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PHENETIC STUDY OF NORTHEAST AND EAST TROPICAL AFRICAN *COMMIPHORA* SPECIES

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ABSTRACT: Phenetic study of Northeast and East Tropical African *Commiphora* species was conducted. Seventy-three species were selected for this study. Forty different characters were considered and thoroughly discussed. The relationship was analyzed using PAUP* version 4.0 b10. The result of this analysis showed seven distinct sections, which, both in circumscription and the species, varied considerably from those recognized previously. Each section is described and discussed. One of these sections was validated and rank of the other one was changed. The distinction of the genus *Commiphora* is briefly reviewed and discussed.

Key words/phrases: *Commiphora*; Phenetic; Sections.

INTRODUCTION

Attempts to circumscribe the genus *Commiphora* began by Berg (1862). Following his grouping, several other workers tried to produce a more reliable classificatory approach to the genus. Notable among others were Engler (1913 and 1931), Sprague (1927) and Chiovenda (1932).

The recent delimitations of the genus have also been attempted by some workers, notably Vollesen (1985, 1986, 1989), Gillett (1991) and Thulin (1999). In fact, Gillett (1991) and Thulin (1999) further followed the circumscription attempts made by Vollesen (1985, 1986, 1989) with some minor changes. However, Vollesen's (1985, 1986, 1989) approach and the characters used in the work to designate the group were not clearly informative. Of the 11 characters used by Vollesen (1985, 1986, 1989), the leaf types, bark peeling pattern, resin and inflorescence types were variable within species and hinder the use of these characters for a sectional delimitation. Therefore, the re-delimitation of the genus into sections seems to be important.

Description of the Genus *Commiphora*

Commiphora Jacq., Hort. Schoenbr. 2: 66, t. 249 (1797); Engl. in A. DC., Monogr. Phan. 4: 7 (1883); Bot. Jahrb. 15: 94 (1893); in Pflanzenfam. 3, 4: 251 (1896); Bot. Jahrb. 26: 368 (1899); Bot. Jahrb. 34: 303 (1905);

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Guillaumin in Ann. Sci. Nat. 9, 10: 279 (1909); Engl. in Bot. Jahrb. 44: 144 (1910); Bot. Jahrb. 46: 289 (1912); Bot. Jahrb: 48: 449 (1913); Planzenw. Afr. 3, 1: 786 (1915); Bot. Jahrb. 54: 292 (1917); Hutch. & Dalz., Fl. W. Trop. Afr. 1: 488 (1928); Engl. in Pflanzenfam. ed. 2, 19a: 429 (1931); Chiov., Fl. Somala 2: 53 (1932); Burtt in Kew Bull. 1935: 101 (1935); Webber in Lilloa 6: 443 (1941); Perr. Bathie in Fl. Madag. 5: 5 (1946); Exell & Mendonca in Consp. Fl. Angol. 1: 298 (1951); Miller in J. S. Afr. Bot. 18: 38 (1952); Wild in Bol. Soc. Brot. 2, 33: 76 (1959); Dale & Greenway, Kenya Trees: 76 (1961); Capuron in Adansonia 2: 270 (1962); White, For Fl. N. Rhod.: 173 (1962); Wild; in Fl. Zamb. 2, 1: 263 (1963); Von Breintenbach, Ind. Tree S. Afr. 3, 2: 429 (1965); De Wint. in Trees S. Afr. 20, 1: 3 (1968); Merxm., Prod. Fl. S. W. Afr. 23: 1 (1968); Van der Walt in Bothalia 11, 1 & 2: 54 (1973); in Boissiera 24: 325 (1975); Gillett in Kew Bull. 34: 569 (1980); Vollesen in Kew Bull. 40: 42 (1985); Van der Walt in Fl. S. Afr., 18, 3: 5 (1986); Vollesen in Fl. Eth. 3: 446 (1989); Gillett in FTEA, 8 (1991), Thulin in Fl. Somalia, 187 (1999), *nom. conserv.* Type species: *C. madagascarensis* Jacq., Hort. Schoenbr. 2: 66, t. 249 (1797).

Niotoutt Adans., Fam. 2: 162 (1763), *nom. rejic.*

Amyris sensu Linn., Mant.: 65 (1767) non Browne; Forsk., Fl. Aegypt.-Arab.: CX, 80 (1775); Vahl, Symb. Bot. 1: 28, t. 11 (1790); Roxb., Fl. Ind. 2: 244 (1832).

Balsamea Geld. in Berl. Ges. Naturf. Fr. Schr. 3: 127 (1782); Engl. in Bot. Jahrb. 1: 41 (1881).

Balessan Bruce, Trav. 5: t. 25 (1790).

Balsamodendrum Kunth in Ann. Sci. Nat. 2: 348 (1824); DC., Prodr. 2: 76 (1825); Sond. in Fl. Cap. 1: 526 (1860);

Balasamodendron, O. Berg in Bot. Ztg. 21: 161 (1862); Marchand in Adansonia 8: 34, 67 (1867-1868); Oliv. in Fl. Trop. Afr. 1: 324 (1868); Hook. f., Fl. Brit. Ind. 1: 529 (1875); Balf. f. in Trans. Roy. Soc. Edinb. 31: 52 (1888); Deflers, Voy. Yemen: 120 (1889).

Hemprichia Ehrenb. in Linnaea 4: 396 (1829); Marchand in Adansonia 8: 69 (1867-1868):

Heudelotia A. Rich. in Guill., Perr. & A. Rich., Fl. Sen. 1: 150, t. 39 (1832).

Protium senu Wight & Arn. in Prod. Fl. Ind.: 176 (1834); Harv. in Fl. Cap. 2: 529 (1862).

Protoniopsin Blume in Mus. Bot. Lugd.-Bat. 1: 229 (1850) *nom. nud.*

Hitzeria Klotzsch in Peters, Reise Mossamb. Bot. 1: 89 (1861).

Balsamoophloeos Berg in Bot. Ztg. 20: 163 (1862).

Spondiopsis Engl., P.O.A.C: 243 (1895).

Trees of variable height or shrubs or many-stemmed shrubs or sometimes flat-toped suffrutex, usually dioecious, rarely monoecious or hermaphrodite, bark often peeling or flacking in papery pieces or strips, rarely not; exudate a gummy resin or liquid and volatile, often aromatic, occurring in phloem, may be copious, scanty or hardly apparent colorless or milky; wood soft, light, consisting mainly of septated fibers; branchlets often thorn-tipped, glabrous, pilose or tomentose. *Leaves* usually 3-foliolate or imparipinnate with opposite leaflet, less often 1-foliolate or simple, petiolate or seldom sessile or subsessile, margins usually crenate, dentate, serrate or biserrate or entire, lamina glabrous, pilose, puberulous, pubescent or tomentose; petioles of a few species with medullary vascular bundles and in most many free traces in ring. Stomata mostly hypostomatic and rarely amphistomatic. *Inflorescences* may be elongated panicles, dichasial cymes, fascicles, uniflorous or raceme; male inflorescence usually longer and looser than the female. *Flowers* pedicellate or sessile, small, regular, greenish yellow or red or dark red, usually unisexual but rarely bisexual, the male with or without a vestigial, rarely functional ovary, the female with reduced, occasionally functional stamens. *Pedicels* of different length, glabrous or pilose, puberulous or pubescent or tomentose. *Receptacle* flat, saucer-shaped, cup-shaped, or funnel shaped. *Calyx* cup-shaped or tubular, with 4 or very rarely 5 valvate lobes. *Petals* 4 or very rarely 5 free, valvate, or slightly imbricate. *Disc* in perigynous flowers adnate to hypanthium, cylindrical, rarely fleshy, and sometimes lobed; in hypogynous flowers not adnate to calyx or corolla, interastaminal, cylindrical, usually with 4 large lobes or with 4 large and small lobes. *Stamens* 8 in two whorls, one whorl shorter and the other longer, in few species 4 only, shorter than, or rarely, as long as the petals. *Ovary* 2- or very rarely, 3-locular, with 2 pendulous ovules in each locules; style short; stigma subcapitate or capitate, obscurely 4 or 2 lobed. *Fruit* an ovoid, ellipsoid or subglobose drupe, usually asymmetrically flattened pericarp composed of fused ectocarp and mesocarp splitting when ripe into 2 or 4 valves in some species or very rarely 3 valves to disclose the hard stone (putamen) which is covered, at least at the base, by a fleshy variously lobed red, orange or yellow pseudoaril; the stone usually consists of a fertile one seeded locule and a sterile locule, both may be fertile; hardly 3 fertile

locules could be seen; the fertile locule may show an oval shield of dehiscence extending downwards from the apex which splits open in germination; two apical pits between the locules may or may not be present.

MATERIALS AND METHODS

Of the ca. 80 species of *Commiphora* occurring in the Northeast and East Tropical Africa, 74 species (*C. wightii* is from India and used here to see its relationship with others) were used for the present phenetic analysis. The species included here were those from Ethiopia and Eritrea (being designated as NE), Kenya, Tanzania and Uganda (being designated as E Tropical Africa). Some of the species were excluded from the present analysis because either they were known from only one collection, and the available material was insufficient to score some of the characters, resulting in high proportions of missing values, or the original literature in which they were described was incomplete to fill the gap from secondary sources. The 74 taxa are listed in Table 1. The data matrix for taxa versus the characters used in the present study is provided in appendix 1.

Characters Used in Sectional Delimitations

Characters were scored from herbarium materials and, wherever possible, during fieldwork from living plants. This information was augmented by data from the literature. Ranges of measurements were averaged to make the value more amenable for statistical tests. Forty different characters, which were considered potentially informative, were used with their character states. The characters and their states are discussed below.

