

Generic status of *Quisqualis* (Combretaceae), with notes on the taxonomy and distribution of *Q. parviflora*

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ABSTRACT

The taxonomic status of *Quisqualis* L., a genus closely related to and sometimes considered congeneric with *Combretum* Loeff., is discussed. The genus *Quisqualis* is maintained to accommodate selected African, Indian, Asian and Malesian species (including *Q. indica* L. and *Q. parviflora* Sond.). Diagnostic characters for *Quisqualis* include: leaves with abundant subepidermal crystalliferous idioblasts, each containing a large druse of calcium oxalate; leaves, stems and flowers with stalked glands but no scales; persistent petiole bases that develop into curved spines; petals well developed; hypanthium tubular or cylindrical, usually longer than 20 mm; stamens and style not or scarcely exerted; style adnate to hypanthium for more than half its length. *Quisqualis* shares a number of morphological similarities with *Combretum* Loeff. subgen. *Cacoucia* (Aubl.) Exell & Stace sect. *Poivreia* (Comm. ex DC.) G. Don. Some species of Combretaceae from West, West Central and East Africa have the style adnate to the upper hypanthium and display features reminiscent of both *Quisqualis* and *Combretum*. These species also have characters of their own and in the past were placed in different sections under *Combretum*. It is suggested that at least some of these species may be best classified in genera distinct from *Combretum* and *Quisqualis*, one of which is *Campylogyne* Hemsley. *Combretum s.str.* is defined on the basis of a combination of characters and includes species of which the upper hypanthium is variable in shape, but when tubular or cylindrical, then always shorter than 20 mm. Other diagnostic characters include: stamens exerted well beyond petals; style exerted and free, but when shortly adnate to upper hypanthium (only at the base or for a short distance), then stamens long-exserted. It is suggested that different pollination strategies have developed independently in the *Combretum–Quisqualis* clade, resulting in convergent morphological trends in floral morphology. These homoplasious similarities in floral morphology are at the root of the difficulties experienced to demarcate genera. An alternative classification is provided for those preferring to include the southern African *Quisqualis parviflora* under *Combretum s. l.* For this purpose, a new combination and name, *Combretum sylvicola* O. Maurin is provided. *Quisqualis parviflora* is confined to the Eastern Cape and KwaZulu-Natal coastal regions and does not extend beyond this area as has been claimed by some. A comparative table to differentiate among four groups in *Quisqualis* and *Combretum* in Africa, as well as a photo of a herbarium specimen and a distribution map of *Quisqualis parviflora*, are provided.

INTRODUCTION

Quisqualis L., a genus comprising ± 17 species, occurs in Africa, India, Asia (China) and Malesia (Exell 1954; Chen & Turland 2007). It shares a number of morphological similarities with *Combretum* Loeff. subgen. *Cacoucia* (Aubl.) Exell & Stace sect. *Poivreia* (Comm. ex DC.) G. Don. In southern Africa, *Combretum mossambicense* (Klotzsch) Engl. and *C. bracteosum* (Hochst.) Brandis belong to this section. *Quisqualis parviflora* Sond. (Figure 1), the only southern African member of the genus, as well as the latter two species of *Combretum*, are characterized by the absence of epidermal glandular scales and leaves with stalked glands on the petiole, midrib, lateral veins and flowers. Scales are always present in subgen. *Combretum* where they are of considerable taxonomic significance, especially at sectional level (Jordaan *et al.* 2011). Stalked glands, on the other hand, are of little use for resolving sections in subgen. *Cacoucia* as well as in genera such as *Quisqualis* and *Calopyxis* Tul. (Stace 1980). Long unicellular combretaceous hairs (non-glandular, sharp-pointed, thick-walled

with a bulbous base) are present in both subgenera of *Combretum* and in *Quisqualis*.

Hennessy (1991) described the leaf lamina of *Combretum bracteosum* as ‘pellucid-punctate’. This distinctive character has now also been observed in *C. bracteosum*, *C. mossambicense*, *Quisqualis parviflora* and *Q. indica* L. These so-called pellucid dots are abundant, spherical, subepidermal, crystalliferous idioblasts, each containing a large druse of calcium oxalate (Figure 2) (see Tilney 2002). These idioblasts are also quite noticeable in dry material as numerous tiny bumps on one or both lamina surfaces when viewed under a stereo light microscope. *Quisqualis* may have extrafloral nectaries (Tilney & Van Wyk 2004), structures not yet recorded in *Combretum*. Furthermore, *C. mossambicense*, *C. bracteosum* and *Quisqualis parviflora* all have hooked or straight spines derived from persistent petioles by means of which they climb in or over vegetation. The flowers vary from white with long protruding stamens in *C. mossambicense*, bright red in *C. bracteosum*, to greenish with included stamens in *Quisqualis parviflora*. *C. mossambicense* has 5-winged, softly hairy fruits, but those of *C. bracteosum* are quite different in being wingless, hairless and indistinctly 5-angled nuts.

