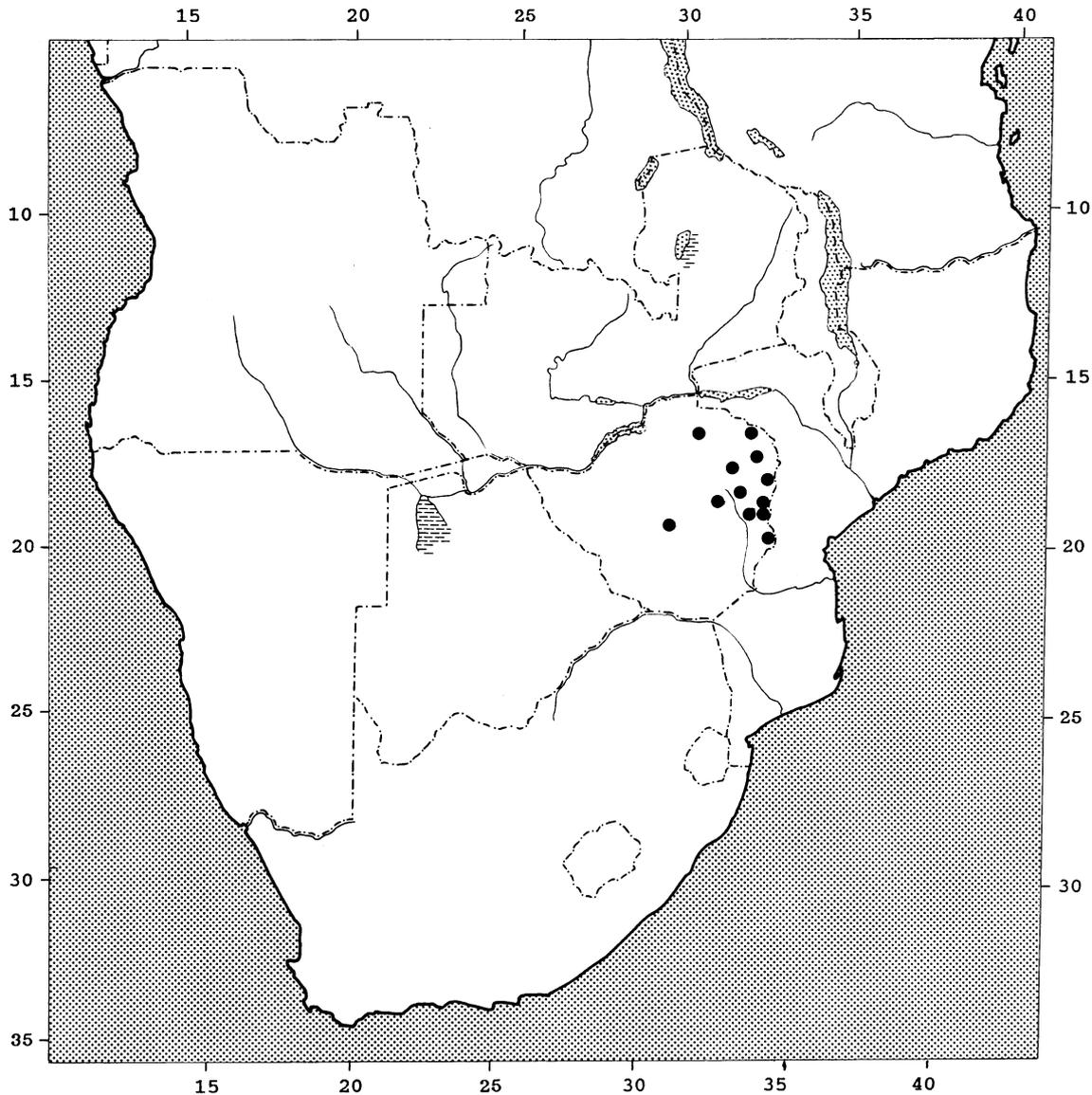
Key to Taxa within *Olinia rochetiana sensu lato*

1. Leaf lamina with conspicuous pattern of reticulate venation on both surfaces, narrowly elliptic; lateral nerve pairs 8 – 10, strongly raised on under-surface; petioles puberulent, 6 – 9 mm long; galled flowers narrow with elongate tubercles; petals 1 – 2 × 0.5 – 1 mm **1. *O. vanguerioides***
 Leaf lamina with conspicuous pattern of reticulate venation on under surface only, broadly elliptic to obovate; lateral nerve pairs 4 – 6, more-or-less level with under-surface; petioles glabrous, shorter than 3 mm; galled flowers swollen; petals 3 – 5 × 1 – 2 mm 2
2. Leaves slightly papery; up to 7 inflorescence units along inflorescence axis **2. *O. huillensis***
 Leaves coriaceous; between 9 – 11 inflorescence units along inflorescence axis 3
3. Leaf lamina discolorous below, broader than long; internodes on terminal branches longer than inflorescence axes **3. *O. ruandensis***
 Leaf lamina concolorous, longer than broad; internodes on terminal branches shorter or equal to inflorescence axes 4
4. Petals 5 on lateral flowers; scales shorter than 1 mm, rarely sealing the hypanthium opening/throat **4. *O. rochetiana***
 Petals 4 on lateral flowers; scales longer than 1 mm, often sealing the hypanthium opening/throat **5. *O. usambarensis***

1. *Olinia vanguerioides* Baker f. (1911: 72); Verdcourt (1978: 323); Verdcourt & Fernandes (1986: 4). Type: Zimbabwe, Umswirizwi head-waters, 1067 m, *Swynnerton* 158 (holotype BM!).

Shrubs or medium to large trees up to 10 m high. *Bark* thin, grey, and finely reticulate. *Branchlets* quadrangular. *Leaves* opposite; lamina dark green on upper surface with pink-mauve tinge, light olive-green on under surface, elliptic, coriaceous; 35.6 – 72.9 × 24.2 – 40.3 mm; margins inrolled; *primary* veins channelled above, light green; *secondary* veins distinctly visible on

both surfaces, parallel to each other on each side of the midvein. *Petiole* pink to red, pubescent, up to 4 mm long. *Inflorescence* puberulent, spreading, light green and thin. *Bracts* caducous, papery. *Flowers* greenish to yellow, sweetly scented; *hypanthium* glabrous, narrow and thin; galled flowers show elongate wart-like tubercles. *Pedicels* distinct, puberulent. *Sepals* rudimentary, often as minute bifid ridges alternating with petals. *Petals* spatulate, 5, short, narrow and thinly textured, yellowish, glabrous on both sides; apex truncate. *Scales* highly puberulent with soft hairs on both surfaces. *Stamens* alternate with petals, attached below sepals; filaments highly reduced or



Map 1. Known distribution of *Olinia vanguerioides*.

absent; anthers covered by hooded scales. *Stigma* globose. *Style* puberulent, shorter than floral tube. *Fruit* globose, 5 – 7 mm in diam., whitish with circular scar at tip 2.5 – 4 mm wide.

DISTRIBUTION. Known only from Zimbabwe (Map 1). Widespread in central, south and eastern Zimbabwe: Umswirizwi head-waters; Inyanga Distr., Inyanga National Park, Inyangombe Watershed; Umtali Distr., Rowa township, Butter North Farm, Tsetsera and Vumba Mts; Makoni Distr.; Matobo Distr.; Melssetter Distr.; Nyahodi R., NW of Tarka Forest; Headlands Distr., Lake Gwani; Chipinga Distr., Chiringa Forest; Wedza Distr., Wedza Mt; Mazoe Distr., Umvukwe and Marandellas Distrs.

SPECIMENS EXAMINED. ZIMBABWE. Bikita Distr., extreme western margin of ravine forest on S cliff face of Mt

Horzi, edge of streamlet between forest margin and bare granite rock, 9 May 1969, *Biegel* 3082 (K, PRE); Chipinga Distr., Chirinda Forest margin, Jan. 1966, *Goldsmith* 9/67 (PRE); Chipinga Distr., main road to Chipinga, just above Msilizwe R. near Chirinda, July 1962, *Goldsmith* 159/62 (PRE); Headlands Distr., Lake Gwani, Dec. 1948, *Greenshaw* s.n. (~ sub SRGH 37362) (K); N of Shiwa Ngandu, Aug. 1938, *Greenway & Trapnell* 5568 (K); Inyanga Distr., Inyanga National Park, Inyangombe Watershed, road to Trout Bick, 2 Jan. 1965, *West* 6245 (K, PRE), *Prope pagum I*, 13 Jan. 1931, *Norlindh & Weimarck* 4257 (BM); Makoni Distr., 15 June 1957, *Chase* 6521a (B, PRE); Marandellas Distr., April 1950, *Wild* 3310 (K), Grassland Research Station, 6 Dec. 1965, *West* 6990 (K); Matobo Distr., Farm Besna Kobila on, stream bank, Dec. 1953, *Miller* 1988 (B, K); Matobo Distr., on stream bank, Dec. 1953,

Milner 1994 (B, K, PRE); Matobo Distr., Farm Besna Kobilá, March 1957, *Milner* 4192 (K); Mazoe Distr., Umvukwes, Ruora Range, Dec. 1952, *Wild* 3928 (B); Melsekter Distr., Nyahodi valley, NW of Tarka Forest Reserve on upper reaches of a tributary of the Nyahodi R., Feb. 1971, *Goldsmith* 7/171 (B); Umtali Distr., Vumba Mt, Feb. 1955, *Chase* 5480 (B, K, PRE); Umtali Distr., Butter North Farm, Tsetsera Mt, near homestead, Nov. 1957, *Chase* 6774 (PRE); Umtali Distr., Rowa township, 5 Feb. 1957, *Chase* 6320 (PRE), 19 Feb. 1955, *Chase* 5480 (BM); Umtali Distr., Vumba Mt, Jan. 1947, *Fisher* 1218 (PRE); from left side of Vumba to farm track to Msasa knoll, July 1948, *Chase* 4173 (BM); Wedza Distr., Wedza Mt near Schulite mine, April 1964, *Wild* 5608 (K), Feb. 1963, *Wild* 5998 (K, PRE); Umswirizwi head-waters, Dec., *Swynnerton* 158 (holotype BM).