1. Habit: shrub or tree (0); special growth forms (1). Most species of *Commiphora* are either shrubs or trees. The character states shrub and tree were coded as a single character since there is an intergradations between the shrub and the tree habit within *Commiphora* and in fact, most species were described as being a shrub or a tree. A good example of this is a popular *C. myrrha*, which was described as shrub and tree by various collectors. Some species are suffrutescent or form a flat-topped crown near ground level ("special growth form"). These were on the other hand coded as another character state within the habit.

2. Plant height: 3 m or more (0); less than 3 m (1). Because most species of *Commiphora* are either shrubs or trees, they normally are higher than 3 meter. Those that are higher than 3 m are coded as one character state and those that are below 3 m in height are coded as another character state for the character plant height.

Table 1 List of 74 taxa of *Commiphora* species included in the present study.

No.	Scientific name of taxa	No.	Scientific name of taxa
1	*C. acuminata* Mattick	38	*C. merkeri* Engl.
2	*C. africana* Engl.	39	*C. mildbraedii* Engl.
3	*C. alaticaulis* Gillett and Vollesen	40	*C. mollis* Engl.
4	*C. albiflora* Engl.	41	*C. mombassensis* Engl.
5	*C. baluensis* Engl.	42	*C. monoica* Vollesen
6	*C. boranensis* Vollesen	43	*C. mossambicensis* Engl.
7	*C. bruceae* Chiov.	44	*C. myrrha* Engl.
8	*C. caerulea* B.D. Burtt	45	*C. oblongifolia* Gillett
9	*C. campestris* Engl.	46	*C. obovata* Chiov.
10	*C. chaetocarpa* Gillett	47	*C. oddurensis* Chiov.
11	*C. ciliata* Vollesen	48	*C. ogadensis* Chiov.
12	*C. confusa* Vollesen	49	*C. ovalifolia* Gillett
13	*C. corrugata* Gillett and Vollesen	50	*C. paolii* Chiov.
14	*C. cyclophylla* Chiov.	51	*C. pedunculata* Engl.
15	*C. danduensis* Gillett	52	*C. pteleifolia* Engl.
16	*C. edulis* Engl.	53	*C. quadricincta* Schweinf.
17	*C. ellenbeckii* Engl.	54	*C. rostrata* Engl.
18	*C. eminii* Engl.	55	*C. samharensis* Schweinf.
19	*C. engleri* Guillaumin	56	*C. sarandensis* B.D. Burtt
20	*C. erlangeriana* Engl.	57	*C. schimperi* Engl.
21	*C. erosa* Vollesen	58	*C. sennii* Chiov.
22	*C. fulvotomentosa* Engl.	59	*C. serrata* Engl.
23	*C. gileadensis* C. Chr.	60	*C. serrulata* Engl.
24	*C. glandulosa* Schinz	61	*C. spathulata* Mattick
25	*C. gowlello* Sprague	62	*C. sphaerocarpa* Chiov.
26	*C. gracilispina* Gillett	63	*C. sphaerophylla* Chiov.
27	*C. guidottii* Chiov.	64	*C. staphyleifolia* Chiov.
28	*C. gurreh* Engl.	65	*C. stolonifera* B.D. Burtt
29	*C. habessinica* Engl.	66	*C. suffruticosa* Teshome in pr.
30	*C. hildebrandtii* Engl.	67	*C. swynnertonii* B.D. Burtt
31	*C. hodai* Sprague	68	*C. terebinthina* Vollesen
32	*C. hornbyi* B.D. Burtt	69	*C. truncata* Engl.
33	*C. horrida* Chiov.	70	*C. ugogensis* Engl.
34	*C. kataf* (Forssk.) Engl.	71	*C. unilobata* Gillett and Vollesen
35	*C. kua* Vollesen	72	*C. velutina* Chiov.
36	*C. lindensis* Engl.	73	*C. wightii* Bhandari
37	*C. madagascarensis* Jacq.	74	*C. zanzibarica* Engl.

3. Plant sex: Non-dioecious (0); dioecious (1). Under the non-dioecious category, species that are hermaphrodite and that are monoecious were coded. It is well known that monoecy is an intermediate stage between hermaphrodite and dioecy in the sense of evolutionary process. Such a hypothesis was put forward for the *Anthospermeae* of the family Rubiaceae by Puff (1986) and literature cited therein. To avoid the multi-state nature of the character and in an attempt to consider the

primitive and derived nature of the character, the dioecy was scored as advanced state as opposed to monoecy and hermaphroditism that were coded as primitive within the group.

4. Plant bark: not peeling (0); peeling (1). *Commiphora* species are known by their exfoliating bark. Most species peel their bark and a few do not (for example *C. albiflora*). What remains after peeling is the greenish under-bark that most likely contains chlorophyll. A study made by Scrivner and Black (1983) entitled 'Bark chlorophyll in five species of Neotropical trees' indicated that *Bursera simaruba*, closely related to *Commiphora*, had greater concentration of chlorophyll in its bark than 3 of the 5 species it compared with. The peeling nature of the plant will obviously serve for different purposes. Because chlorophyll exists within the bark, peeling may provide light access to the photosynthetic layers of the trunk and it impedes the establishment of epiphytes on the bark. This, on the other hand, will enable the plant to photosynthesize during the long dry and harsh seasons when the plant remains leafless. However, Becerra and Venable (1999) considered bark peeling as primitive states for *Bursera*. They have also recognized the opposite reversions for the section *Bullockia*, where smooth bark is an ancestor to bark peeling pattern. In the present analysis, bark peeling is considered as an advanced state over the non-peeling pattern as it is the situation that enables the plant to cope successfully with the dry conditions.

5. Thorns: absent (0); present (1). Some species of *Commiphora species* have thorns (for example *C. schmiperi*) and others are thornless (as in *C. baluensis*). It has been believed that the thorn/spine can be developed from almost any part of the plant or represent a modification of any plant organ. It is usually a tough, woody structure with a sharp pointed end. According to Bell (1991), if a thorn is in the axil of an existing leaf or has scar where a leaf has dropped off, then the thorn represents a modified stem. Species of thorny *Commiphora* have leaves on their thorns (as in *C. gurreh*), showing that it may be a modification of their stem. Therefore, this modified part of the plant is here considered a derived state.

6. Petiole length: 1.5 cm or more (0); less than 1.5 cm (1). A reduction in length is advancement.

7. Petiole vascularization: Many free traces in ring (0); many free traces in ring with medullary bundles (1). It has been a well-established fact that the presence of vascular bundle in cylinder is a primitive state as

compared to the scattered bundles (Radford *et al.*, 1974). The presence of medullary bundle found scattered in the ring may be a move toward an advanced direction. As a result, species with the medullary bundle in the ring within *Commiphora* species are considered as advanced over the species lacking the feature and coded accordingly.

8. Petiole trichomes: absent (0); present (1).

9. Leaflet length: 3.5 cm or more (0); less than 3.5 cm (1). Another interesting feature in *Commiphora* species is the remarkable variation in leaf size and leaf indumentum. Leaf size and shapes are considered to have adaptive significance in ecological context. Hairy, small and sclerophyllous leaves seem to be more important in an adaptation to water and nutrient stress. The pubescent nature of the leaves may enable *Commiphora* species to maintain a layer of air, which does not move and can act as an insulator in reducing water loss by evapotraspiration from the plant organ. Besides, most *Commiphora* species occur in seasonally dry-arid and semi-arid habitats and produce leaves that usually last for a few months only. This provides an opportunity for the plant to avoid excess loss of water. It must be expected that there is a strong correlation between temperature and the arid environment in which *Commiphora* resides. Therefore, it appears that leaf size and leaf indumentum have important impact on leaf energy budgets. Small leaves (as in *C. gurreh*) and hairy ones (as in *C. edulis, C. baluensis, C. velutina*,) can regulate their temperature better than large and glabrous leaves, whose temperature can increase above ambient when exposed to high levels of solar radiation in the arid environment eventually resulting in the loss of scarce water through transpiration. As a result small leaf size and hairiness provide advantage to *Commiphora* species to survive in the arid environment.

10. Leaflet width: 1.6 cm or more (0); less than 1.6 cm (1). It is clear that measurements of certain parts are scored in ranges. Here, however, the ranges were averaged to fit for the purposes of analysis. Thus, the studied species were grouped into two based on assumed relationships. Since the pattern of evolution of leaves in *Commiphora* is reduction in size, the smallness is here considered as advancement in the group.

11. Leaflet trichomes: absent (0); present (1). Species like *C. corugata, C. guidottii, C. edulis, C. hildebrandtii, C. ogadensis, C. alaticaulis, C. ugogensis, C. glandulosa* and others have leaflet trichomes on the leaves as opposed to other species (e.g. *C. kua, C. ellenbeckii, C.*

madagascarensis, etc.) which lack that state. However, the density of pubescence and the length of the different trichomes considerably vary to the extent that it was not possible to make a hypothesis of homology. In support of this notion Van der Walt and Van der Schijff (1973) had clearly indicated that the number of ordinary hairs on the petiole and leaves vary not only from one species to another, but in many cases in different petioles and leaves of the same species. Despite this variability in the density and length of indumentum, presence and absence is the consistent character within the species. Thus, the different types of trichomes within the group were also considered with a similar coding scheme in the three characters to follow.

12. Leaflet multicelled glandular hairs: absent (0); present (1).

13. Leaflet unicellular hairs: absent (0); present (1).

14. Leaflet multicellular hairs: absent (0); present (1).

15. Stomatal position: amphistomatic (0); hypostomatic (1). A few species of *Commiphora* species are known to be amphistomatic. This stomatal type is observable in *C. myrrha, C. kua, C. boranensis,* and a few others. Contrary to this, most species happen to have hypostomatic stomatal position. The fact that some species are having stomata on upper surface is clearly a disadvantage for the water budget in the arid and semi-arid habitats for the plants as the solar radiation hits the upper surface rather than the lower portion of the leaf and eventually leads the plant to a transpirational loss.