Quisqualis parviflora, according to Carr (1986), has 5-winged fruits. However, we could not find any fruiting material of this species in South African herbaria and it is possible that Carr inferred the fruit morphology from generic descriptions which are based mainly on non-African material. The 4-winged fruit attributed to *Quisqualis parviflora* and depicted in plate 1925 of *The*

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FIGURE 1.—*Quisqualis parviflora*, Ward 9831 in PRE.

Flowering Plants of Africa (Carr 1986) is said to have come from Mariepskop, Mpumalanga. Considering the known distribution of this species in southern Africa (Figure 3), the fruit most probably belonged to a member of *Combretum* and not to *Quisqualis*. Tony Abbott (pers. comm.) has confirmed that he has not seen any fruits on this species in the Umtamvuna Nature Reserve for the last 30 years. As Carr (1986) states, even flowering seems to be a rare event, only a handful of flowering specimens exist in South African herbaria. On the other hand, the paucity of flowering material in herbaria may well be due to the fact that the flowers are inconspicuous and borne in the canopy of tall forest trees well out of the reach of plant collectors. The flowering and reproductive behaviour of *Q. parviflora* is clearly in need of further investigation.

History of the genus *Quisqualis*

The genus *Quisqualis* was established by Linnaeus (1762). Hooker (1867), Lawson (1871) and Brandis (1898) separated *Quisqualis* from *Combretum* on the basis of its elongated, tubular, upper hypanthium which is subterete throughout and not constricted towards the base—a character state absent in typical *Combretum*. They attributed to *Quisqualis* several species from Asia, tropical and southern Africa. Engler & Diels (1900), on the other hand, recognized *Quisqualis* based on the alleged presence of dehiscent fruit, compared to indehiscent fruit in *Combretum*. However, this character proved to be unreliable because many species of *Combretum* have tardily dehiscent fruit.

Exell (1931) proposed a new circumscription of *Quisqualis* and *Combretum* based on the insertion of the style in the upper hypanthium: if the style is adnate to

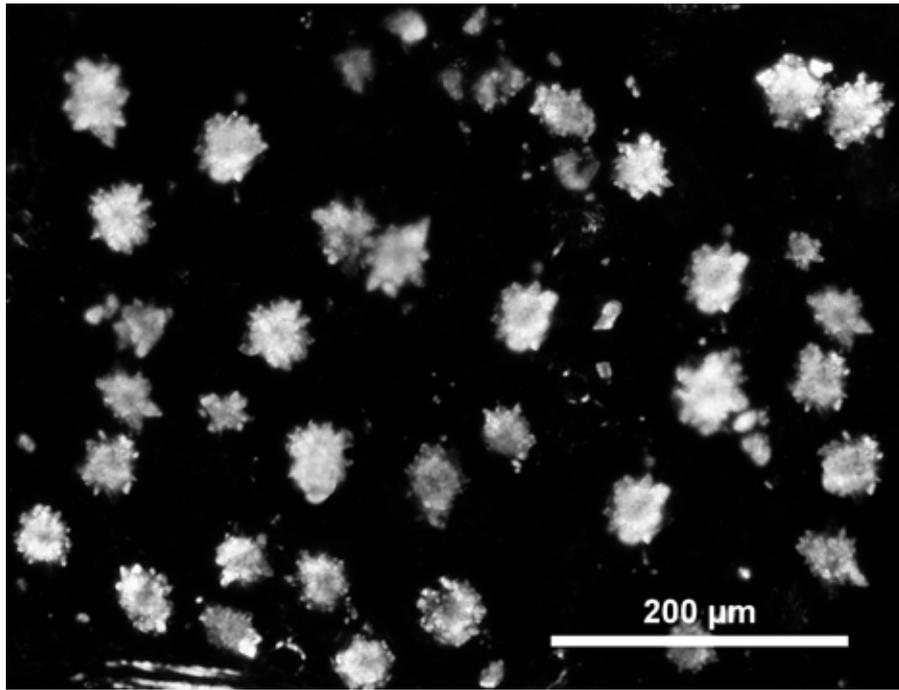


FIGURE 2.—Paradermal section of leaf blade of *Combretum mosambicense* showing subepidermal, crystalliferous idioblasts under polarized light. Each idioblast contains a large druse of calcium oxalate.