HABITAT. In crevices or among granite boulders/rocks; near streams in kloof forest or on edge of relic forests; solitary or often among *Polysphaera*, *Erythroxylon*, *Hymenodictyon*, *Combretum*, *Ochna*, *Uvaria* and *Clerodendrum* evergreen thicket among rocks.

CONSERVATION STATUS. Least Concern (LC). The distribution of this species is limited to Zimbabwe where it is widespread (central, south and eastern parts and the highlands along the border with Mozambique). The number of collections in herbaria

indicates great abundance in the areas of occurrence. Although there are no precise records of population numbers nor information on possible habitat destruction, some labels indicate that the species is common where it was collected.

PHENOLOGY. Flowering between Dec. – Feb. and fruiting between March – June.

VERNACULAR NAME. Zimbabwean *Olinia*.

NOTES. *Olinia vanguardoides* has only been recorded in Zimbabwe, but it is possible that its distribution extends into northern Mozambique and south-western Malawi. Specimens collected in Malawi, Mafingi Hills at approximately 2134 m alt. (*Chapman* 56), and southern region of Mt Mlanje (*Chapman & Chapman* 8207) have smaller, leathery leaves, inflorescences and flowers. Apart from the small leaves and flowers, the specimens resemble most of the Angolan material of *O. huillensis* in overall leaf morphology, pattern of venation, floral indumentum, and could constitute a different taxon (further field and laboratory investigations are recommended to determine the appropriate taxonomic status).

2. *Olinia huillensis* Welw. ex A. & R. Fern. (1962: 15).

Type: Angola, Huila region, between Lopollo and Humpata, *Welwitsch* 991 (holotype LISU; isotype BM!).

Key to Infraspecific Taxa of *Olinia huillensis*

- 1. Slender tree, 4 – 6 m high; terminal branches slender, light green to grey; leaves thin, papery and evergreen; inflorescence axes and peduncles slender, narrow; pedicels 2 – 4 mm long; petals 6.6 – 9.8 mm long **2a. subsp. huillensis**
- Shrub, up to 3 m high; terminal branches short and thick; leaves coriaceous and deciduous; inflorescence axes and peduncles robust and compact; pedicels 1 – 2.5 mm long; petals 4.9 – 7.4 mm long **2**
- 2. Leaves obovate, apex distinctly notched with a mucro, concolorous; hypanthium thick-walled, wider, shorter or equal to petals; petals obovate, wider than 3.5 mm; restricted to South Africa, Mpumalanga province **2b. subsp. burttidavii**
- Leaves broadly elliptic, apex slightly notched to emarginated, discolorous; hypanthium thin-walled, narrow, longer than petals; petals broadly spatulate, narrower than 3 mm; common in north-western Malawi and southern Zambia **2c. subsp. discolor**

2a. subsp. huillensis

Trees or slender shrubs, up to 6 m high. *Bark* light grey. *Leaves* thinly leathery to papery, elliptic; apex emarginate with a short mucro, slightly concolorous to distinctly discolorous, both surfaces glabrous; margins flat; *primary* vein light green (mature), flat, slightly pinky-red (young), glabrous; *secondary* veins slightly to just visible above, conspicuous below. *Petiole* short, light green to yellow, glabrous, 1.5 – 2 mm long. *Inflorescence* sparsely pubescent (younger) or completely glabrous (mature) and spreading. *Bracts* leathery, linear to oblong, caducous. *Flowers* pentamerous, sessile to

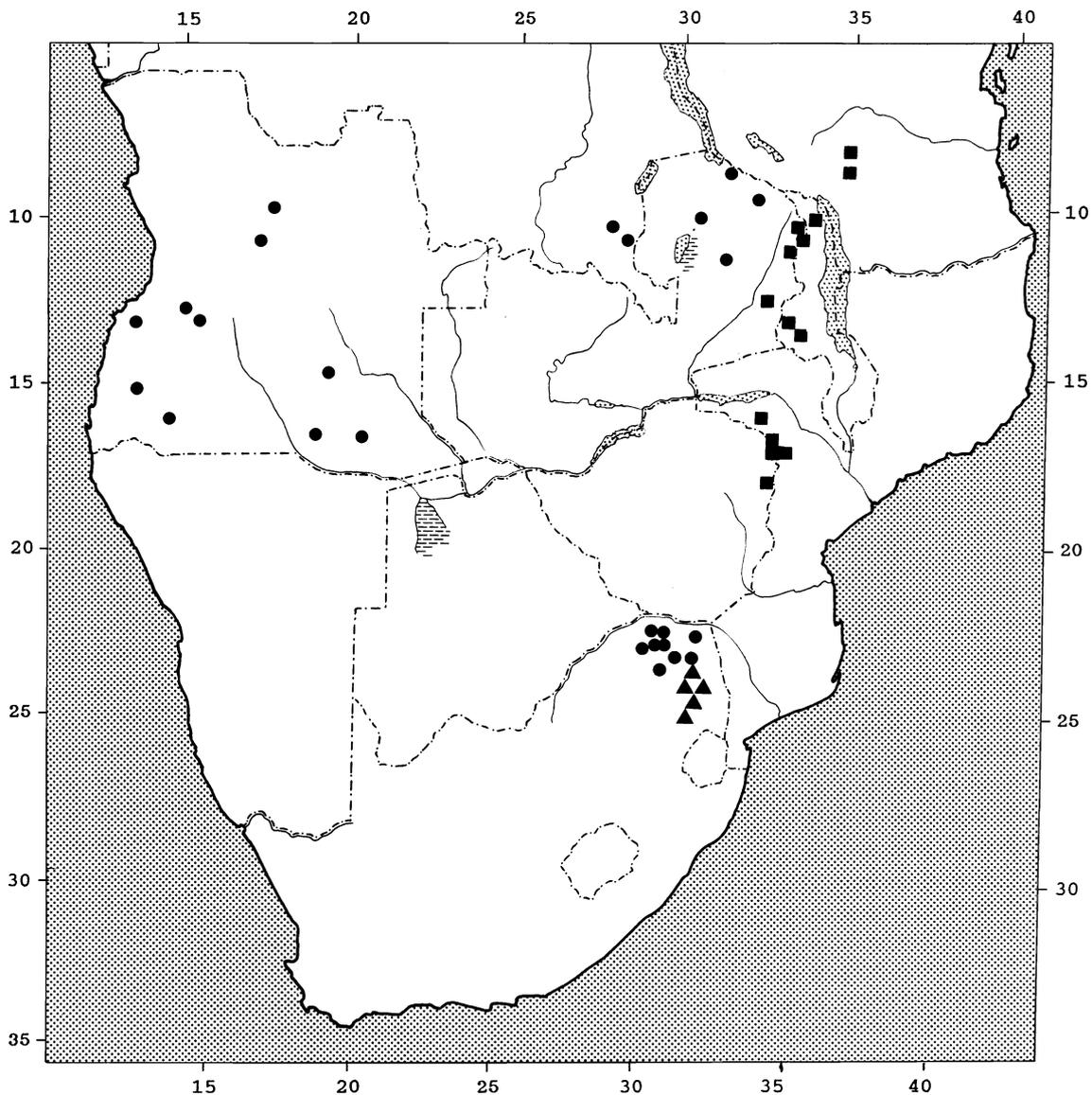
sub-sessile; *hypanthium* slightly narrow, 4 – 6 mm long, puberulent with very short hairs; *pedicel* distinct, markedly puberulent. *Sepals* rudimentary, appear as minute bifid ridges, alternate with petals. *Petals* spatulate to oblong, 5, glabrous, thick-textured, apex truncate with a short mucro, greater or equal to the hypanthium in length. *Scales* inflexed, sealing inside of tube, markedly puberulent. *Style* pubescent. *Fruit* obovoid and roughly fissured (preserved material), 6 – 8 mm in diam.; hypanthium scar not distinctly marked, 3 – 5 mm in diam.

DISTRIBUTION. From Angola (Benguela, Huilla, Lubango and Tundavala; Huambo Distr., Moco Mt)

through Zambia (Abercon, Mushitu Distr., Isoka and Mpika Distrs in Northern Province, Mafingi Mt; Makutus, Eastern Province, and Lundazi), to South Africa (Soutpansberg, Blouberg and Tate Vondo Forests, Leolo and the Wolkberg Mts in Limpopo Province; and Bourkes Luck in Blyderivierspoort, Mpumalanga Province). Map 2.

SPECIMENS EXAMINED. ANGOLA. Huila, Lubango, Tundavala, 2200 m alt., 9 Dec. 1962, *Barbosa* 10365 (K, PRE), 8 Dec. 1971, *Borges* 314 (K, PRE); Huila, between Lopollo and Humpata, 30 Dec. 1859, *Welwitsch* 991 (BM); Huambo Distr., Mt Moco, Dec. 1973, *Huntley et al.* 58 (K, PRE); Huila, Humpata, 25 Nov. 1955, *Mendes* 844 (BM, PRE); Benguela, R. Cuito, near Quipei, c. 1500 m alt., 11 May 1937, *Exell & Mendonça*

1900 (BM). **SOUTH AFRICA.** Limpopo Province, Soutpansberg, Mt Letjuma, 28 Jan. 1968, *Nicholson* 653 & 655 (PRE), 21 Dec. 1998, *Sebola* 432 (J); Vivo, Farm Llewellyn 35 LS, 1640 m alt., 4 July 1985, *Venter* 10744 (PRE), 28 Nov. 1999, *Sebola* 442 (J); Hangklip, 32 km NE of Makhado (Louis Trichardt), 18 Feb. 1946, *Gerstner* 5935 (PRE); Soutpansberg, Entabeni, in Mr Menzel's garden, Dec. 1930, *Obermeyer* 905 & 1216 (PRE), 13 Jan. 1935, *Phillips* s.n. (J); Soutpansberg, Bosley 773 MS, 15 March 1985, *Raal* 379 (PRE); Soutpansberg, Heights above Lake Fundudzi, 17 Nov. 1904, *Story* 4860 (PRE); Soutpansberg, on the crest of mountain, on the farm Zwarthoek 794 MS, at 1550 m altitude, 13 May 1994, *Balkwill et al.* 9107 (J); Tate Vondo Forest, 10 Dec. 1976, *Hemm* 035 (J); Mahovhohovho a



Map 2. Known distribution of *Olinia huillensis* subsp. *huillensis* (●), *O. huillensis* subsp. *burttdavii* (▲) and *O. huillensis* subsp. *discolor* (■).