16. Peduncle length: more than 2.5 mm (0); 2.5 mm or less (1). According to this character, the studied species are roughly arranged into two non-overlapping groups based on their relative relationship. Accordingly, *C. kua, C. ellenbeckii, C. boranensis, C. corrugata*, etc. are those having short peduncle length as compared to, for example, *C. monoica, C. rostrata, C. baluensis*, etc, which have long peduncle.

17. Pedicel length: 1.5 mm or more (0); less than 1.5 mm (1).

18. Inflorescence: loose and long pedunculate (0); congested, fasciculate or solitary (1). Within the genus, different forms of inflorescence types exist, such as panicle, raceme, long pedunculate cymes /cymes, short cymes, solitary and fasciculate types. In *Commiphora* species, this characteristic shows considerable variation not only within the genus but also in the different sexes of the plant (e.g., *C. suffruticosa*, where the male is fasciculate and the female is solitary). As a result of this

variability, panicle, raceme and long pedunculate cymes/cymes were coded as loose and long pedunculate type and short cymes, solitary and fasciculate types as congested ones. A close observation of the inflorescence pattern in *Commiphora* may presumably indicate that, because of reduction, some evolutionary process has taken place that enabled the plant toward developing short and congested inflorescence types. Wild (1959) suggested that the evolution of inflorescence characters evolved from elongated paniculate cymes to progressively much reduced and abbreviated cymes. Besides the above analogy, insects are likely to visit many flowers of congested inflorescence at one visit (before flying to another) more than those flowers of long and divaricately branched inflorescence thereby enhancing pollination.

19. Flower sex: bisexual (0); unisexual (1). A few species of *Commiphora* tend to have bisexual flower (e.g. *C. schimperi* and *C. obovata*) while most are known to be unisexual.

20. Calyx length: more than 2 mm (0); 2 mm or less (1). Argument as for character 16.

21. Calyx indumentum: absent (0); present (1). The presence of hairs, as explained above under character 9 appears to be advantageous. Still the density of hairiness varies differently showing pubescent as in *C. unilobata*, pilose as in *C. mossambicensis*, puberulous as in *C. mildebrandii* and tomentose as in *C. ciliata*. This remarkable feature of calyx is here coded for its presence and absence.

22. Corolla length: more than 4 mm (0); 4 mm or less (1). Argument as for character 16.

23. Corolla indumentum: absent (0); present (1). Argument as for character 21.

24. Length of long stamens: 4.4 mm or more (0); less than 4.4 mm (1). *Commiphora* species exhibit staminal dimorphism in most cases (having short and long stamens), although there are some exceptions like *C. monoica*. However, some species like *C. corrugata* were observed to show 4 equal sized stamens and 8 dimorphic stamens in different seasons. Consequently, staminal dimorphism was not considered here for two reasons; it occurs in almost all species and it is variable within the species depending on seasons. Rather some species are known to have longer long stamens (e.g., *C. terebinthina, C. alaticaulis*) and others have shorter long stamen (e.g., *C. gurreh, C. ciliata*). Note that a

flower with longer stamens is likely to have longer floral part.

25. Anther length of long stamens: 1 mm or more (0); less than 1 mm (1). See character 16 for discussion.

26. Length of short stamens: 2.5 mm or more (0); below 2.5 mm (1). The length of the short stamens was also considered as a character, since there is variation in its length. Species such as *C. myrrha, C. samharensis* are known to have shorter short stamens in comparison with those having longer short stamens, for example, *C. paolii* and *C. edulis*.

27. Anther length of short stamens: 0.6 mm or more (0); below 0.6 mm (1). Argument as for character 16.

28. Pistil length: more than 2 mm (0); 2 mm or less (1). Pistil length is here considered in the sense that it represents ovary, style and stigma length. Species such as *C. habessinica, C. suffruticosa* and *C. fulvotomentosa* have remarkably longer pistil length with their style more pronounced. On the other hand, *C. gurreh, C. sphaerocarpa* and *C. boranensis* have a shorter pistil.

29. Drupe length: more than 10.5 mm (0); 10.5 mm or less (1). The drupe of *Commiphora* species had been considered the best taxonomic tool in distinguishing the different species within the genus. While supplementing this idea under the taxonomic and phylogenetic significance of the drupe, Van der Walt (1975) indicated that number of valves in which the mature drupe split, shape and size of the drupe, indumentum of the drupe, shape and surface of the putamen and color and structure of the pseudoaril were characters that were used in the classification of the genus. Although it is possible to make distinction between the different species as mentioned above, hypothesis of homology cannot be developed from the shapes of the stone (putamen) and that of the drupe, since it shows variation within the species. Based on the general assumption made by Radford *et al.* (1974) the larger drupe, be it in length, width or thickness, is considered as primitive state. Species like *C. unilobata, C. ugogensis* and *C. serrata* are known to have large drupe size.

30. Drupe width: 7 mm or more (0); less than 7 mm (1). Argument as for character 29.

31. Drupe thickness: 7 mm or more (0); less than 7 mm (1). See character 29 for argument.

32. Drupe indumentum: absent (0); present (1). In some species the drupe is hairy, such as in *C. engleri, C. fulvotomentosa, C. alaticaulis, C. mollis* and in others it is glabrous as in *C. horrida, C. hodai; C. quadricincta, C. cyclophylla* etc. This variability within the group is coded as present and absent leaving the density and length of hairs for the reasons discussed above under character 11.

33. Pericarp valve: two valved (0); partially four or four valved (1). Opening of the valve of the ripe drupe exposes the fleshy and bright red colored pseudoaril that attracts birds. Obviously, this assists in the dispersal process. *C. serrulata, C. ciliata, C. boranensis* and *C. velutina* are some of the species having 4-valved drupes while *C. hornbyi, C. caerulea, C. eminii, and C. kataf* are good examples of species with 2-valved drupe. Four valved is then an advanced character in the sense that it exposes more pseudoarilar surface than the 2-valved ones.

34. Pseudoaril arm: two or otherwise (0); four armed (1). Pseudoaril is another important taxonomic tool for distinguishing species of *Commiphora*, since it shows distinct variation from the rest of the characters. Some species are known to have four-armed pseudoaril, notably *C. habessinica, C. kua* and *C. glandulosa.* Others have a variable pseudoaril. *C. monoica*, for example, has an irregularly armed, thin psuedoaril that covers most of the stone, whereas species such as *C. erlangeriana* and *C. unilobata* have pseudoaril that extends on one side of the stone appearing as one arm. Still some are having two broad arms almost to the extent that it covers the stone to the top as in *C. baluensis.* Another variation in the pseudoaril nature is the existence of cup like ones that are only observable at the bottom of the stone, although at times it forms indistinct arms. This type is seen in, for example, *C. corrugata.* The pseudoaril also covers the whole stone and fused with it as in *C. schimperi* and *C. africana.* Having considered these variations in pseudoaril, hypothesis of homology was developed as four armed and non-four armed ones, four armed being advancement. The fact is that four armed ones are easily picked by the birds than the other arms and help in dispersal.

35. Pseudoaril's extent of stone coverage: Covering the whole stone (0); not covering the whole stone (1). Wild (1959) indicated the evolution of the pseudoaril trend "from a fleshy pseudoaril covering the lower 1/3 of the endocarp to forms in which it encloses the whole endocarp or becomes so intimately associated with the endocarp that it appears to be absent

and finally to forms with four variously developed arms." Taking the species under investigation into consideration, however, the most primitive type of pseudoaril seems reasonably to be the one that covers the whole stone. This type of pseudoaril was also realized by Engler (1931) as the most primitive one.

36. Number of fertile locules: two (0); one (1). Most species of *Commiphora* are known to have one locule, while a few have two locules as in *C. myrrha, C. madagascarensis* and in *C. kua.* In an attempt to produce one viable seed, a species with one locule is at advantage over the one having two locules.

37. Stone length: 7 mm or more (0); less than 7 mm (1). See character 29 for discussion.

38. Stone width: 5 mm or more (0); less than 5 mm (1). See character 29 for discussion.

39. Stone thickness: more than 3.5 mm (0); 3.5 mm or less (1). See character 29 for discussion.

40. Stone surface: smooth (0); rugose (1). It seems reasonable to hypothesize that pseudoaril is more firmly attached to the rough surfaced stone than to the smooth surfaced ones. This means that it takes some time and energy for the birds to remove it from the former types.

Excluded Characters

Besides the characters discussed above, other characters were also investigated but not included in the analysis either for their highly multistate nature and large amount of interaspecific variation, or because it was difficult to establish the necessary hypothesis for coding the states. Such characters include leaf types, the smell of the exudates, the peeling pattern of the bark and shapes of all parts. Some characters including ovary width, stigma width and staminoides lengths were omitted because of the high frequency of missing values.

Data Analysis

Attempt was made to analyze the data based on phenetic approach. The data were analyzed using PAUP* version 4.0 b10 (Swofford, 2002) run on a Macintosh computer. For this analysis UPGMA (Unweighted Pair Group Method of Arithmetic means or sometimes known as Unweighted Average Linkage method) was chosen and a standard distance measure set at mean character difference. Podani (1994) described this method as more efficient

than the others because the distance of the two clusters to be joined is calculated as the arithmetic average of all between-cluster distances.