the hypanthium, it is a *Quisqualis*. Based on his generic concept, Exell (1931) transferred the following African species to *Quisqualis*: *Combretum hensii* Engl. & Diels, *C. latialatum* Engl. ex Engl. & Diels, *C. littoreum* Engl. and *C. exannulatum* (O.Hoffm.) Engl. & Diels. These species of *Combretum* were earlier classified, together with *C. oxystachyum* Welw. ex M.A.Lawson, in *Combretum* sect. *Campylogyne* (Hemsl.) Engl. & Diels (Engler & Diels 1899). Subsequent to Exell's (1931) new definition of *Quisqualis*, some specimens from tropical Africa classified under *Combretum* were found in which the style is very shortly adnate to the upper hypanthium. To avoid this ambiguity, Exell & Stace (1964, 1966) redefined *Quisqualis* and separated it from *Combretum* by a combination of two characters: 1, adnation of the style to the hypanthium and 2, the non-exsertion of stamens from the flower. Exell & Stace (1964) provided a useful key to distinguish between *Quisqualis* and *Combretum*. Jongkind (1991), on the other hand, proposed the amalgamation of *Quisqualis* with *Combretum* based on the adnation of the style to the upper hypanthium which he encountered in some otherwise undisputed species of *Combretum*. He formally transferred a number of species from *Quisqualis* to *Combretum* (Jongkind 1991, 1992, 1999). Based on leaf anatomical evidence, Tilney (2002) supports the classification of Jongkind (1991). Stace (2007) and Mabberley (2008) follow Jongkind's lumping of the two genera.

Quisqualis in Africa

The style is free from the hypanthium in nearly all species of *Combretum* in Africa and only in a few is there a certain degree of adnation to the upper hypanthium. For example, *C. ghesquierei* Liben from the Democratic Republic of Congo (DRC) has 4-merous (mostly 5-merous in other species) flowers with the style only adnate to the very base of the upper hypanthium, but with long-exserted stamens. Liben (1968) separated this species from all of the other members of *Combretum*

in West Central Africa and placed it in a group of its own. Furthermore, Jongkind (1990) found that the style is fused to the upper hypanthium for more than 2 mm in *C. grandiflorum* G.Don from West tropical Africa (Guinea, Liberia and Sierra Leone, through Ivory Coast to Ghana). It has bright red, 5-merous flowers with the upper hypanthium infundibuliform, 12–20(–25) mm long, glabrous or sparsely hairy, petals 10–15 mm long, glabrous or with few hairs on veins outside, but with the stamens long-exserted. Engler & Diels (1899) placed this species, together with other West African species, in a section of their own, namely sect. *Grandiflorae*, based on the nearly glabrous petals. Stace (1981) placed this section in synonymy with subgen. *Cacoucia* sect. *Poivrea*, a step which seems morphologically poorly supported. Although *C. grandiflorum* also has leaves with abundant crystalliferous idioblasts as in *C. mosambicensis* and *C. bracteosum*, and bright red flowers as in *C. bracteosum*, it has no stalked glands and almost glabrous petals. The petals in the latter two species are densely hairy. With its long-exserted stamens, *C. grandiflorum* still fits better morphologically with *Combretum* than with *Quisqualis*. We suggest it be retained in *Combretum* sect. *Grandiflorae* as proposed by Engler & Diels (1899). Crystalliferous idioblasts in the leaves of *C. grandiflorum* may not be homologous to those in the leaves of members of sect. *Poivrea*, but is perhaps a similarity due to convergence.