Phiphidi, Waterfall, along Tshirovha R., 13 April 1980, *Van Wyk* 4156 (PRE); Ha-Khakhu, near Shop, along the road, 5 July 1979, *Netshungani* 922 (PRE); Blouberg Mt, 1524 m alt., 1 June 1980, *Davidson* 3504 (J); Blouberg, SW end of western plateau, path to 'ten-ten' stove, 26 April 1997, *Winter* 1892 (J); Sekhukhuniland, Lulu Mts, Farm Het Fort, on summit of upper slopes at 2134 – 2225 m alt., 7 Jan. 1939, *Barnard & Mogg* 988, 1027 (J, PRE); Serala Peak, Farm Forest 8 KT, 22 Oct. 1985, *Venter* 11075 (PRE); Leolo Mts, Farm Driekop 253 KT, 8 March 1984, *Venter* 10020 (PRE); Wolkberg, Farm Haffenden heights 35 KT, W of Lekgalameetse Nature Reserve, overlooking Mohlapitse valley, from highest point locally, 1347 m alt., 25 July 1999, *Winter* 3539 (J); Mpumalanga Province, Middelburg Distr., Farm Hoogstepunt, 3 Sept. 1936, *Mogg* 16934 (PRE); Blyde R. Canyon Nature Reserve, Bourkes Luck, Sept. 1968, *Davidson* 379 (J); Blyderivierspoort Nature Reserve, N of The Pinnacle, edge of escarpment, 27 Jan. 1981, *Balkwill et al.* P1/1 (J); Potgietersrust (Mokopane), on the Farm Portugal 55 KS, c. 18 km ESE of Potgietersrust near farm Grootvlei, 8 April 1956, *Maguire* 2874 (J). **TANZANIA.** Arusha Distr., Meru Mt, NW flank on Mt, edge of forest, 31 Dec. 1966, *Richards* 21852 & 21864 (K). **ZAMBIA.** Eastern Province, Lundazi, upper slopes of Kangampande Mts, Nyika Plateau, 2134 m alt., 3 May 1952, *White* 2579 (K); Makutus, 26 Oct. 1972, *Fanshawe* F11531, F11534 (K); Northern Province, Isoka Distr., Mafingi Mt, 8 km W of Chisenga Rest House, 28 Nov. 1952, *Angus* 838 (K); Northern Province, Mpika Distr., on rocky slopes of Muchinga escarpment, 48 km S of Shiwa Ngandu on Mpika road, 29 Nov. 1952, *Angus* 883E (K).

HABITAT. Often growing on rocky slopes or above upper limit of evergreen forests growing in ravines; often associated with *Phillipia*, *Podocarpus* and *Ochna*; 1300 – 2225 m.

CONSERVATION STATUS. Least Concern (LC). There are many gatherings by different collectors from at least fifteen localities in three southern African countries (Map 2), suggesting that this taxon is both widespread and common. In addition, none of the habitats in which it occurs is considered to be under threat.

NOTES. The most southerly distribution is probably the Waterberg range, Thabazimbi distr., 30 km W of Vaalwater on the farm Sterkstroom 262 KQ, 2424 BD, at an altitude of 1400 m based on a sterile specimen, *Balkwill & Balkwill* 4438 (J). Attempts to collect fertile material from the same locality have been unsuccessful, thus making it uncertain as to whether the specimen represents subsp. *huillensis* or subsp. *burttdavii*.

2b. subsp. burttdavii *Sebola* **subsp. nov.** Frutices ad 3 m alti; cortex atro-cinereus. Folia late elliptica, coriacea, glabra insuperficiebus ambabus; margines cum tinctus rubra; basi cuneatus; apex saepe incisus, recurvatus et

obliquus ad latus ex lamina profunde emarginatus. Secundarius vena bis-reticulatus, conspicuus superne; tertiaris vena conspicuus infra. Petiolus brevis, rubescens, sparsim puberulus supra. Monates inflorescentiarum compectus, crassus et distinctus quadrangulus. Pedicellus leviter glaucus, brevissimus, 0.5 – 1 mm longum. Hypanthium latus et crassus, glabra, usque 12 mm longum. Petala spatulate ad leviter oblongus, apiculatus, crassus, glabra in superficiebus ambabus, rubescens ad maturitas. Typus: South Africa, Mpumalanga Province, Graskop distr., The Pinnacle, *Sebola* 225 (holotypus J!; isotypi BM!, K!, PRE!).

O. usambarensis sensu Burt Davy (1926: 200).

Shrubs up to 3 m high; bark dark-grey. *Leaves* 30.3 – 53.3 × 31.1 mm, broadly elliptic, coriaceous, glabrous on both surfaces; margins with a tinge of red; base cuneate; apex often incised, recurved and slanted to one side of blade becoming deeply emarginate; *primary* veins loop twice, conspicuous above; *secondary* veins conspicuous below. *Petiole* short, reddish, sparsely pubescent above, 1.5 – 2 mm long. *Inflorescence* units compact; axes thick, distinctly quadrangular. *Bracts* caducous. *Flowers* pentamerous; *pedicel* slightly glaucous, very short, 0.5 – 1 mm long. *Hypanthium* broad and thick-walled, glabrous, up to 12 mm long. *Sepals* rudimentary, showing small bifid ridges barely more than 1 mm long, alternate with petals. *Petals* spatulate to slightly oblong, apiculate, thickly textured, glabrous on both surfaces, pink and turning red at maturity, 4.9 – 7.4 mm long. *Scales* hooded, opposite petals, markedly pubescent and often yellowish, 2.5 – 3 mm long and 3 mm wide. *Stamens* alternate with petals, attached below scales; filaments highly reduced or absent; anthers covered by hooded scales. *Stigma* capitate. *Style* slightly pubescent, 2 – 4 mm long. *Ovary* inferior, five-locular. *Fruit* pink, becoming red when mature, ovoid, 10 – 14 mm in diam., apex marked by hypanthium scar/rim 5 – 7 mm in diam.

DISTRIBUTION. Known from South Africa, Mpumalanga Province, The Pinnacle in Graskop area, Mt Sheba, Lost City in Pilgrim's Rest area. Map 2.

SPECIMENS EXAMINED. SOUTH AFRICA. Mpumalanga Province, Pilgrim's Rest, Mt Sheba, Lost City, 2 May 1980, *Balkwill* M.S. 1-79 (J); 12 Dec. 1997, *Sebola* 225 (holotype J!; isotypes BM, K!, PRE!) & 324 (holotype J); Mt Sheba NR, 1980 m alt., Nov. 1978, *Kerfoot* K8196 (J); April 1975, *Heaner & De Jager* s.n. (J); Hill near Mt Sheba, 26 Oct. 1968, *Davidson* s.n. (J); Pilgrim's Rest, upper edge of berg, 29 Jan. 1906, *Burt Davy* 1482 (BOL), *Burt Davy* 5220 (J, cited by Burt Davy as *O. usambarensis*), 10 Dec. 1963, *Van der Schyff* 6348 (PRE), Van der Merwe Bush, 30 Jan. 1906, *Burt Davy* 1425 (PRE); Graskop, on slopes of escarpment, 25 Oct. 1945, *Lock* s.n. (PRE); slopes of escarpment, 2 Nov. 1942, *Forest Research Officer, Pretoria* 2, (J); Mariepskop,

27 Nov. 1924, *Keet* 1347 (PRE); Mariepskop, in fynbos area, near the radar installations, 26 March 1988, *Balkwill et al.* 4037 (J); Sikorora Mts, Macoutsi R, Dec. 1922, *Van Dam* s.n. (PRE); Mariepskop, summit of mountain, along path to trig. station, 5 Dec. 1961, *Van der Schyff* 5835 (BOL, J, K), 23 Oct. 1962, *Van der Schyff* 6200 (PRE); Mac Mac Pools, 23 Oct. 1985, *Hilliard & Burt* 18451, (PRE); Lydenburg distr., Vygenhoek Farm, W of Lydenburg, 2 Dec. 1997, *Burgoyne* 6579 (PRE); Tzaneen, Wolkberg 643T, New Agatha Forest Reserve, 24 April 1971, *Muller & Scheepers* 196 (PRE).

HABITAT. On windswept rocky outcrops or in mist-prone environments; 1475 – 2500 m.

CONSERVATION STATUS. Data Deficient (DD). The distribution is restricted to the eastern part of South Africa on rocky outcrops, where it overlaps with that of subsp. *huillensis*. Its recorded area of occupancy is approximately 7,000 km² mainly in nature conservation areas, where there are no apparent threats to its habitat due to human activities (development and agricultural practices (pers. obs.)). Both the numbers of individuals per locality and the number of localities appear limited. It thus appears that field work to determine the likely IUCN Red List Category is necessary.

NOTES. *Olinia huillensis* subsp. *burttdavii* differs from the typical subsp. *huillensis* by its shrubby, often dwarf, habit (not tree-like), up to a maximum of 3 m high, branching at or below 0.5 m (not branching at more than 1 m high). Leaves are thick and deciduous; margins slightly recurved with a tinge of red. Terminal branches and inflorescence units are short, compact and distinctly quadrangular. Hypanthia or floral tubes and petals are glabrous, broad and deep red.

2c. subsp. *discolor* (Mildbr.) Sebola, comb. & stat. nov.

O. discolor Mildbr., *Notizbl. Bot. Gart. Berlin-Dahlem* 11: 669 (1932). Type: Tanzania, Iringa Province, Lupembe, Likanga-Bushes, *Schlieben* 20 (holotype BM!).