RESULTS

The UPGMA tree produced from the phenetic analysis is shown Fig. 1. The tree clearly shows that there are seven distinct groups, although there are two big basal groups. Of the seven clusters clearly seen on the UPGMA tree, the first cluster is formed by the taxa ranging from *C. gileadensis* to *C. gowlello*, the second from *C. rostrata* to *C. samharensis*, the third from *C. madagascarensis* to *C. quadricincta*, the fourth from *C. glandulosa* to *C. myrrha*, the fifth from *C. stolonifera* to *C. africana*, the sixth from *C. caerulea* to *C. staphyleifolia* and the seventh from *C. acuminata* to *C. erlangeriana*. These clusters are here recognized as sectional clusters.

DISCUSSION

The present morphological phenetic analysis of the genus *Commiphora* confirmed the recognition of seven sections. In naming these, the International Code of Botanical Nomenclature (Anonymous, 2000) has been followed. Key to sections and short description of the sections recognized are provided below.

Key to Sections of *Commiphora* Jacq.

1. Pseudoaril covering the whole stone; flower mostly bisexual; stone surface strictly rugose.....Section *Schimperianae.*

   Pseudoaril not covering the whole stone; flower strictly unisexual; stone not as above..... 2.

2. Trichomes on petiole absent; leaflet multi-celled glandular hair absent; leaflet unicellular and multicellular hair absent; leaflet usually glabrous.....3.

   Trichomes on petiole present; leaflet multi-celled glandular hair; leaflet unicellular hair and leaflet multicellular hairs mostly present; leaflet hairy.....5.

3. Thorn usually absent; petiole more than 1.5 cm long; inflorescence long and pedunculate.....Section *Cupulares.*

   Thorn usually present; petiole usually less than 1.5 cm long; inflorescence fasciculate and solitary.....4.

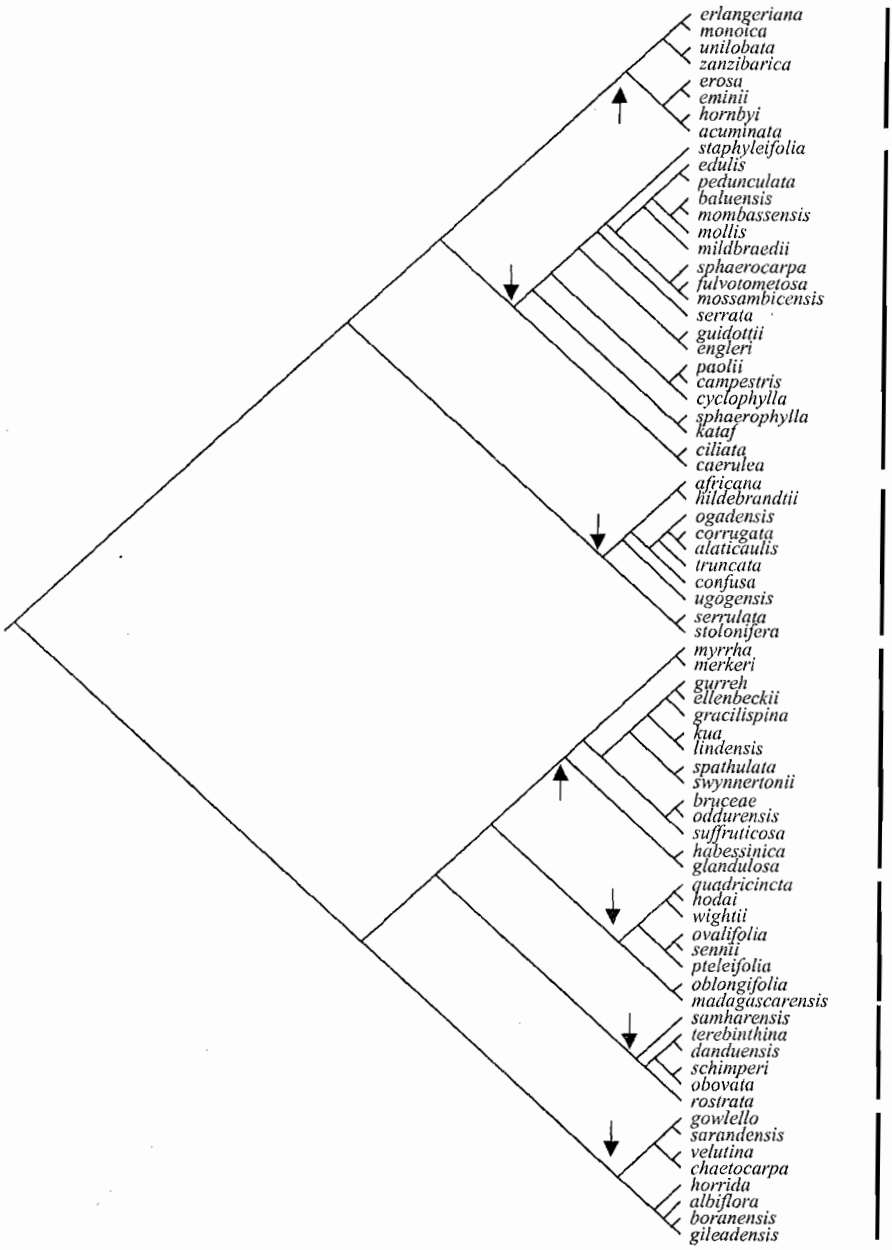

Fig. 1. Slanted UPGMA revealing the different clusters. Arrows and lines indicate the different clusters. Note that only the epithet names are used for all the species included in the analysis.

4. Pericarp more or less 4-valved; stone width usually less than 5.5 mm, drupe less than 7 mm thick..... Section *Coriaceae.*

Pericarp more or less 2-valved; stone width often greater than 5.5 mm; drupe greater than 7 mm thick.....Section *Commiphora.*

5. Peduncle longer than 1.5 mm; drupe longer than 10.5 mm long; stamen often shorter than 4.4 mm..... Section *Hemprichia.*

Peduncle shorter than 1.5 mm; drupe shorter than 10.5 mm long; stamen usually longer than 4.4 mm.....6.

6. Leaflet shorter than 3.5 cm; calyx shorter than 2 mm; stone less than 3.5 mm thick..... Section *Opobalsameae.*

Leaflet longer than 3.5 mm; calyx longer than 2 mm; stone thicker than 3.5 mm.....Section *Africanae.*

The Sections

1. Section *Opobalsameae*

Sect. *Opobalsameae* (Engl.) Vollesen in Kew Bull. 40: 44 (1985). Type species: *C. gileadensis* (L.) C. Chr.

Basionym: *Commiphora* § Artengruppe *Opobalsameae* Engl., *Bot. Jahrb.* 48: 454 (1912), without indication of rank. Type *C. gileadensis* (L.) C. Chr., lectotype selected by Wild (1959).

Syn: Subsect. *Ancistrophora* Chiov. Tom. Cit. **Fl. Somala** 2: 111 (1932); Subsect. *Foliaceae* Chiov., tom.cit., **Fl. Somala** 2: 94 (1932); *Commiphora* § Subgenus Opobalsameae (Engl.) Wild in *Bol. Soc. Brot. Ser*, 2: 94 (1959).

Trees, shrubs or flat topped usually unarmed except in *C. gowlello* and *C. horrida*; bark often peeling, sex dioecious; branchlets pubescent or very rarely glabrous; exudates mostly watery and aromatic in most cases; petiole usually less than 1.5 cm, hairy, petiole vascular number at lamina base less than 7, in its vascularization many free traces in ring; leaf types three foliolate, pinnate, one foliolate and rarely hetrotrifoliolate; leaflet less than 3.5 cm and 1.6 cm wide, hairy, shape elliptic some times obovate rarely oblong sub-orbicular and spathulate, margin entire crenate serrate rarely dentate and sub-entire, apex rounded to emarginate rarely acute or sub-acute, base rounded to acute and cuneate. Inflorescence fasciculate or solitary. Peduncle less than 2.5 mm; pedicel usually less than 1.5 mm. Flower unisexual; calyx 2 mm or less, shape mostly cupular triangular rarely ovate triangular; corolla 4 mm or less mostly glabrous and rarely hairy. Long stamens less than 4.4 mm, its anthers less than 1 mm. Drupe ovoid ellipsoid rarely globose or sub-globose, length 10.5 mm or less, width less

than 7 mm, less than 7 mm thick, usually glabrous and rarely hairy. Pseudoaril not covering the whole stone; number of fertile locules one. Stone shape ovoid ellipsoid rarely globose or subglobose, less than 7 mm long, less than 5.5 mm wide, 3.5 mm or less thick and often with smooth surfaces.

Included species: *C. gileadensis, C. boranensis, C. albiflora, C. horrida, C. chaetocarpa, C. velutina, C. sarandensis* and *C. gowlello.*

2. Section *Schimperianae*

Sect. *Schimperianae* Engl. ex Teshome, comb. nov.

Basionym: Commiphora § Artengruppe *Schimperianae* Engl. *Bot Jahr.* 48: 459 (1912). **Syn**: Series Glabrae Sect. Serratifoliolatae § *Schimperianae* Chiov. tom. cit, **Fl. Somala** 2: 63 (1932); Section *Rostratae* (Engl.) Wild in *Bol. Soc. Brot., Sèr.* 2, 33: 88 (1959), Vollesen in *Kew Bull.* 40 (1): 45 (1985), Gillett in **FTEA**, 15 (1991), Type, *C. rostrata* Engl. Type species: *C. schimperi* (O. Berg) Engl. chosen here.