Nine species in Africa were at one time or another placed under *Quisqualis* (Liben 1968; Wickens 1973). Six of these are from the most western parts of West Central Africa (Angola, adjacent DRC, Gabon and Cameroon), namely *Q. exannulata* (O.Hoffm.) Exell, *Q. falcata* Welw. ex Hiern, *Q. hensii* (Engl. & Diels) Exell, *Q. latialata* (Engl. ex Engl. & Diels) Exell, *Q. mussaendiflora* (Engl. & Diels) Exell and *Q. pellegriniana* (Exell) Exell. Two species grow along the east coast of Africa, namely *Q. parviflora* in South Africa and *Q. littorea* (Engl.) Exell in Somalia, Kenya and Tanzania. The ninth

TABLE 1.—Comparison of proposed four groups of African *Combretum* and *Quisqualis*. See footnotes for more information on each group

Group	Species	Inflorescence type	Flower		Shape of upper hypanthium	Stalked glands	Scales	Crystal-liferous idioblasts in leaf	Stamen length	Style		
			bracts	maturation (anthesis)						colour	length	orientation
1	<i>Campylogyne exannulata</i>	racemes	large, leafy, along whole axis, $\frac{2}{3}$ length of flower	\pm synchronous	rose-purple	absent	absent	absent	scarcely exerted	well exerted	geniculate	short
2	See footnote	dense subcapitate racemes	large, $\pm \frac{1}{2}$ length of flower, only at base	pronounced acropetal	pale green, yellow and red	present	absent	present	included/scarcely exerted	scarcely exerted	straight	long
3	<i>Quisqualis s.str.</i>	very lax elongated spikes or umbellate	elliptic to linear, along whole axis, much shorter than $\frac{1}{3}$ of flower	\pm synchronous	greenish, white and red	present	absent	present	included	scarcely exerted	straight	long
4	<i>Quisqualis hensii</i> *	dense capitate racemes	$\frac{2}{3}$ length of flower	\pm synchronous	?	present	absent	absent	well exerted	well exerted	straight	short
4	<i>Combretum grandiflorum</i> **	subcapitate racemes	leaf-like, elliptic, $\pm \frac{1}{3}$ length of flower, early caducous	\pm synchronous	bright red	absent	absent	absent	well exerted	well exerted	straight	short
4	<i>Combretum</i> subgen. <i>Cacoucia</i> sect. <i>Poivrea</i> ⁺	subcapitate racemes	leaf-like, ovate, $\pm \frac{1}{3}$ length of flower, early caducous	\pm synchronous	bright red or white tinged pink	present	absent	present	well exerted	well exerted	straight	not
4	<i>Combretum s.str.</i> [•]	elongated or subcapitate spikes or racemes	shorter than $\frac{1}{3}$ of flower	\pm synchronous	yellow, white, red	present or absent	present or absent	absent	well exerted	well exerted	straight	not

Group 1: (= *Quisqualis exannulata*) (Angola, DRC).Group 2: West Central African and East African group: *Combretum inflatum*, *Quisqualis falcata*, *Q. latialata*, *Q. littorea*, *Q. mussaendiflora*, *Q. pellegriniana* (Angola, Gabon, DRC, Nigeria, Cameroon, Tanzania, Kenya, Somalia).Group 3: *Quisqualis parviflora*, *Q. indica* (African form), plus Indian, Asian & Malasian species.Group 4: *(DRC, Gabon); ⁺*Combretum mossambicensis*, *C. bracteosum* (southern & tropical Africa); ** and other members of *Combretum* sect. *Grandiflorae* (Liberia to Ghana); [•](Africa).

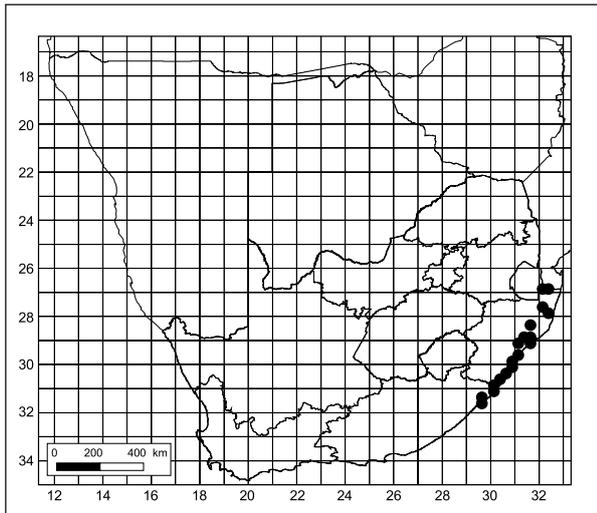


FIGURE 3.—Known distribution of *Quisqualis parviflora*.

species, *Q. indica* L., is reputed to be a native of Asia, but is now widely cultivated as a horticultural subject in the tropics.