Shrubs up to 2 m high. *Leaves* obovate to elliptic, 35.7 – 57 × 20.5 – 33.5 mm, base cuneate, symmetrical; apex slightly notched to emarginate, distinctly discolorous; margins slightly undulate, coriaceous, glabrous on both surfaces; *primary* veins slightly raised above; *secondary* veins conspicuous on abaxial surface. *Petiole* short, sparsely pubescent above, up to 1.5 mm long. *Inflorescence* units compact to slightly sparse; axes thick, distinctly quadrangular. *Bracts* leathery, caducous. *Flowers* perigynous, 5-merous. *Pedicel* glaucous, very short, 0.5 – 1 mm long. *Hypanthium* narrow, longer than petals, up to 20 mm long; *sepals* as in subsp. *burttdavii*; *petals* broadly spatulate, narrower than 3 mm, up to 3 mm long. *Scales* as in subsp. *burttdavii*; *Stamens* attached below sepals; filaments highly re-

duced or absent; anthers covered by hooded scales, subsessile, up to 1 mm diam. *Style* pubescent, short, up to 1 mm long. Fruit globose.

DISTRIBUTION. Occurs in Zambia, Nyika Plateau; and Malawi, N of Lake Malawi to Tanzania, in Mufindi Distr., Iringa Province, Kigogo Forest Reserve; Ufipa Distr., Mbisi forest. Also in Zimbabwe, Chimanimani Mts and Mozambique, Manica and Tete Provinces. Map 2.

SPECIMENS EXAMINED. TANZANIA. Ufipa Distr., Mbisi forest, 13 Sept. 1960, *Richards* 13102 (K); Iringa Distr., Mafindi, Kigogo Forest Reserve, 18 Dec. 1961, *Richards* 15759; Iringa Distr., Kigogo, Dec. 1953, *Carmichael* 324 (K); Iringa, Mufindi, Farm Iringa, 6 Nov. 1938, *Hartmann* 127 (B); Iringa Province, East Mufindi, Nov. 1928, *Haarer* 1647 (K); Iringa Mt, Ibagama, Ukwama, 1 May 1958, *Ede* 3 (K, PRE); Sao Hill, Mufindi Distr., Nov. 1964, *Proctor & Shibani* 2708 (K); S. Highlands Province, Irundi, Iringa Distr., 9 Nov. 1955, *Benedicto* 80 (K); Msima Stock farm, Iringa Province, 1932, *Emson* 291 (K); *s. loc.*, *Schlieben* 20 (BM, isotype). **ZAMBIA.** Nyika Plateau, 14 Nov. 1967, *Richards* 22531 (K). **MALAWI.** Northern Province, eastern side of Mafinga Hills, Nov. 1952, *Chapman* 56 (K); Southern Region, Mt Mulanje, Lutchenya Plateau, 12 Nov. 1986, *Chapman & Chapman* 8207 (PRE); Nyika Plateau, path to Chipopoma Waterfall, 27 Nov. 1967, *Richards* 22770 (K).

HABITAT. Forest and forest margins; 1768 – 2250 m.

CONSERVATION STATUS. Least Concern (LC). This taxon is widely distributed in north western Malawi, western Tanzania, north eastern Zimbabwe and northern Mozambique.

NOTES. Verdcourt (1975) did not see most of the specimens cited here during his preparation of the *Flora of Tropical East Africa*, but later referred to them, in particular *Richards* 13102, as an “odd variant of *O. rochetiana*”. Information on herbarium sheets indicates the specimen *Richards* 13102 lacks the characteristic venation pattern of *Olinia usambarensis*, as well as having a larger floral tube and different indumentum. Analysis of floral and vegetative features of the material collected on Nyika plateau (Zambia), at Kigogo Forest Reserve in Mufindi distr. (Tanzania) and around the Chimanimani Mts (eastern Zimbabwe and northern Mozambique) indicates that these specimens are more closely related to *O. huillensis* than they are either to *O. usambarensis*, *O. rochetiana* or *O. ruandensis*.

3. *Olinia ruandensis* Gilg (1914: 575). Type: Rwanda, Rugege-Wald, *Mildbraed* 1027 (holotype B†; isotype K!).

O. macrophylla Gilg (1914: 575). Type: Zaire (Democratic Republic of the Congo), Ruwenzori, Butaguta-Tal to Waldgrenz, *Mildbraed* 2541 (holotype B†; isotype K!).

Shrubs up to 6 m high; bark grey and slightly peeling. *Branches* pale and quadrangular. *Leaves* 46 – 63 × 27 – 39 mm, discolorous, broadly elliptic; apex acuminate; base rounded to cuneate; *primary* veins channelled or impressed above, prominent below; *secondary* veins faintly visible above, just visible below, second loop before margins invisible above. *Petiole* 2.5 – 6 mm long, glabrous. *Inflorescence* units sparsely pubescent, slightly compact but loose. *Bracts* caducous or rarely persistent, pubescent, thinly papery and nerved. *Bracts* papery, caducous. *Flowers* perigynous, 5-merous. *Hypanthium* narrow, glabrous, 10 – 14 mm long. *Sepals* rudimentary, often as bifid minute ridges, alternating with petals. *Petals* 3.5 – 4.7 mm long, oblong, bluntly apiculate, hairy on margins, glabrous on outside and inside, broader than long. *Pedicels* 2 – 4 mm long, pubescent. *Scales* yellowish, 2 – 5 mm long, markedly puberulent. *Stamens* attached below scales; *filaments* highly reduced or absent; anthers covered by hooded scales. *Stigma* slightly terete, shorter than hypanthium tube. *Style* slightly glabrous. *Ovary* inferior, five-locular. *Fruit* 6 – 9 mm in diam., globose, often with pale to whitish lenticels, apex with a circular hypanthium scar 4 – 6 mm in diam., sharp point marks remnant of style.

DISTRIBUTION. Occurs in Rwanda, Butare; Tanzania, Mbeya Distr. Kikondo, SE of Mbogo Mt, and in Mpanda Distr. Kungwe Mahali Peninsula; Zaire (Democratic Republic of the Congo), Kakunda parc national de l'Upemba; Haut-Katanga, Kasumbalesa, Colline Kibwe I; and Zambia, Mwinilunga Distr., Luakera Falls, N of Mwinilunga. Map 3.

SPECIMENS EXAMINED. RWANDA. Butare, Rugege – Wald, Aug. 1907, *Mildbraed* 1027 (K, isotype); TANZANIA. SE to Mbogo Mt, 7 Nov. 1966, *Gillett* 17617 (K); Mpanda Distr., Kungwe Mahali Peninsula, 7 Sept. 1959, *Harley* 9550 (B, K); Mbeya Distr., Kikondo, 22 Oct. 1956, *Richards* 6727 (K); Southern Highlands Province TT, Njombe Distr., Njombe-Kifonya road, Ubena, May 1953, *Eggeling* E.6576 (K); Iringa, Usima Stock, 1932, *Emson* 254 (K); ZAIRE (DEMOCRATIC REPUBLIC OF THE CONGO). Haut-Katanga, Ruwenzori, Butaguta, Feb. 1908, *Mildbraed* 2541 (K, isotype); Haut-Katanga, Kasumbalesa, Colline Kibwe I, 20 March 1971, *Lisowski* 98 (K); Kakunda parc national de l'Upemba, Nov. 1974, *de Witte* 3085 (PRE); ZAMBIA. Abercon, Mushitus, 6 Nov. 1958, *Fanshawe* F.4954 (K); Abercon, Lake Chila, 11 Nov. 1958, *Robson & Fanshawe* 499 (PRE); Mwinilunga Distr., Luakera Falls, N of Mwinilunga, 24 Nov. 1937, *Milne-Redhead* E. 3381 (K, PRE); Zambezi R. above Rapids, Mwinilunga Distr., 15 Nov. 1962, *Richards* 17233, 21850, 21848 (K).

HABITAT. Growing in forests and forest margins; 1200 – 2250 m.

CONSERVATION STATUS. Least Concern (LC). This species is widely distributed from the Democratic Republic of the Congo to Zambia, and up to the great Lakes in Rwanda.

VERNACULAR NAME. Mbagwe (Kisambaa).

4. *Olinia rochetiana* A. Juss. (1846: 812); Liben (1973: 235; t. 1); Verdcourt (1975: t. 1; 1978: 323); Verdcourt & Fernandes (1986: 2). Type: Ethiopia, *Rochet* (holotype P; isotype K!).