Thorny trees or shrubs 3 m or more in height; bark usually peeling in small flakes; sex hermaphrodite and dioecious; branchlets glabrous; exudates often watery and has aromatic smell very rarely faintly scented as in *C. samharensis*. Petiole glabrous, its vascularization many free traces in ring and its vascular number at the lamina base is mostly less than 7. Leaf types three foliolate rarely heterotrifoliolate or simple, leaflet multicelled glandular hairs absent, shape elliptic obovate sub orbicular rhombic spathulate or their combinations (here after same for margin, apex, base and shapes of any structures), margin crenate dentate entire serrate sub entire, apex acute emarginate rounded sub acuminate truncate, base cuneate acute rounded, venation pattern semicraspedodromous and rarely kladodromous as in *C. rostrata*. Stomatal position hypostomatic. Inflorescence cymes, fascicle or solitary. Flower unisexual or bisexual. Calyx usually more than 2 mm long, glabrous, shape broad or ovate triangular rarely cupular triangular; corolla more than 4 mm long, glabrous, color reddish or rarely yellowish green as in *C. schimperi*, tip recurved. Long stamen greater than 4.4 mm, its anther usually 1mm or more in length. Drupe 7 mm or more thick, glabrous, shape ellipsoid obovoid ovoid and rarely globose. Pericarp mostly 2-valved; pseudoaril covers the whole stone; number of fertile locules one; stone usually 7 mm or more in length, shape ovoid obovoid ellipsoid and rarely subglobose, surface rugose.

Included species: *C. rostrata, C. obovata, C. schimperi, C. danduensis, C.*

terebinthina and *C. samharensis*.

3. Section *Commiphora*

Sect. *Commiphora* Jacq., Hort. Schoenbr. 2: 66, t. 249 (1797). Type species: *C. madagascarensis* Jacq., as for the genus.

Thorny trees or shrubs 3 m or taller than that; bark peeling in small flakes rarely in large papery flakes; sex dioecious; branchlets glabrous; petiole trichomes absent. Leaf types heterotrifoliolate, three foliolate or one foliolate, leaflet trichomes absent, shape elliptic oblong obovate ovate sub orbicular and rhombic, margin serrate dentate crenate and entire, apex acute rounded sub acute acuminate and rarely truncate, base cuneate rounded or acute. Inflorescence fasciculate solitary or rarely short cymose. Peduncle usually shorter than 2.5 mm. Flower sex unisexual; calyx glabrous; corolla often shorter than 4 mm or less, glabrous, color mostly reddish rarely yellowish or greenish. Long stamen shorter than 4.4 mm, its anther mostly shorter than 1 mm. Drupe 7 mm or wider and thick, glabrous, shape ovoid ellipsoid rarely globose and obovoid. Pseudoaril more or less four armed and not covering the whole stone except in *C. madagascarensis*; number of fertile locules often one. Stone 7 mm or longer than that, width 5 mm or more, shape ovoid ellipsoid rarely subglobose and obovoid.

Included species: *C. madagascarensis, C. oblongifolia, C. pteleifolia, C. senni, C. ovalifolia, C. wightii, C. hodai* and *C. quadricincta.*

4. Section *Coriaceae*

Sect. *Coriaceae* Engl. ex Wild in *Bol. Soc. Brot., Ser.* 2, 33: 89 (1959). Type species: *C. myrrha* (Nees) Engl. selected here.

Basionym: *Commiphora* § Artengruppe *Coriaceae* Engl. *Bot. Jahrb.* 48: 89 (1912), without indication of rank. Type *C. myrrha* (Nees) Engl. (= *C. coriaceae* Engl.), lectotype selected by Wild (1959), *C. lindensis* Engl.

Syn: Section *Abyssinicae* (Engl.) Gillett; in Fl. TEA (1991); Type, *C. habessinica* (O. Berg) Engl. as '*abyssinica*'

Thorny shrub or tree very rarely flat topped; bark often peeling; sex dioecious; branchlets glabrous; exudates in most cases milky and rarely watery; petiole shorter than 1.5 cm, trichomes often absent. Leaf types one foliolate rarely heterotrifoliolate and three foliolate, leaflet unicellular and multicellular hairs absent, leaflet multicelled glandular hairs absent except in *C. glandulosa*, shape obovate elliptic rarely sub orbicular oblong ovate or spathulate, margin dentate crenate entire sub entire serrate biserrate and

laciniate, apex acute rounded truncate sub acute, base cuneate rarely acute or rounded. Inflorescence fascicle solitary or congested cymes. Peduncle often shorter than 2.5 mm. Flower unisexual; calyx more or less glabrous; corolla glabrous, color red yellowish and greenish. Drupe usually longer than 10.5 mm, less than 7 mm thick, glabrous, shape ellipsoid ovoid and globose. Pericarp 2-valved except in *C. suffruticosa* and *C. oddurensis*; pseudoaril mostly four armed and not covering the whole stone. Stone often less than 5.5 mm, shape ellipsoid ovoid rarely subglobose.

Included species: *C. glandulosa, C. habessinica, C. suffruticosa, C. oddurensis, C. bruceae, C. swynnertonii, C. spathulata, C. lindensis, C. kua, C. gracilispina, C. ellenbeckii, C. gurreh, C. merkeri* and *C. myrrha*.

5. Section *Africanae*

Sect. *Africanae* (Engl.) Wild in *Bol. Soc. Brot., Ser.* 2, 33: 87 (1959). Type species: *C. africana* (A. Rich.) Engl. selected here.

Basionym: *Commiphora* § Artengruppe *Africanae* Engl. *Bot. Jahrb.* 48: 462 (1912), without indication of rank. Type *C. africana* (A. Rich.) Engl.

Syn: Section *Hildebrandtianae* (Engl.) Vollesen in *Kew Bull.* 40 (1): 44 (1985), Gillett in **FTEA**, 73 (1991), Type, *C. hildebrandtii* (Engl.) Engl. (= *Balsamea hildebrandtii* Engl.); Section *Ugogenses* (Engl.) Gillett in **FTEA**, 71 (1991), Type, *C. ugogensis* Engl.

Shrub or trees 3 m or more in height; bark some times peeling in small flakes and rarely not; sex dioecious; branchlets hairy very rarely glabrous; exudates mostly milky and rarely watery; petiole trichomes present, its vascular number at the lamina base 7 or more, vascularization many free traces in ring. Leaf types three foliolate rarely heterotrifoliolate and pinnate, leaflet usually 3.5 cm or longer than that, more than 1.6 cm wide, trichomes present (both multicellular and unicellular hairs), shape elliptic obovate rarely ovate oblong sub entire rhombic spathulate, margin crenate dentate serrate rarely biserrate and laciniate, apex truncate acute acuminate rarely sub acute rounded and emarginate, base cuneate rounded and or acute, leaf venation kladodromous and semicraspedodromous. Stomatal position mainly hypostomatic very rarely amphistomatic. Inflorescence fasciculate solitary and congested cymes. Peduncle usually shorter than 2.5 mm. Flower unisexual; calyx often more than 2 mm, hairy; corolla usually more than 4 mm, shape broad triangular, color yellowish rarely red white and greenish. Long stamen often as long as 4.4 mm or more; short stamens as long as 2.5 mm or more, its anther 0.6 mm or more than that. Drupe often 10.5 mm or

less long, shape ovoid ellipsoid globose rarely obovoid and rounded. Pericarp 2-valved except in *C. serrulata*. Pseudoaril not covering the whole stone except in *C. africana* and *C. stolonifera*; number of locules one. Stone usually 5.5 mm wide or more, often more than 3.5 mm thick, shape ovoid ellipsoid globose rarely obovoid subglobose and cordate, surface mostly rugose.

Included species: *C. stolonifera, C. serrulata, C. ugogensis, C. confusa, C. truncata, C. alaticaulis, C. corrugata, C. ogadensis, C. hildebrandtii* and *C. africana.*

6. Section *Hemprichia*

Sect. *Hemprichia* (Ehrenb.) Schweinf. In *Bull. Herb. Boiss. 7, App.* 2: 283 (1989). Type species: *C. kataf* (Forssk.) Engl. chosen here.

Basionym: *Hemprichia* Ehrenb., in *Linnaea* 4: 396 (1929), Type: *C. kataf* (Forssk.) Engl. (= *Amyris kataf* Forssk.)

Syn: Section *Campestres* (Engl.) Vollesen in *Kew Bull.* 40 (1): 43 (1985), Gillett in **FTEA**, 32 (1991), Type, *C. campestris* Engl.; Section *Ciliatae* Vollesen in *Kew Bull.* 40 (1): 43 (1985), Gillett in **FTEA**, 84 (1991), Type, *C. ciliata* Vollesen; Section *Latifoliolatae* (Engl.) Vollesen in *Kew Bull.* 40 (1): 44 (1985), Gillett in **FTEA**, 49 (1991), Type, *C. mossambicensis* Engl.; Section *Pedunculatae* (Engl.) Vollesen in Kew Bull. 40 (1): 44 (1985), Gillett in Fl. TEA, 73 (1991). Type, *C. pedunculata* (Kotschy & Peyr.) Engl.

Trees or shrub usually more than 3 m; bark often peeling; thorn usually absent; sex dioecious; petiole often 1.5 cm or longer than that, trichomes present except in *C. mildbraedii*. Leaf types pinnate or trifoliolate, leaflet more or less hairy, shape elliptic obovate ovate oblong rarely sub orbicular rhombic or spathulate, margin entire serrate dentate crenate, apex acuminate acute rounded emarginate, base rounded cuneate acute and rarely truncate. Inflorescence long pedunculate cymes panicle and very rarely solitary. Peduncle more or less more than 2.5 mm; pedicel 1.5 mm or more. Flower unisexual; calyx often hairy. Long stamen usually shorter than 4.4 mm and its anther smaller than 1 mm. Drupe more or less more than 10.5 mm long, 7mm or more wide and thicker than that, shape ellipsoid ovoid obovoid globose and subglobose. Pericarp often 2 valved; pseudoaril not covering the whole stone; number of fertile locules one. Stone 7 mm or longer than that, often 5.5 mm or wider than that, shape ellipsoid ovoid globose or subglobose, surface more or less smooth.