In Africa, herbarium specimens attributed to *Quisqualis indica* L. have been recorded from both gardens and the wild in West, East and South Africa. The cultivated Asian form of *Q. indica* has become semi-naturalized in close proximity to human dwellings, such as in the Nairobi Arboretum (e.g. *Williams 396, 529* and *Greenway 1821*, all in PRE). However, a number of herbarium specimens somewhat resembling *Q. indica* were collected from natural habitats (near streams or in damp places) along the woodland escarpment in the Iringa District, Tanzania, e.g. *Lovett & Congdon 1093, 300*, *Taylor et al. 8493* (MO, PRE) and *Greenway & Kanuri 14816, Napper 1685* (PRE). These specimens require further study and may well turn out to be an indigenous African form of *Q. indica*, or a new species. The Tanzanian taxon differs in its petals being well developed, up to 23 mm long with abruptly acuminate apices. *Q. indica* in Asia has petals up to 12 mm long with round to blunt apices. Wickens (1973) noted the differences between the indigenous Tanzanian form and typical Asian *Q. indica*, but refrained from taking any formal taxonomic decisions on the status of the African form. In both forms the flowers are white becoming dark red with age, especially on the inside, whereas the leaves have subepidermal, crystalliferous idioblasts, stalked glands, and combretaceous hairs, with hair-tuft domatia in the axils of veins beneath.

Leaves of *Quisqualis latialata* have black (in herbarium material) stalked glands and combretaceous hairs on both sides, but lack crystalliferous idioblasts; the petals are yellow becoming red with age with a yellow edge; its upper hypanthium is described as cylindrical-infundibuliform, very short, less than 6 mm long; the inflorescence is always terminal, contracted into a dense subcapitate raceme. Leaves of *Q. littorea* also have black stalked glands, combretaceous hairs and hair-tuft domatia in the axils of veins below; the hypanthium is narrowly tubular, up to 20 mm or occasionally up to 25 mm long, petals 6 mm long and apex rounded. *Q. pel-*

legriniana has very thick pubescent young leaves that become puberulous with age and stems with unusual long, flattened, stalked glands mingled with combretaceous hairs, whereas *Q. littorea* and *Q. falcata*, both have almost papery, puberulous leaves. The stamens and styles are included or very slightly exerted in *Q. falcata*, *Q. latialata*, *Q. pellegriniana* and *Q. littorea*, but the first three species have a short (6–10 mm long) upper hypanthium, whereas in *Q. littorea* the hypanthium can be up to 25 mm long. Liben (1968) lowered the rank of *Q. mussaendiflora* (Engl. & Diels) Exell to a variety of *Q. falcata*. Jongkind (1992, 1999) placed *Q. pellegriniana* and *Q. littorea* in synonymy under *Combretum falcatum* (= *Quisqualis falcata*), resulting in two widely disjunct distribution ranges for the expanded *Q. falcata*, a classification not accepted by us because there are slight, though quite marked differences between these taxa. In 1991, Jongkind described *Combretum inflatum* from Gabon, a species with tubular greenish flowers and an adnate style which seems closely related to *Q. falcata* and *Q. latialata*. Jongkind (1999) provided a key and illustration (pl. 14) to show the differences between *C. inflatum*, *Q. falcata* and *Q. latialata*. They all have greenish flowers, conspicuous floral bracts, whereas the leaves have stalked glands, lacking any scales or idioblasts. The inflorescences of these species are dense, congested capitate racemes with few, long, elliptic to falcate floral bracts, the latter best developed towards the base of the inflorescence axis. The inflorescences also display pronounced acropetal maturation, with the flowers opening sequentially over a period of time from the base to the apex. This phenomenon is so far only displayed by these six species. In essentially all other members of *Combretum* and *Quisqualis* in Africa, floral anthesis in any one inflorescence is more or less synchronous.