O. abyssinica Engl. (1921: 624), nom. nud.

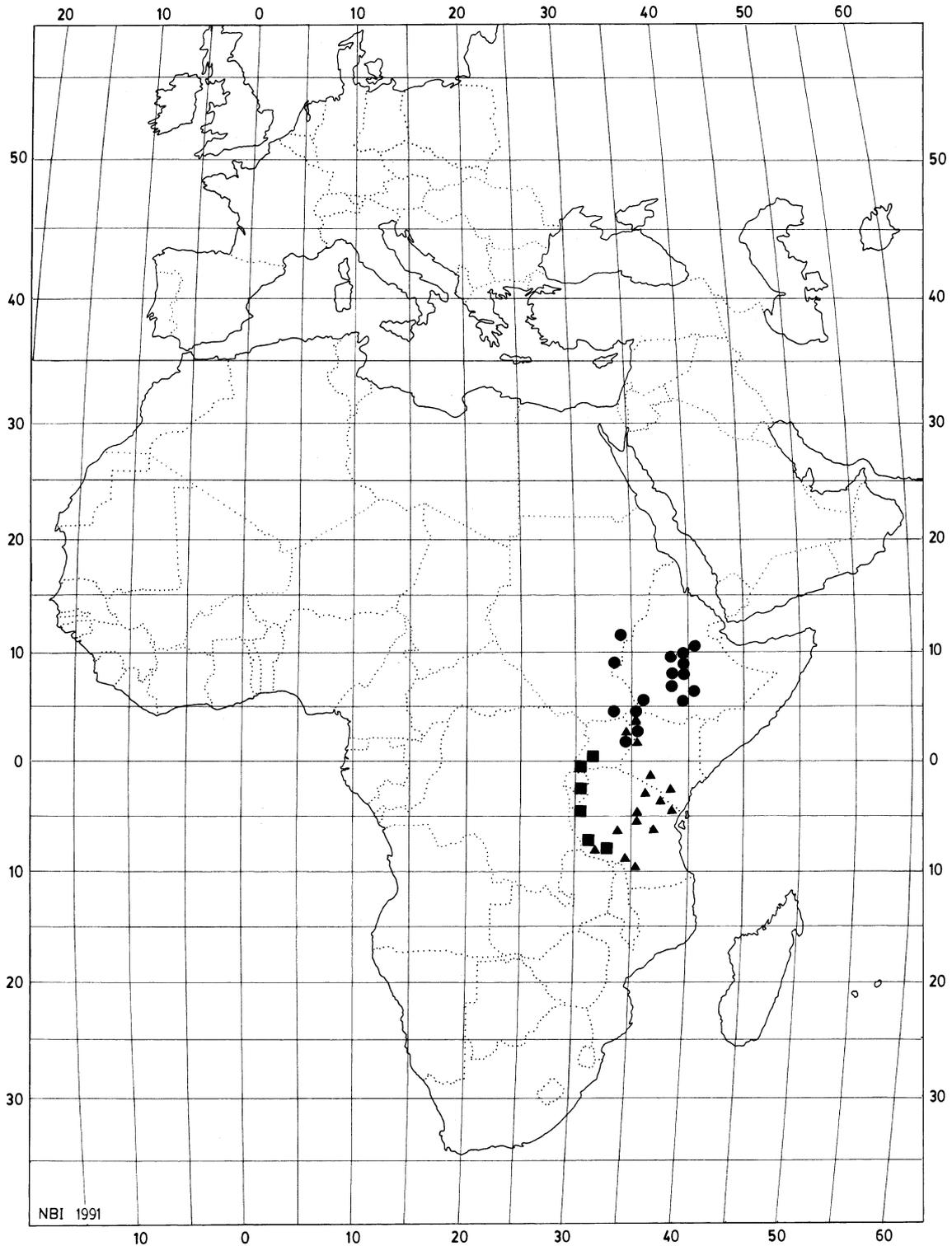
O. ternata Gilg ex Engl. (1921: 624), nom nud.

Tephea aequipetala Delile (1846: 340). *O. aequipetala* (Delile) Cufod. (1959: 603). Type: possibly the same as for *Olinia rochetiana*.

Shrubs or medium to large trees up to 15 m high; bark grey, with peeling scales; younger branches light grey and quadrangular. *Leaves* simple, opposite, decussate; lamina often large, broadly elliptic to obovate, slightly discolorous, glabrous on both surfaces, 41.1 – 64.5 × 28.7 – 53.4 mm; base tapering to rounded or slightly cordate; apex notched or broadly emarginate; margins smooth; *primary* veins slightly channelled above; *secondary* veins branch from midrib at 45° – 60° and loop more than once before the margins, slightly conspicuous above, distinctly conspicuous below. *Petiole* light green-yellow, glabrous, up to 3 mm long; *stipules* rudimentary and brown. *Inflorescences* axillary and terminal, dichasial cyme; inflorescence units 12 – 28 mm long, compact or loose; *peduncle* sparsely pubescent, 8 – 24 mm long. *Bracts* caducous, papery and creamy white or leathery and pink, ovate or elliptic, 4.6 – 7.7 × 2.8 – 5.4 mm, markedly pubescent on both surfaces (for papery ones), glabrous on dorsal surfaces (for leathery ones). *Flowers* bisexual, perigynous, 5-merous, subsessile; *pedicel* glaucous, 0.5 – 1.5 mm long. *Hypanthium* broad and thick, glabrous to sparsely pubescent or highly puberulous, throat with hooked scales alternating with petals. *Sepals* rudimentary, often as minute bifid ridges. *Petals* spatulate to slightly oblong, apex slightly apiculate to rounded, base slightly narrow, glabrous on abaxial surfaces but pubescent on margins, adaxial and the base, creamy white or pink, turning red at maturity, 4.3 – 10.5 × 1.6 – 3.7 mm. *Scales* puberulent, enclose stamens, 1 – 2.5 mm long, 0.5 – 1.5 mm wide. *Stamens* alternating with petals, attached below scales; *filaments* highly reduced or absent; anthers covered by hooded scales. *Stigma* capitate or terete. *Style* glabrous, 2 – 6 mm long. *Ovary* five-locular. *Fruit* light green, pink to red when mature, globose, 6 – 15 mm in diam., glabrous, apex marked by hypanthium scar 4 – 10 mm in diam.

DISTRIBUTION. Known from north-eastern and central Ethiopia, south-eastern Sudan, Uganda, north-eastern Kenya and Tanzania. Map 3.

SPECIMENS EXAMINED. ETHIOPIA. Menagesha State Forest, 19 Jan. 1994, *Afewerk Kasso* 20 (ETH), *Amshoff* 10279 (B); Near Addis Ababa, March 1975, *Chaffey* 476 & 415



Map 3. Known distribution of *Olinia rochetiana* (●), *O. ruandensis* (■) and *O. usambarensis* (▲).

(K); Asella, lower slopes of Mt Cilalo, 14 Feb. 1966, *De Wilde* 10043 (PRE); Mt Uociacia, 6 March 1966, *De Wilde* 10279 (ETH); Kaffa Province, SE of Folla, 1 Dec. 1970, *Friis et al.* 532 (K), 6075 (ETH); Arssi Province, between Asella & Chilalo Mts, 18 Nov. 1972, *Tewolde* 1242 (ETH);

Addis Ababa, Mr Abel's garden, 14 Jan. 1927, *Scott* s.n. (K); Sidamo region, N of Waddera, 20 Dec. 1980, *Haugen* 1838 (ETH); Sole, near Shashemene, 11 Feb. 1954, *Mooney* 5688 (K); Soyuma Choko Hill, 15 km S of Shashemene, Sidamo, 11 Feb. 1954, *Mooney*

5726 (B, ETH, K); Kaffa Province, 7 km E of Jimma, 22 Dec. 1961, *Meyer* 7784 (K); Arshi region, 5 – 10 km from Assela, 19 March 1983, *Sebsebe* 319, 1374 (ETH); ±14 km from Assela Abay Ras Hotel, on way to Assassa, 7 July 1981, *Sebsebe* & *Melaku* 766 (ETH); Arusi Province, 15 km S of Assela, 12 Oct. 1964, *Selassie* 392 (ETH); Kaffa, SW Ethiopia, June 1975, *Chaffey* 476 (ETH), 10 km S of Assela, 11 Feb. 1964, *Selassie* 71 (ETH); Choa, near Ankober, *Rochet* 18 (K, holotype); Shoa Province, Square 68 B, Forest at upper rim of Wonchi Crater Lake, 11 Dec. 1971, *Ash* 1396 (K); Central Ethiopia, 64 km NE of Addis Ababa, on Dessie road, 11 Jan. 1953, *Gillett* 14824 (B, K, PRE); Sidamo region, Arero Awraja, Dec. 1974, *Tadesse* 6891 (ETH). **SUDAN.** Imatong Mts, 10 March 1976, *Howard* 81 (K). **KENYA.** N of Mt Kenya, Kentrout farm, 1 March 1981, *Gilbert* 6029 (K); Kiambu Distr., Muguga N, 18 Feb. 1962, *Verdcourt* 3283 (B, K, PRE); Cabarnet, W of Baringo, *Jex-Blake* 6867 (K); Isiolo (K1 & K4) to Mathews Range and Mt Nyiruki, Siruan, plateau, 1 Jan. 1959, *Newbould* 3367 (K); Nyanza Province, Mt Elgon, Trans-Nzoia Distr., 19 – 20 Feb. 1935, *Taylor* 3435 (BM); Njong Forest, Dec. 1940, *Van Someren* 1396 (K); Mau Forest, *Gardner* 321 (K); Musasia, *Gardner* 1026, (PRE); Masai Distr., Nguruman Range, Lebetero Hills, Jan. 1961, *Van Someren* EA12289 (K); Narok Distr., Olorukto Mau area, 13 May 1961, *Glover et al.* 1007 (K, PRE); Muguga, 21 km E of Nairobi, 7 March 1958, *Verdcourt* 2139 (PRE); Narok Distr., Oltarakwai (Narosura), 18 Aug. 1961, *Glover et al.* 2486 (PRE). **TANZANIA.** Laitokitok, NE slope of Kilimanjaro, 28 July 1956, *Bally* 10701 (K). **UGANDA.** Tororo Distr., Namwamba valley, near Kyanjoki, 17 Jan. 1935, *Taylor* 3142 (BM, K).

HABITAT. Occurs in mountain forests and along ravines; 1950 – 2896 (3000) m.

CONSERVATION STATUS. Least Concern (LC). This species is widely distributed in east Africa from the Ethiopian highlands through Sudan, Uganda, Kenya, and Tanzania. Herbarium label information from various collectors in different countries, provinces and districts indicates a diverse habitat tolerance and local abundance in areas in which it was collected.

VERNACULAR NAMES. Téphé (amhara; *vide* Delile 1846), guna (galla: Shashamanna), nole (sidamo).

NOTES. The distribution overlaps considerably with that of *Olinia usambarensis* along the Mt Elgon range between Kenya and Uganda, and along the Rift Valley in Kenya (Narok) to the west in Masai Distr.

The type for *Olinia rochetiana* might probably be the same as for *O. aequipetala*, which is the specimen collected by Rochet d'Héricourt (*Rochet* 18) during his voyages to Ethiopia. *Verdcourt* (1975) does not cite a particular specimen as the type for *O. rochetiana* (citing merely Rochet d'Héricourt with the holotype deposited at P and the isotype at K), but does for *O.*

aequipetala (*Rochet* 18, holotype MPU). It is therefore uncertain whether the specimen at MPU is the same as that at P. Examination of the specimens determined as *O. rochetiana* at both MPU and P might provide some insight on the correct typification of this species.