Included species: *C. caerulea, C. ciliata, C. kataf, C. sphaerophylla, C.*

cyclophylla, C. campestris, C. paolii, C. engleri, C. guidottii, C. serrata, C. mossambicensis, C. fulvotomentosa, C. sphaerocarpa, C. mildbraedii, C. mollis, C. mombassensis, C. baluensis, C. pedunculata, C. edulis and *C. staphyleifolia.*

7. Section *Cupulares*

Sect. *Cupulares* (Wild) Teshome, comb. nov., Type species: *C. zanzibarica* (Baill.) Engl. chosen here.

Basionym: Subsect. *Cupulares* Wild in *Bol. Soc. Brot., Ser.* 2, 33: 90 (1959). Type species: *C. zanzibarica* (Baill.) Engl.

Syn: *Commiphora* § Artengruppe *Spondioideae* Engl. *Bot. Jahrb*, 48: 453 (1912), Type *C. spondioides* (= *C. zanzibarica* Engl.); Section *Arillopsidium* Engl.; in *E.J.* 10: 283 (1888); Vollesen, in *Kew Bull*, 40 (1): 43 (1985); Gillett, in **FTEA**, 61 (1991); Type, *C. glaucescens* Engl.; Section *Monoicae* Vollesen in *Kew Bull.* 40 (1): 44 (1985), Type, *C. monoica* Vollesen.

Unarmed tree or shrubs usually 3 m or more in height; branchlets glabrous but rarely puberulous; sex dioecious and monoecious; petiole1.5 cm or more, trichomes often absent. Leaf types pinnate or trifoliolate; leaflet length often 3.5 cm or more, 1.6 cm or wider than that, trichomes absent, shape ovate elliptic oblong obovate rhombic, margin entire serrate crenate, apex acuminate acute rounded, base rounded cuneate acute or rarely truncate. Stomatal position hypostomatic. Inflorescence panicles long cymes and racemes. Peduncle longer than 2.5 mm; pedicle usually 1.5 mm long or more than that; flower unisexual; calyx glabrous, shape ovate triangular rarely cupular and broad; corolla glabrous, color reddish yellowish or greenish. Drupe often 7 mm wide and thick or more than that, glabrous shape ellipsoid globose obovoid and ovoid. Pericarp 2-valved; pseudoaril not covering the whole stone; number of fertile locules one. Stone often 7 mm or longer than that, 5.5 mm or wider than that, thicker than 3.5 mm, shape ellipsoid ovoid rarely oblong, surface usually smooth.

Included species: *C. acuminata, C. hornbyi, C. eminii, C. erosa, C. zanzibarica, C. unilobata, C. monoica* and *C. erlangeriana.*

The sections recognized as a result of the present study are distinct groups based on morphological characters. Albeit the presence of a big split at the top of the dendrogram, it was not reasonable to intercalate sub-generic rank for the fact that there were no clear cut couplet of characters leading to the distinction of the big split. As a result, only the sectional ranks are recognized. Taking the pattern of clustering of the sections or their

relationships into consideration, section *Opobalsamae* shares certain characters with section *Commiphora*, *Coriaceae* and section *Africanae*. These characters are the fasciculate and solitary nature of the inflorescence and the shorter peduncle. On the other hand, it shares a smoothness of stone surface with sections *Hemprichia* and *Cupulares*. Nevertheless, it has its own distinguishing features from the rest of the sections. Small leaflet length and width, shorter peduncle and calyx, smaller drupe width and stone length and smaller stone thickness are the characters that are attributable to the section *Opobalsamae*.

Section *Opobalsamae* (Engl.) Vollesen is here emended because of the additional data set and addition of the species from the East Tropical Africa. For example, *C. gowlello* of Vollesen's (1989) section *Commiphora* was moved to section *Opobalsamae*. Similarly, Gillett's (1991) *C. sarandensis* of the section *Hildebrandtianae* is moved here to section *Opobalsamae*. The addition of these species to the section suggests that these species share more morphological features with the species presently included in the section *Opobalsamae* than the species of the other sections. As a result, in the present study the total number of sections is reduced to seven. The reduction in the number of sections and the amendment of formerly recognized sections are entirely based on the intercalation of more morphological data set and consideration of more species from different Flora regions. For similar reasons, the other sections recognized in the present study contain more species.

Members of the section *Schimperianae* are distinct for their pseudoaril that covers the whole stone. Morphological features such as absence of petiole trichomes, absence of multi-celled glandular hairs and more or less absence of leaflet trichomes are those shared between sections *Schimperianae*, *Commiphora*, *Coriaceae* and *Cupulares*. It also shares the rugose stone surface, more or less longer short stamens, long stamens and longer corolla with section *Hemprichia*. The thorny nature of section *Schimperianae* is also a binding feature observed in section *Commiphora* and *Coriaceae*.

The type section, section *Commiphora*, also shares a number of features with other sections. For example, absences of petiole trichomes, multi-celled glandular hairs, unicellular and multicellular hairs, the over all leaf trichomes, absence of calyx and corolla indumentum are those that are shared with sections *Schimperianae*, *Coriaceae* and *Cupulares*. The thorny nature is shared between this section and sections *Schimperianae* and *Coriaceae*. Other remarkable characters shared between sections

Commiphora, *Opobalsamae* and *Hemprichia* are the presence of shorter long stamens and its anthers. Section *Commiphora* also shares tree or shrub habit with members of the sections, *Schimperianae*, *Africanae*, *Hemprichia* and *Cupulares*. Albeit this habit, members of the section *Commiphora* are distinct for their height, the glabrous nature of their branchlets, more or less four armed pseudoaril and their thick and wide stones. Similarly, on the basis of the present character matrix, section *Coriaceae* is distinct for its small petiole length, smaller drupe thickness and smaller stone width. However, it shares longer sized drupe with sections *Commiphora* and *Hemprichia*. Members of section *Africanae* are distinct for their longer short stamen's anther and broad triangular corolla.

Section *Hemprichia* is the largest section with more species than the others. It is characterized by having larger organs. For example, it has usually pedunculate and long inflorescence, the character shared with section *Cupulares*. The pedicel length, the peduncle length, drupe length, drupe width, drupe thickness, stone length and stone width are all the largest. The pseudoaril of the section *Hemprichia* does not cover the whole stone, the morphological feature shared also by most of the sections except section *Schimperianae*. Similarly, absence of thorn and longer petiole are characters that made section *Cupulares* distinct from the rest. Moreover, variations also exist between these clusters when the overall morphological features are compared.

A comparison of the recognized sections of *Commiphora* was made to see which of the sections exhibited more primitive and/or advanced states based on the selected characters. The missing value for each section was also considered to see if it might affect the comparison (Fig. 2).

The figure shows that the highest primitive state is recorded from sections *Cupulares* and *Schimperianae*. However, there are more missing values and less advanced conditions in section *Cupulares* than in section *Schimperianae* suggesting that the possible primitive group is section *Cupulares*. The most advanced section seems to be section *Opobalsameae* that has more advanced states as compared to the other sections.

Commiphora and other Burseraceae

Below are some comments on the distinction and the phylogenetic relationships of the genus *Commiphora* within the family Burseraceae and more specifically with the tribe Bursereae to which the genus belongs. It should be clear that this comparison is solely based on the secondary data

for the other genera of this family. Highlight on the sub-familial division and the characters used are presented here first.

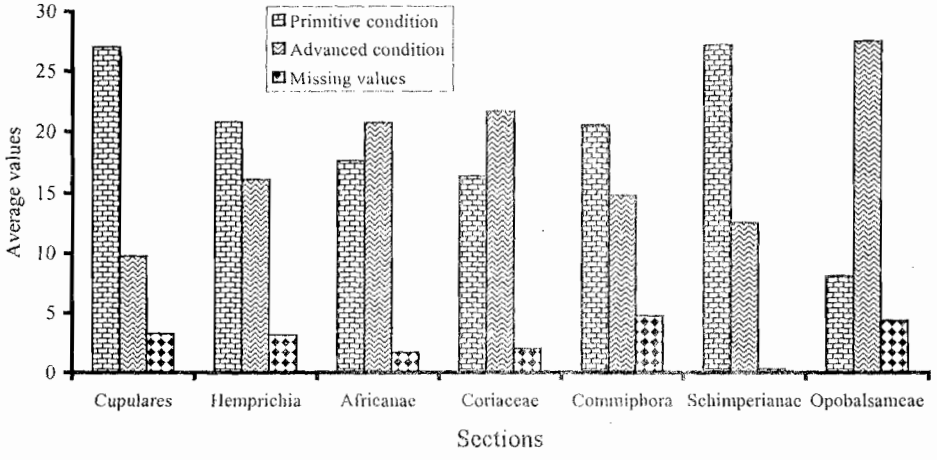

Fig. 2. Primitive and advanced states in the sections of *Commiphora* recognized in the present study.

Since the first description of the family Burseraceae by Kunth (1824), other workers such as Cronquist (1981) and Takhtajan (1997) have attempted to circumscribe the family. It is believed that the family is closely related to the families Rutaceae, Simaroubaceae and Anacardiaceae.

Few workers, notably Marchand (1867-1868), Engler (1913, 1915, 1931) and Guillaumin (1909), attempted circumscription at the sub-familial level. Although he considered his circumscription artificial and unsatisfactory, Marchard (1867-1868) classified the family based on whether the petals are free or connate and divided the family into three tribes: the Protieae, with convex receptacle, hypogynous stamens, and free petals; the Hedwigieae, with convex receptacle, hypogynous stamens and connate petals; the Garugeae, with concave receptacle, perigynous stamens and free petals. Guillaumin (1909) on the other hand, developed keys for the genera of this family using anatomy, morphology of drupe, seed and flower.