5. *Olinia usambarensis* *Gilg ex Engl.* (1894: 63; 277); *Engl. & Prantl* (1894: t. 74, fig. A – G); *Engl.* (1921: 624, t. 277, Fig. A – G); *Robyns* (1948: 650, t. 67); *Brenan* (1949: 395); *Eggeling & Dale* (1952: 290, t. 14); *Brenan* (1954: 441); *Dale & Greenway* (1961: 350, t. 22); *White* (1962a: 269); *Von Breitenbach* (1963: 107). Type: Tanzania, Kwa Mshuza, *Holst* 9115 (holotype B†; isotypes BM!, K!).

O. volkensii *Gilg ex Engl.* (1895: C 285). Type: Tanzania, Kilema, Useri, *Volkens* 1816 (holotype B†; isotypes BM!, K!), Karrakia-Schlucht, *Volkens* 2000 (isotypes B†, K!). **synon. nov.**

Shrubs or small trees up to 5 m high. *Bark* grey, rough. Branchlets quadrangular; internodes short and thick. *Leaves* oblong to elliptic, persistent at and subtending inflorescence axes and units, caducous on internodes, discolorous, glabrous on both surfaces, 28.6 – 57.9 × 22.2 – 38.4 mm, apex rounded to emarginate, base slightly cuneate to cordate; *primary* veins channelled above, sparsely pubescent above, especially on lower or proximal half of the lamina; *secondary* veins loop twice, network conspicuous on both surfaces. *Petiole* distinct, glabrous, 4.5 – 8 mm long. *Inflorescence* units more than 11 per axis, compact, markedly puberulent, broader than long, thick, 20 – 35 mm long. *Bracts* retained after anthesis, papery, white, abaxial surface glabrous, adaxial surface and margins puberulous; obovate, slightly oblanceolate; 3.3 – 7.5 mm long, 4.2 – 5.7 mm wide. *Flower* 4- or 5-merous. *Hypanthium* yellowish to creamy-white, pubescent, up to 10 mm long, galled flowers swollen. Sepals rudimentary, present as stipular bifid ridges, alternate with petals. *Petals* 4 (lateral flowers) or 5 (terminal flowers), spatulate, large and very showy (2.5 – 5 mm long), broader than long (up to 2.5 mm wide), slightly thick, yellowish brown, glabrous on both sides. *Scales* hooded, opposite petals, markedly pubescent. *Stamens* 4 (lateral flowers) or 5 (terminal flowers) alternate with equal number of petals, attached below scales; filaments highly reduced or absent; anthers covered by hooded scales. *Stigma* capitate. *Style* pubescent, 2 – 4 mm long. *Ovary* inferior, 4- or 5-locular. *Fruit* pink to red, globose, up to 8 mm in diam., glabrous; apex marked by hypanthium scar 6 – 10 mm in diam.

DISTRIBUTION. Known from Tanzania (Usambara and Kilimanjaro Mts), central to south western Kenya, and Uganda around Mt Elgon and environs). Map 3.

SPECIMENS EXAMINED. TANZANIA. Usambara, Kwa Mshuza, Aug. 1893, *Holst* 9115 (isotypes BM, K.); NE of Mt Meru, Arusha National Park, 7 Jan. 1972, *Greenway & Fitzgerald* 14970 (K, PRE); Arusha Region, Mbulu Distr., Gidaghandajek on W Slope of Hanang, 2134 m alt., 28 Oct. 1968, *Carmichael* 1577 (K); Masai Distr., Loliondo Mt, 2316 m alt., 23 June 1969, *Carmichael* 1703 (K); North Province, Moshi Distr., Mt Kilimanjaro, Sanya Sawmill at Ngare, alt. c. 1737 m, 13 Jan. 1954, *Hughes* 193 (ETH, K); Usangu, *Goetze* 994, 1452 (K); Mbeya region, Makete Distr., Kipengere Mts, Ndumbi forest, slopes of Mt Orwe, 2300 – 2600 m, 22 Nov. 1986, *Goldblatt & Love* 8245 (K, PRE); Iringa region, Mufindi Distr., Ngwazi, at 1830 m alt., 8 May 1987, *Lovett & Lovett* 2115 (PRE); Iringa, Ludewa, along road to Mlangali, at 2200 m alt., 15 Nov. 1987, *Mwasumbi et al.* 13740 (PRE); Mbeya Distr., Mbeya Peak, at 2500 m alt., 31 Aug. 1962, *Kerfoot* 4229 (PRE), 21 Jan. 1991, *Lovett & Kayombo* 476 (PRE); Mbeya Distr., S. H. Province, alt. c. 2438 m, Oct. 1959, *Proctor* 1508 (PRE); S. H. Province, Rungwa, NE of Rungwa Mt, at 2591 m alt., Oct. 1959, *Proctor* 1445 (PRE); Kilimanjaro, alt. c. 1800 m, 22 Dec. 1933, *Schlieben* 4417 (B, BM); Moshi Distr., Kilimanjaro, Laitokitok, c. 2300 m alt., *Schlieben* 5128 (B, BM, K); Morogoro Distr., Uluguru, alt. c. 2400 m, 23 Feb. 1933, *Schlieben* 3565 (B, BM); Kyimbila Distr., N of Lake Nyasa, *Stolz* 1721, 2288, 2367 (K); Tanga Province, Lushoto-Gare track, 24 Feb. 1960, *Willan* 484 (K); Kilimanjaro, Rongai Forest, Kibo-Nordseila, 25 Dec. 1932, *Geilinger* 4988 (K); Mkusi, W of Usambara, 2600 m alt., 2 Feb. 1954, *Grant & Gardner* H59/54/1 (PRE); Tanga Province, Lushoto Distr., Shume Forest Reserve, Nov. 1957, *Semsei* 2724 (B); Lushoto Distr., Lushoto-Mlalo, roadside, 4 Dec. 1982, *Sigara* 257 (K); 8 Dec. 1959, *Willan* 472 (PRE); Shoa Province, Square 69B, Mt Zuquaila, 31 km SE of turnoff at Ducam, c. 10 km W Debre-Zeit, 3 Feb. 1974, *Ash* 2346 (K); Kilema, Useri, Feb. 1894, *Volkens* 1816 (BM, K), Karrakia-Schlucht, 1800 – 2000 m alt., *Volkens* 2000 (K). **KENYA.** Aberdares National Park, 3 km N from Shamata Gate, *Beentje* 3256 (K, PRE); Subukia escarpment (Thomson Falls to Lake Solai road), 21 Jan. 1959, *Bogdan* 4762 (K); Cherangani foothills, E of Kitale, 21 Jan. 1964, *Brunt* 1399 (K); Mt Kenya, April 1935, *Synge* S1712 (K); NE Elgon, 2316 m alt., Feb. 1955, *Tweedie* 1287 (K, PRE); Mt Kenya, Sirimam track, 24 Jan. 1961, *Polhill* 325 (K); Muchenge, NW Kenya, alt. 2835 m, *Hutchinson* 402 (PRE); SE of Mt Elgon, alt. c. 1981 – 2286 m, Jan. 1931, *Jackson* 337a (K). **UGANDA.** Kuburon, Elgon, c. 2073 m alt., Jan. 1936, *Eggeling* 2484 (K); Mt Elgon, Oct./Nov. 1930, *Lugard* 202 (K); Karamoja Distr., Northern Province, Bokora, Napak, alt. c. 2286 m, Jan. 1957, *Philip* 797 (K); Sebei Distr., Eastern Province, Kere Village, N of Elgon, c. 1981 m alt., 10 Jan. 1963, *Stylos* 299 (K).

HABITAT. Often in gorges, steep slopes or rocky outcrops, edges of forest or disturbed mountain forest among *Podocarpus*, *Nuxia*, *Hagenia*, *Fauvea*, *Protea*, *Halleria*; 1981 – 2850 m.

PHENOLOGY. Flowers from Oct. – Dec. and fruits in Jan. – May.

LOCAL NAMES. Kenya: Mwathanthia, Musasia, Muthangira (Meru); Kaptalonget, Nerekio (Sebei); Merikwa (Kamas); dalecho (amhara); Ethiopia: dalecho (amhara).

USES. Root used in East Africa as a stomach and gastric tonic.

CONSERVATION STATUS. Least Concern (LC). This species is widely distributed at high altitudes in mountain ranges in east Africa, largely in and around nature conservation areas, which would presumably limit human access and prevent destruction to habitats. It was collected in more than 20 districts in a variety of habitats within Tanzania, although collected in fewer districts in both Uganda and Kenya.

NOTES. Burt Davy (1926) erroneously recorded *Olinia usambarensis* in South Africa on the basis of misidentification of his specimen (*Burt Davy* 5220) collected in Graskop, Pilgrim's Rest area in Mpumalanga Province. However, numerical phenetic analyses place this specimen among the material determined in this study as *O. huillensis* subsp. *burttdavii*, which differs from *O. usambarensis* by its shorter obovate leaves and thickly textured and glabrous hypanthia.

The specimens *Stolz* 1721, 2288, 2367 (K); *Goetze* 994, 1452 (K); *Proctor* 1508 (K, PRE); *Goldblatt & Love* 8245 (K, PRE) form a sub-cluster (the OTUs marked LL in Figs. 1 & 2) separable from the others in this group by their distinctly coriaceous leaves, which are obovate to elliptic, discolourous, margins inrolled, and longer petioles. The inflorescence units are markedly pubescent, compact and shortly pedunculate. Hypanthia are slightly broader, markedly puberulent and shortly pedicellate. Petals are short, yellowish, pubescent on adaxial surface and lower part of abaxial surface. Styles are markedly pubescent. All specimens were found at altitudes above 2000 m in Tanzania (i.e. North of Lake Nyasa, Kyimbila Distr.; Ussangu; Mbeya Distr., S. H. Province, 2438 m; Makete Distr., Kipengere Mts, Ndumbi forest, slopes of Mt Orwe, 2300 – 2600 m). Although this cluster fits the ecological concept of species (Van Valen 1976) and could accordingly be assigned a subspecific rank to be consistent with the categorisation of variation within *Olinia huillensis*, more sampling at the population level in these areas is needed to assess the morphological variation in more detail before formally recognising this entity.