Engler (1913) proposed a sub-familial classification into three tribes and maintained this classification in subsequent publications (Engler, 1915, 1931). Engler (1913) classified the tribes based on the degree of concrescence of the pyrenes: the Protieae have completely free pyrenes which may be in contact; the Bursereae (published as Boswellieae; and corrected by later workers for it contains the type genus) have the pyrenes partly connate but separable and the Canarieae have the pyrenes completely

fused. This classification of Engler (1913) was adopted and used by later workers such as Leenhouts (1956) and Clarkson *et al.* (2002). Although later workers corrected Engler's (1913) Boswellieae as Bursereae, Engler did not validly publish the name Bursereae in the subsequent works nor did the later workers identify its validity including Clarkson et al (2002). Thus, considering the ICBN rule, the name should appear as Bursereae Engl. ex Teshome, characters as described above. The proposed sub-familial division and the genera belonging to them as adopted by Clarkson *et al.* (2002) is given in Table 2.

Table 2 Sub-familial division of Burseraceae and the genera belonging to them as adopted from Clarkson *et al.* (2002).

Tribe	Genera
Bursereae Engl. ex Teshome	*Aucoumea* Pierre
	Beiselia Forman
	Boswellia Roxb.
	Bursera Jacq.
	Commiphora Jacq.
	Triomma Hook. f.
Canarieae Engl.	*Canarium* L.
	Dacryodes Vahl
	Haplolobus Lam
	Pseudodacryodes R. Pierlot
	Rosselia Forman
	Santiria Blume
	Scutinanthe Thwaites
	Trattinnickia Willd.
Protieae Marchand emend. Engl.	*Crepidospermum* Hook. f.
	Garuga Roxb.
	Protium Burm. f.
	Tetragastris Gaertn.

a) *Commiphora* and *Aucoumea*

The genus *Aucoumea* Pierre is monotypic genus in the family represented by *Aucoumea klaineana* Pierre and recorded from Gabon. The general architecture of its drupe including its winged pyrenes resembles the drupe of *Boswellia* and *Triomma*. In the figure presented by Engler (1913: 418), the extrastaminal disk and the five merous floral parts are a characteristic of the genus *Triomma* and that of *Boswellia*. Staminal dimorphism, the dehiscent nature of the drupe and the nature of the cotyledon is more or less suggesting an affinity with *Commiphora*.

b) *Commiphora* and *Beiselia*

The discovery of the Neotropical genus *Beiselia* Forman and the circumscription of the species *Beiselia mexicana* Forman were thoroughly discussed by Forman (1987) and Forman *et al.* (1989). On the basis of these

accounts *Beiselia* shares some characters with *Commiphora*, among other things, the presence of resin, the pinnate leaves, the nature of the male (in 1-3 flowered cymose fascicles in *Beiselia*) and the female flower (single along the axis in *Beiselia*) are typical for some species of *Commiphora*. The triangularly lobed calyx, the valvate petals, the intrastaminal disc, the 2-ovules per locules, the flat cotyledon of *Beiselia* is also characters shared by some members of the genus *Commiphora*.

The basic chromosome number in *Beiselia* was reported x = 13 (Forman *et al.*, 1989), the most common number in the family in general and in *Commiphora* as well (Gillett, 1980 and literature cited therein). Although the two genera share some common features, they also differ in some remarkable features, such as the absence of a pseudoaril in *Beiselia* and the nature of the drupe in *Beiselia* in which it is closer to that of *Boswellia* than to *Commiphora*.

c) *Commiphora* and *Boswellia*

Boswellia is a genus that often occurs in the same habitat as *Commiphora*. They occur together over a huge area of the Horn of Africa and other parts of the paleotropics. According to Vollesen (1989), Gillett (1991) and Thulin (1999) these two genera share a number of similarities and differences. They are related in any one or more of the following characters: the peeling of the outer bark that leaves the greenish under bark, which is also a characteristics of most *Commiphora* species (for example *C. baluensis*), the aromatic exudates hardening to resin in both, the soft wood often with latex and the dehiscent drupe in both genera. *Boswellia* is known to possess 5 calyx lobes and petals, ten stamens, woody modified drupe that has three or four stones and also lack thorns and pseudoaril. *Commiphora* on the other hand is characterized by having four calyx and petals (very rarely 5), 8 or less often 4 stamens, fleshy or leathery drupe that has one stone, a brightly colored pseudoaril and thorns in many of its members. From the aforementioned information, it seems reasonable to assume that *Boswellia* is more primitive than *Commiphora* in having numerous floral parts and characterized by the lack of pseudoaril, which according to Van der Walt (1975), is a modification of the endocarp. The somatic chromosome number in two species of *Boswellia* (*B. sacra* and *B. frereana*) was reported 2n = 22 (Thulin and Warfa, 1986) which is also different in *Commiphora* from the information at hand now.

d) *Commiphora* and *Bursera*

Several authors, notably Engler (1913, 1931), McVaugh and Rzedowski (1965), Forman *et al.* (1989) and Chithra and Henry (1997) have treated the genus Bursera. Moreover, in an attempt to screen out the distinction between the genera *Bursera* and *Commiphora*, Gillett (1980) had made an extensive comparison and finally reached at the conclusion that the two genera were distinct and should be kept separate. However, the two genera share a number of remarkable characters. *Bursera* is known to have a peeling bark, a characteristic also common in *Commiphora,* such as in *C. boranensis, C. baluensis* and *C. kua* and in most of the other species; the inflorescence in *Bursera* was reported to be paniculate (Chithra and Henry, 1997) which still occurs in some species of *Commiphora* such as *C. guidotti* Chiov. and *C. unilobata* Gillett and Vollesen. The fruit in both genera is drupaceous and has valves. Another remarkable feature that occurs in both is the presence of pseudoaril, a character seemingly unique to both genera in the family. Although both happen to have pseudoarils, the pseudoaril arm in *Bursera,* when not covering the whole stone, appears to occur on the sutural faces while it occurs on both sutural and facial faces in *Commiphora.* According to Forman *et al.* (1989), the pollen morphology of a few species of both genera used for comparison was found to have an indistinctly reticulo-echinate tectum. In the same account, anatomical comparison of *Commiphora hildebrandtii* Engl. and *Bursera kerberi* Engl. showed almost no difference. More importantly, the recent phylogeny-based study by Clarkson et al. (2002) put the two genera closer to one another. However, the two genera are more or less geographically separated having different center of diversity, *Bursera* in Mexico and *Commiphora* in the Horn of Africa, albeit some intergradations of both, *Commiphora* in South America and *Bursera* in India. Generally speaking, the similarity between the two genera outweighs the differences when judged from the available literature. A conclusion about combination or separation of the two genera is out of the scope of the present study, but it seems reasonable to work for further comparisons between the two genera that are based on adequate sampling of species from both groups. The comparison by Gillett (1980) is no longer sufficient to draw conclusions.

e) *Commiphora* and *Triomma*

According to Leenhouts (1956) *Triomma* Hook. f. is a monotypic genus that is confined to Western Malaysia. *Triomma* is characterized by five merous flowers, five stamens, free sepals and extrastaminal disk, three celled pistil,

three winged dry woody and dehiscing fruit that contains three woody valves. This genus shares most characters with *Aucoumea* and *Boswellia* and is more likely to be related to them than to the other genera of the family Burseraceae. In the phylogenetic study of the family Burseraceae made by Clarkson *et al.* (2002), *Triomma* appears to be closer to *Boswellia*, the idea that confirms the suggestion that the two genera are closely related. The free pyrenes of *Aucoumea*, *Boswellia* and *Triomma* are winged with which it differs from *Commiphora*. Although the detailed investigation on *Triomma* is lacking, the dehiscent drupe of the genus is the character with which it resembles *Commiphora*.

CONCLUSION

The present study indicated that *Commiphora* species in NE and E Tropical Africa could be grouped into seven sections. These sections are based on the morphological characters with which the clusters are distinctly distinguished from one another. The sections recognized in the present study are section ***Opobalsamae*** (Engl.) Vollesen, section ***Schimperianae*** Engl. ex Teshome, section ***Commiphora***, section ***Coriaceae*** (Engl.) Wild, section ***Africanae*** (Engl.) Wild, section ***Hemprichia*** (Ehrenb.) Schweinf. and section ***Cupulares*** (Wild) Teshome. Moreover, sections previously recognized by Vollesen (1989) and Gillett (1991) were emended in the present study due to the additional morphological data set. The combined treatment of the species of *Commiphora* occurring in NE and E Tropical Africa has significantly reduced the number of recognized sections to seven. Ten sections are placed in synonymy.

According to this study, the present sections share features particularly in the presence or absence of thorns, size relationships and presence or absence of indumentum of various organs or structures, pattern of inflorescence branching, the overall architectural pattern of flora parts with its sexes and that of the drupes, the fascinating nature of the fleshy psuedoaril and the nature of the stone that show prodigious variations within the clusters. However, further studies should combine the morphology and DNA sequence data (attempts to make DNA sequence of eight species using ITS showed promising result) of all *Commiphora* species of the world to make the detailed treatment of the genus. The distinction of *Commiphora* from *Bursera* should also be further studied.

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Appendix 1 Taxa versus characters used for phenetic analysis (Numbers are those under material and methods.)