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Appendix 1. Index of exsiccatae.

Alphabetical listing of all specimens examined according to: collector number (taxon number in this paper, herbarium acronyms).

Afework-Kasso 20 (4, ETH), *Amshoff* 10279 (4, B); *Angus* 838 (2a, K); *Angus* 883E (2a, K); *Ash* 1396 (4, K); *Ash* 2346 (5, K).

Balkwill et al. 9107 (2a, J); *Balkwill et al.* P1/1 (2a, J); *Bally* 10701 (4, K); *Barbosa* 10365 (2a, K, PRE); *Barnard & Mogg* 988, 1027 (2a, J, PRE); *Beentje* 3256 (5, K, PRE); *Benedicto* 80 (2c, K); *Biegel* 3082 (1, K, PRE); *Bogdan* 4762 (5, K); *Borges* 314 (2a, PRE, K); *Brunt* 1399 (5, K).

Carmichael 324 (2c, K); *Carmichael* 1577 (5, K); *Carmichael* 1703 (5, K); *Chaffey* 476 & 415 (4, K); *Chaffey* 476 (4, ETH); *Chapman* 56 (2a, K); *Chapman & Chapman* 8207 (2a, PRE); *Chase* 4173 (1, BM); *Chase* 5480 (1, B, BM, K, PRE); *Chase* 6320 (1, PRE); *Chase* 6521a (1, B, PRE); *Chase* 6774 (1, PRE).

Davidson 3504 (2a, J); *Davidson* 379 (2a, J); *De Wilde* 10043 (4, PRE); *De Wilde* 10279 (4, ETH); *De Witte* 3085 (2a, PRE).

Ede 3 (2c, K, PRE); *Eggeling* 2484 (5, K); *Eggeling* E.6576 (3, K); *Emson* 254 (3, K); *Emson* 291 (2c, K); *Exell & Mendocça* 1900 (2a, BM).

Fanshawe F.4954 (3, K); *Fanshawe* F11531, F11534 (2a, K); *Fisher* 1218 (1, PRE); *Friis et al.* 532 (4, K), 6075 (4, ETH). *Gardner* 321 (4, K); *Gardner* 1026, (4, PRE); *Geilinger* 4988 (5, K); *Gestner* 5935 (2a, PRE); *Gilbert* 6029 (4, K); *Gillett* 17617 (3, K); *Gillett* 14824 (4, B, K, PRE); *Glover et al.* 1007 (4, K, PRE); *Glover et al.* 2486 (4, PRE); *Goetze* 994 (5, K); *Goetze* 1452 (5, K); *Goldblatt & Love* 8245 (5, K, PRE); *Goldsmith* 9/67 (1, PRE); *Goldsmith* 7/171 (1, B); *Goldsmith* 159/62 (1, PRE); *Grant & Gardner* H59/54/1 (5, PRE); *Greenshaw* s.n. (~ Salisbury 37362) (1, K); *Greenway & Fitzgerald* 14970 (5, K, PRE); *Greenway & Trapnell* 5568 (1, K).

Haarer 1647 (2c, K); *Harley* 9550 (3, B, K); *Hartmann* 127 (2c, BM); *Hemm* 035 (2a, J); *Holst* 9115 (5, K); *Howard* 81 (4, K); *Hughes* 193 (5, ETH, K); *Huntley et al.* 58 (2a, K, PRE); *Hutchinson* 402 (5, PRE).

Jackson 337a (5, K); *Jex-Blake* 6867 (4, K).

Kerfoot 4229 (5, PRE).

Lisowski 98 (2a, K); *Lovett & Kayombo* 476 (5, PRE); *Lovett & Lovett* 2115 (5, PRE); *Lugard* 202 (5, K).

Maguire 2874 (2a, J); *Mendes* 844 (2a, BM & PRE); *Meyer* 7784 (4, K); *Miller* 1988 (1, K, B); *Milner* 1994 (1, K, B, PRE); *Milner* 4192 (1, K); *Milne-Redhead* E. 3381 (3, K, PRE); *Mogg* 16934 (2a, PRE); *Mooney* 5688 (4, K); *Mooney* 5726 (4, B, ETH, K); *Mwasumbi et al.* 13740 (5, PRE).

Netshiungani 922 (2a, PRE); *Newbould* 3367 (4, K); *Nicholson* 653 & 655 (2a, PRE);

Norlindh & Weimarck 4257 (1, BM).

Obermeyer 905 & 1216 (2a, PRE).

Philip 797 (5, K); *Phillip* s.n. (2a, J); *Polhill* 325 (5, K); *Proctor* 1445 (5, PRE); *Proctor* 1508 (5, PRE); *Proctor & Shibani* 2708 (2c, K).

Raal 379 (2a, PRE); *Richards* 13102 (2c, K); *Richards* 15759 (2c, K); *Richards* 21852 & 21864 (2a, K); *Richards* 17233, 21850, 21848 (3, K); *Richards* 22531 (2c, K); *Richards* 22770 (2a, K); *Richards* 6727 (3, K); *Robson & Fanshawe* 499 (3, PRE); *Rochet* 18 (4, K).

Schlieben 3565 (5, B, BM); *Schlieben* 4417 (5, B, BM); *Schlieben* 5128 (5, B, BM, K); *Scott* s.n. (4, K); *Sebola* 432 (2a, J); *Sebola* 442 (2a, J); *Sebsebe* 319, 1374 (4, ETH); *Sebsebe & Melaku* 766 (4, ETH); *Semsei* 2724 (5, B); *Selassi* 392 (4, ETH); *Selassi* 71 (4, ETH); *Sigara* 257 (5, K); *Stolz* 1721, 2288, 2367 (5, K); *Story* 4860 (2a, PRE); *Styles* 299 (5, K); *Swynnerton* 158 (1, BM); *Synge* S1712 (5, K).

Tadesse 6891 (4, ETH); *Taylor* 3142 (4, BM, K); *Taylor* 3435 (4, BM); *Tewolde* 1242 (4, ETH); *Torstein-Haugen* 1838 (4, ETH); *Tweedie* 1287 (5, K, PRE).

Van Someren EA12289 (4, K); *Van Someren* 1396 (4, K); *Van Wyk* 4156 (2a, PRE); *Venter* 10020 (2a, PRE); *Venter* 10744 (2a, PRE); *Venter* 11075 (2a, PRE); *Verdcourt* 2139 (4, PRE); *Verdcourt* 3283 (4, B, K, PRE).

West 6245 (1, K, PRE); *West* 6990 (1, K); *White* 2579 (2a, K); *Wild* 3310 (1, K); *Wild* 3928 (1, B); *Wild* 5608 (1, K); *Wild* 5998 (1, K, PRE); *Willan* 484 (5, K); *Willan* 472 (5, PRE); *Winter* 1892 (2a, J); *Winter* 3539 (2a, J).

Appendix 2

Table 3. List of voucher specimens studied.

OUTa	Collector & No., herbarium ^b , Provenance, district/province, and locality
NE225	<i>Venter</i> 10744, (PRE), South Africa: Limpopo province, Zoutpansberg, Vivo farm, Llewelyn 35 LS
NE226	<i>Venter</i> 11075 (PRE), South Africa: Seralla Peak, Farm Forest Reserve 8KT
NE227	<i>Davidson</i> s.n. (J), South Africa: Mpumalanga, Pilgrims Rest, near Mt Sheba
NE228	<i>Balkwill</i> ms 1-79, (J), South Africa: Mpumalanga, Mt Sheba Nature Reserve.
NE229	<i>Kenfoot</i> 8196 (J), South Africa: Mpumalanga, Mt Sheba Nature Reserve.
NE230	<i>Van Der Schyff</i> 5835 (J, K), South Africa: Mpumalanga, Mariepskop, along path to TRIG Station
NE231	<i>Forest Research Officer</i> 2 (PRE), South Africa: Mpumalanga, Graskop, on slopes of escarpment
NE232	<i>Keet</i> 1347 (PRE), South Africa: Mpumalanga, Mariepskop
LJ001	<i>Sebola</i> 241 (J), South Africa: Limpopo province, Soutpansberg regio, Vivo, Lejuma farm
PN05	<i>Sebola</i> 367 (J), South Africa: Mpumalanga, Graskop, The Pinnacle
VG104	<i>Goldsmith</i> 159/62 (PRE), Zimbabwe: Chipinga Distr., along main road to Chipinga just above Msilizwe R. near Chirinda
VG105	<i>West</i> 6245 (BM, K, PRE), Zimbabwe: Inyanga Distr., Inyanga National Park, Inyangombe Watershed
VG106	<i>Wild</i> 3310 (BM, PRE), Zimbabwe: Marandellas Distr., Delta among granite boulders
VG107	<i>Fisher</i> 1218 (PRE), Zimbabwe: Umtali Distr., Vumba Mt
VG108	<i>Goldsmith</i> 9/67 (PRE), Zimbabwe: Chipinga Distr., Chirinda Forest margin
VG109	<i>Greenshaw</i> s.n. (Salisbury No. 37362) (K), Zimbabwe: Headlands Distr., Lake gwani
VG110	<i>Chase</i> 6521a (BM, K, PRE), Zimbabwe: Makoni Distr.
VG111	<i>Wild</i> 5608 (K), Zimbabwe: Wedza Distr., Wedza Mt, Near Schulite mine
VG112	<i>Wild</i> 3928 (BM, PRE), Zimbabwe: Mazoe Distr., Umvukwes, Ruorra Range
VG113	<i>Miller</i> 1994 (BM, K, PRE), Zimbabwe: Matobo Distr.
VG114	<i>Greenway & Trapnell</i> 5568 (K), Zimbabwe: N of Shiwa Ngandu
VG115	<i>Goldsmith</i> B. 7/171 (J, BM, PRE), Zimbabwe: Melsester Distr., Nyahodi valley, NW of Tarka Forest Reserve on upper reaches of a tributary of the Nyahodi R.
VG116	<i>Miller</i> 4192 (BM, PRE), Zimbabwe: Matobo Distr., Farm Besha Kobila
VG117	<i>Miller</i> 1988 (B, BM, Kew), Zimbabwe: Matobo Distr., Farm Besna, Kobila on stream bank fringing
VG118	<i>Norlindh & Weimark</i> 4257 (BM), Zimbabwe: Inyanga, Inyanga National Park, Inyangombe Watershed, road to Trout Bick
VG119	<i>Wild</i> 5998 (B, PRE), Zimbabwe: Wedza Distr., Wedza Mt in kloof forest.
VG121	<i>Chase</i> 6774 (PRE), Zimbabwe: Umtali Distr., Butter North Farm, Tsetsera Mt
VG122	<i>Swynnerton</i> 158 (BM, PRE), Zimbabwe: Umswirizwi head-waters
VG123	<i>Biegel</i> 3082 (K), Zimbabwe: Bikita Distr., extreme western margin of ravine forest on S cliff face, Mt Horzi edge of streamlet
VG124	<i>Chase</i> 5480 (B, K, PRE.), Zimbabwe: Umtali Distr., Vumba Mt
VG125	<i>Chase</i> 6320 (B, PRE), Zimbabwe: Umtali Distr., Rowa township, Leutenya's Reserve
AA01	<i>Mendes</i> 844 (BM, K, PRE), Angola: Huila Distr.
AA02	<i>De Witte</i> 3085 (PRE), Zaire (DR Congo): Kankunda National Park, l'Upemba
AA03	<i>Huntley, Roberts & Ward</i> 58 (BM, K, PRE), Angola: Huambo Distr., Mt Moco, Main forest
AA04	<i>Richards</i> 21864 (K, PRE), Tanzania: Arusha Distr., Mt Meru
AA05	<i>Richards</i> 21852 (P, PRE), Tanzania: Arusha Distr., NW of Mt Meru, on verge of forest
AA06	<i>Barbosa</i> 10365 (PRE), Angola: Huila Distr., Lubango, Tundavala
AB01	<i>Boges</i> 314 (K), Angola: Huila Distr., Lubango, Tundavala 18 km junction to miradoure da Fenda
AB02	<i>Fanshawe</i> F11531 (K, PRE), Zambia: Makutus
AB03	<i>White</i> 2579 (PRE), N Rhodesia (Zambia): Eastern Province, Lundazi Distr., Nyika Plateau, Mt Kangampande slope
AB04	<i>Chapman</i> 56 (K), Malawi, N Province, E Mafingi Hills
LL01	<i>Stolz</i> 2288 (K), Tanzania: Kyimbila Distr., N of Lake Nyasa.
LL02	<i>Stolz</i> 2367 (K), Tanzania: Kyimbila Distr.
LL03	<i>Goetze</i> 994 (K), Tanzania: Ussangu
LL04	<i>Stolz</i> 1721 (K), Tanzania: Kyimbila Distr., N of Lake Nyasa
LL05	<i>Proctor</i> 1508 (K), Tanzania: Mbeya Distr., S. H. Province
LL06	<i>Goetz</i> 1452 (K), Tanzania: Nyika plateau
LL07	<i>Goldblatt & Lovett</i> 8245 (K, PRE), Tanzania: Mbeya region, Makete Distr., Kipengere Mts, Ndumbi forest, slopes of Mt Orwe
ML01	<i>Proctor</i> 2708 (S Shabani ?) (K, PRE, J), Tanzania: T7 Sao Hill, Mufindi Distr.
ML02	<i>Emsen</i> 291 (K), Tanzania: Iringa Distr., Msima stock farm
ML03	<i>Richards</i> 15759 (K), Tanzania: Iringa Distr., Mafindi Kigogo Forest Reserve
ML04	<i>Carmichael</i> 324 (K, PRE), Tanzania: Iringa Distr., Kigogo
ML05	<i>Haaver</i> 1647 (K), Tanzania: Iringa province, E of Mufindi
ML06	<i>Richards</i> 13102 (K, PRE), Tanzania: Ufipa Distr., Mbisi forest
ML07	<i>Richards</i> 22531 (K), Zambia: Nyika Plateau, 2 miles from Zambia rest house
ML08	<i>Hartmann</i> 127 (K), Tanzania: Iringa, Mufindi, farm Iringa
LP01	<i>Moony</i> 5726 (K), Ethiopia: Soyuma, Choko Hill, 15 m S of Shashamane, Sidamo
LP02	<i>Gardner</i> 321 (K), Kenya: Mau Forest
LP03	<i>Van Someren</i> EA 12 289 (K), Kenya: Masai Distr., Nguruman Range, Lebettero Hills
LP04	<i>Mooney</i> 5688 (K), Ethiopia: Sole near Shashamane
LP05	<i>Hughes</i> 193 (K), Kenya: North Province, Moshi Distr., Mt Kilimanjaro, Sonya Sawmills at Ngare
LP07	<i>Willan</i> 484 (K, PRE), Tanzania: Tanga Province, Lushuto-Gare Track
LP08	<i>Taylor</i> 3142 (K, PRE), Uganda: W Province, Toro Distr., Ruwenzori, Namwamba valley, near kyanjoki

Table 3. (continued).

OUTa	Collector & No., herbarium ^b , Provenance, district/province, and locality
LP09	<i>De Wilde</i> 10279 (K), Ethiopia: Mt Uociacia, ±15 km W of Addis Ababa
LP10	<i>Hugh Scott</i> s.n. (K), Ethiopia: Addis Ababa, Mr Abel's Garden
LP11	<i>Kasso</i> 20 (K), Ethiopia: Manegesha State Forest, 46 km SW Addis Ababa
LP12	<i>Demissew</i> 1374 (ETH, K), Ethiopia: Arshi region, 5 – 10 km from Assela on road to Geba
LP13	<i>Haugen</i> 1838 (ETH, K), Ethiopia: Sidamo region, N of Waddera.
LP14	<i>Selassie</i> 71 (ETH, K), Ethiopia: Arussia Province, 10 km S of Asala
LP15	<i>Berham</i> 1242 (ETH, K), Ethiopia: Arrsi Province, between Asella and Chilalo Mt
LP16	<i>Meyer</i> 7784 (ETH, K, PRE), Ethiopia: Kaffa Province, 7 km E of Jimma
LP17	<i>Chaffey</i> 476 (& 415?) (ETH, K), Ethiopia: near Addis Ababa
LP18	<i>Chapman</i> 8207 (K), Malawi: Southern region, Mt Mulanje, Lutchenya plateau
LP19	<i>Friis et al.</i> 532 (K), Ethiopia: Kaffa Province, SE of Folla, ±15 km N of Ghibe-bridge (Addis – Jimma road)
LP20	<i>Glover et al.</i> 1007 (K, PRE), Kenya: Narok Distr., Olokurto, Mau area
LP21	<i>Schlieben</i> 4417 (K), Tanzania: Kilimanjaro
MP01	<i>Gillet</i> 17617 (K), Tanzania: SE to Mbogo Mt
MP02	<i>Richards</i> 17233 (K), Northern Rhodesia (Zambia): Mwinilunga Distr., Zambezi R., above Rapids, 5 miles from Kalene mission
MP03	<i>Milne-Redhead</i> 3381 (K), Northern Rhodesia (Zambia): Mwinilunga Distr., Luakera falls, N of Mwinilunga
MP04	<i>Richards</i> 6727 (K), Tanzania: Mbeya Distr., Kikondo
MP05	<i>Gilbert</i> 6029 (K), Kenya: N of Mt Kenya, Kentrout farm
MP06	<i>Harley</i> 9550 (K), Tanzania: Mpanda Distr., Kungwe-Mahali Peninsula
MP07	<i>Verdcourt</i> 3283 (K), Kenya: Kiambu Distr., Muguga N
MP08	<i>Greenway & Fitzgerald</i> 14970 (K), Tanzania: NE of Mt Meru, Arusha National Park
BR01	<i>Lugard</i> 202 (K), Uganda: Mt Elgon
BR02	<i>Jackson</i> 337a (K), Uganda: SE of Mt Elgon
BR03	<i>Brunt</i> 1399 (K), Kenya: E of Kitale, Cherangani foothills
BR04	<i>Philip</i> 797 (K), Uganda: N Province, Karamoja Distr., Bokora, Napak
BR05	<i>Eggeling</i> E.2484 (J, K) Uganda: Kaburon, Elgon
BR06	<i>Beentje</i> 3256 (K), Kenya: Aberdares, NP N, 3 km up from Shamata Gate
BR07	<i>Linder</i> 3547 (J, K, PRE), Zaire (DR Congo): du kivu, Ruwenzori Mts
BR08	<i>Humbert</i> 8866 (K), Congo Belge: Ituri, gorge de la Butagu
BR09	<i>Styles</i> 299 (K), Uganda: Eastern Province, Sebei Distr., N of Elgon, Kere village
BR10	<i>Polhill</i> 325 (K), Kenya: Mt Kenya, Sirimam track.
BR11	<i>Sunge</i> S.1712 (K), Kenya: Mt Kenya, NW Slopes at edges of <i>Podocarpus-Juniperus</i> forest
BR12	<i>Ash</i> 2346 (K), Tanzania: Shoa Province, square 69.B, Mt Zauqualla, 31 km SE of turn off at Ducam, ~ 10 km W Debre-Zeit
BR13	<i>Hutchins</i> 402 (K), Kenya: Muehege NW Kenia
BR14	<i>Tweedie</i> 1287 (K), Uganda: NE of Mt Elgon
BR15	<i>Bogdan</i> 4762 (K), Kenya: Subukia Escarpment, Thomsons falls to lake Solai road

^aOperational taxonomic units represent specimens used in the phenetic study

^bAbbreviations for herbaria according to Holmgren *et al.* 1990

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