Taxa/characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
erlangeriana	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	1	0	0	1	0	1	0	?	?	?	0	0	0	0	0	0	1	1	0	0	0	1
staphyleifolia	0	1	1	0	0	0	?	1	0	0	1	?	?	?	?	1	0	0	1	0	1	1	1	1	1	?	?	?	0	0	0	0	0	0	1	1	0	0	0	1
unilobata	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
guidottii	0	0	1	1	0	0	1	1	0	0	1	0	1	1	0	1	1	0	1	0	1	1	1	1	0	1	0	?	0	0	0	1	0	0	1	1	0	1	0	0
paolii	0	0	1	1	0	0	0	1	1	1	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
edulis	0	0	1	1	0	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0
baluensis	0	0	1	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0
sphaerophylla	0	0	1	1	0	1	?	1	0	1	1	?	?	?	?	0	0	0	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	1	0
myrrha	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	1	0	?	0	0	1	0	0	1	1	0	0	1	1	1
samharensis	0	0	0	1	1	1	0	0	1	1	1	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1
terebinthina	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	0	1	
schimperi	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
obovata	0	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	1
africana	0	0	1	1	1	0	0	1	0	0	1	1	1	1	1	1	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1
danduensis	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	1	1
monoica	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	1	1	1	0	0	0
pedunculata	0	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	0	1	0	1	1	1	0	0	?	0	0	1	1	0	1	1	1	0	0	0	1
hildebrandtii	0	0	1	1	0	0	0	1	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	0	0	0	1	1	1	1	0	0	1
ogadensis	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	0	1	1
corrugata	0	0	1	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	1	0	1	0	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	1
truncata	0	0	1	1	0	1	1	?	1	0	1	?	?	?	?	1	1	1	1	0	1	0	1	0	0	?	?	?	1	1	0	0	0	1	1	1	1	0	1	1
confusa	0	0	1	1	1	1	0	1	1	1	1	0	1	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1	1	1	1	0	0	1
alaticaulis	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	0	?	0	0	1	1	0	0	1	1	0	0	1	1
rostrata	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	?	0	1	1	0	1	0	0	1	0	1	1	1
ciliata	0	0	1	1	0	0	0	1	0	0	1	1	1	1	0	1	0	1	1	1	1	0	0	1	0	1	0	1	0	0	1	0	1	0	1	1	0	0	1	0
erosa	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	1	1	0	0	0	1	1	1	0	1	0	0

Appendix 1 (Continued ...)

Taxa/characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
sphaerocarpa	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1	1	1	0	0	0	1
mildbraedii	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0
cyclophylla	0	0	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0	1	1	1	0	1	0	1	1	?	?	?	0	0	0	0	0	1	1	1	0	0	0	0
campestris	0	0	1	1	1	0	0	1	1	0	1	0	1	1	0	0	0	0	1	1	1	0	0	0	1	0	0	?	0	0	0	0	0	1	1	1	0	0	0	0
serrulata	0	0	1	1	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	0	0
gurreh	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1
quadricincta	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	0	0	0	0	1	1	1	1	0	1	0	0
hodai	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	1	1	1	1	1	0	1	0	1	1	?	?	?	0	0	0	0	1	1	1	1	0	1	0	1
habessinica	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0
bruceae	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	?	1	1	1	0	0	1	1	1	1	1	0	0
ellenbeckii	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	1	1	1	0	1	0	1	1	1	0	?	1	1	1	0	0	1	1	1	1	1	1	0
kua	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	1
suffruticosa	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	0	0
gowlello	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1
horrida	1	1	1	1	1	1	?	1	1	1	1	?	?	?	0	1	1	1	1	1	0	1	0	1	1	?	?	?	1	1	1	0	1	0	1	1	1	1	1	0
albiflora	0	0	1	0	0	1	0	1	1	1	1	1	1	0	0	1	0	1	1	1	0	1	0	1	0	?	?	0	1	1	1	0	1	0	1	1	1	1	1	0
boranesis	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1
gileadensis	0	0	1	1	0	1	?	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	?	?	?	1	1	1	0	1	0	1	1	1	1	1	0
velutina	0	0	1	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	?	1	1	1	1	1	1	1	1	1	1	1	0
oblongifolia	0	0	1	1	1	1	?	0	1	1	0	0	0	0	?	1	1	1	1	1	0	1	0	1	1	?	?	?	1	0	0	0	0	0	1	1	0	0	1	1
ovalifolia	0	0	1	1	1	1	?	0	0	0	0	0	0	0	?	1	1	1	1	0	0	1	0	1	1	?	?	?	0	0	0	0	0	1	1	1	0	0	0	1
madagascarensis	0	0	1	1	1	0	?	0	1	1	0	0	0	0	?	1	1	1	1	1	0	1	0	1	1	0	0	?	0	0	0	0	0	0	0	0	0	1	1	1
ugogensis	0	0	1	1	1	1	?	1	0	0	1	?	?	?	?	1	1	1	1	1	1	1	1	0	0	0	0	?	0	0	0	1	0	1	1	1	0	0	0	1
hornbyi	0	0	1	1	0	0	?	0	1	0	0	?	?	?	?	0	0	0	1	1	0	1	0	1	0	1	0	?	0	0	1	0	0	0	1	1	0	0	0	0
caerulea	0	0	1	1	0	1	?	1	0	0	1	?	?	?	?	1	0	0	1	1	1	1	1	1	0	0	0	?	0	0	0	0	0	0	1	1	0	0	1	0
acuminata	0	0	1	1	0	0	?	1	0	0	0	0	0	0	?	0	0	?	1	1	0	0	0	?	?	?	?	?	1	0	1	0	0	1	1	1	0	0	0	0
chaetocarpa	0	0	1	1	1	1	?	1	1	1	1	?	?	?	?	1	1	1	1	1	1	1	0	1	1	?	?	?	1	1	1	1	0	?	?	?	?	?	?	?

Appendix 1 (Continued ...)

Taxa/characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
eminii	0	0	1	0	0	0	?	0	0	0	0	?	?	?	?	0	0	0	1	1	0	1	0	1	1	1	1	?	0	0	0	0	0	1	1	1	0	0	0	0
engleri	0	0	1	1	0	0	?	1	0	0	0	?	?	?	?	0	1	0	1	0	1	0	0	1	1	1	0	?	0	0	0	1	0	0	1	1	0	0	0	0
fulvotomentosa	0	0	1	0	0	0	?	1	0	0	1	?	?	?	?	0	0	0	1	1	1	0	1	1	1	0	1	?	0	0	0	1	0	1	1	1	0	0	0	1
glandulosa	0	0	1	1	1	1	?	1	0	0	1	1	0	0	?	1	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1	0	0	1	1	1	1	0	0	1
gracilispina	0	1	1	1	1	1	?	0	1	1	0	0	0	0	?	1	1	1	1	1	1	0	0	1	1	1	1	?	1	1	1	0	0	1	1	1	1	1	1	1
kataf	0	0	1	1	0	0	?	1	1	1	1	0	1	1	?	0	0	0	1	1	1	1	1	1	1	1	1	?	1	0	0	1	0	0	1	1	0	1	1	0
lindensis	0	0	1	1	1	1	?	0	0	0	0	0	0	0	?	1	1	1	1	1	0	1	0	1	1	0	1	?	1	1	1	0	0	1	1	1	1	1	1	0
merkeri	0	0	1	1	1	1	?	0	1	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	1	1	1	0	1	1	1
mollis	0	0	1	1	0	0	?	1	1	1	1	?	?	?	?	0	0	0	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	1	1	1	0	0	0	0
mombassensis	0	0	1	1	0	0	?	1	0	0	1	?	?	?	?	0	0	0	1	0	1	0	1	1	1	1	1	?	0	0	0	0	0	1	1	1	0	0	0	0
mossambicensis	0	0	1	0	0	0	?	1	0	0	1	?	?	?	?	0	0	0	1	1	1	1	1	1	1	1	1	?	1	0	1	1	0	1	1	1	0	0	0	1
oddurensis	0	0	1	1	1	1	?	0	1	1	0	0	0	0	?	1	1	1	1	?	0	?	0	?	?	?	?	?	1	1	1	0	1	1	1	1	1	1	0	1
pteleifolia	0	0	1	0	1	0	?	0	0	0	0	0	0	0	?	1	0	1	1	0	0	0	0	0	0	0	1	?	0	0	0	0	0	1	1	1	0	0	0	0
sarandensis	0	1	1	1	0	0	?	1	0	0	1	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	0	?	1	1	1	0	0	1	1	1	1	1	1	0
sennii	0	0	1	1	1	0	?	0	0	0	0	0	0	0	?	1	0	1	1	0	0	1	0	1	1	?	?	0	0	0	0	0	1	1	1	1	0	0	0	0
serrata	0	0	1	0	1	0	?	1	0	1	1	?	?	?	?	0	0	1	1	0	1	0	0	1	1	0	1	?	0	0	0	0	0	1	1	1	0	0	0	0
spathulata	0	0	1	1	1	1	?	0	1	1	0	0	0	0	?	1	1	1	1	1	0	1	0	1	1	1	1	?	1	1	1	0	0	0	0	1	0	1	0	0
stolonifera	0	1	1	1	1	0	?	1	0	0	1	1	1	1	?	0	0	0	1	1	1	0	0	0	1	0	0	?	1	1	1	0	0	0	0	1	0	1	0	1
swynnertonii	0	0	1	1	1	1	?	0	1	1	0	0	0	0	?	1	1	1	1	1	0	0	0	1	1	1	1	?	1	1	1	0	0	0	0	1	1	1	1	0
zanzibarica	0	0	1	1	0	0	?	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
wightii	0	0	0	?	1	1	?	0	1	1	0	0	0	0	?	1	1	1	0	1	0	1	0	1	1	?	?	?	0	0	0	0	0	1	1	1	0	0	0	0