Quisqualis hensii and *Q. exannulata* have long (up to 20 mm), protruding styles, the latter twice as long as the stamens in *Q. hensii*, a state not found in any other species of *Quisqualis* examined. *Q. hensii* is also the only member of *Quisqualis* with long, exerted stamens. Although *Q. hensii* has the style adnate to the hypanthium for ± 2 mm, stalked glands on the leaves, stems and flower axis, it has flowers with an infundibuliform upper hypanthium, 9–11 mm long. Initially *Q. hensii* was included in *Combretum* sect. *Campylogyne* by Engler & Diels (1899), then transferred to *Quisqualis* sect. *Combretopsis* Exell (1931), provisionally associated with *Combretum* (Exell & Stace 1964) and subsequently placed in a section of its own, namely *Combretum* sect. *Pseudoquisqualis* by Exell (1968) and Stace (1981). Anatomically, *Q. hensii* has a distinctive type of epidermis, discussed in detail by Stace (1965, 1980) as well as an unusual indumentum, namely: a mixture of stalked glands; normal combretaceous compartmented hairs; and on young leaves, thin-walled non-compartmented unicellular hairs. The indumentum is very rare in the family (Stace 1965). Although *Q. hensii* has some adnation of the style to the hypanthium, it still fits better in *Combretum* because of its short upper hypanthium and long-exserted stamens and style (Table 1).

Quisqualis in Asia, Malesia and eastern Africa

The Asian and Malesian species of *Quisqualis*, namely *Q. caudata* Craib, *Q. conferta* (Jack) Exell, *Q.*

parvifolia Exell, *Q. sulcata* Slooten and *Q. indica* L. (Exell 1954) and the East and southern African species (*Q. indica* and *Q. parviflora*) all have tubular hypanthiums from 10–25 mm long or up to 90 mm long in *Q. indica*, with \pm included or shortly exerted stamens and styles. *Q. parviflora* and *Q. indica* have hairs and occasionally stalked glands on the hypanthium, petiole, midrib and lateral veins of the leaves as well as abundant subepidermal crystalliferous idioblasts similar to those in *Combretum mossambicense* and *C. bracteosum*.

A resolution on the taxonomic status of Quisqualis

From the above overview of *Quisqualis* in Africa and Asia, it is obvious that there is a great need for further comparative studies to try and resolve the many uncertainties still prevailing. In our judgement, there is still ample morphological evidence to distinguish between *Combretum* and *Quisqualis*. The two genera can easily be keyed out in southern and East Africa, Malesia (Exell 1954) and China (Chen & Turland (2007). Chen & Turland (2007), for example, separate *Quisqualis* and *Combretum* on the basis of a combination of characters, namely, 1, length of the hypanthium; 2, degree of stamen exertion; and 3, adnation of the style to the hypanthium. If the hypanthium is (17–)50–90 mm long, the stamens are not or scarcely exerted from the hypanthium and the style is partly adnate to the hypanthium, then it is a *Quisqualis*. *Combretum* on the other hand has the hypanthium usually shorter than 20 mm, the stamens usually well exerted from the hypanthium and the style mostly free or shortly adnate to the inside of the hypanthium.

In the case of the few African species of *Combretum* (*C. hensii*, *C. grandiflorum*, *C. ghesquieriei*) where the style is shortly adnate to the hypanthium, the long-exserted stamens and short hypanthiums can still be used to separate these species from *Quisqualis*. These three species can therefore remain in *Combretum*, placed in three different sections in subgen. *Cacoucia* as classified before by Exell (1968) and Stace (1981), Engler & Diels (1899) and Liben (1968), respectively.

We suspect the other six combretaceous species from West Central and East Africa previously placed in *Quisqualis* (Table 1) may well constitute one or more genera of their own. *Quisqualis exannulata* from Angola and the DRC has rose-purple flowers, lacks stalked glands and has leaves without abundant crystalliferous idioblasts. It is most unusual in having a geniculate style which is adnate to the hypanthium and long exerted beyond the petals, whereas the stamens are scarcely exerted. The hypanthium is infundibuliform, slightly curved, 25–35 mm long and has a double constriction, one just above the lower hypanthium and another above the portion where the style bends and becomes free from the hypanthium. The flower bracts are large, leafy, ovate, venose, up to $\frac{2}{3}$ of flower length and present along the whole length of the inflorescence axis, although decreasing somewhat in size towards the apex. It was previously placed in a genus of its own, namely *Campylogyne* by Hemsley (1897), a classification which we support. Differentiation among these four groups in *Quisqualis* and *Combretum* in Africa is presented in Table 1.

Potential shared characters for *Quisqualis s.l.* (if one includes *Q. hensii* and *Q. exannulata* despite their anomalous floral structure), may include the persistent petiole bases that develop into curved spines, petals minutely to densely hairy or pilose, fruits 5-winged or 5-angled, characters also shared with species of *Combretum* subgen. *Cacoucia* sect. *Poivreia*. However, spiny petioles could have evolved independently in these taxa because all are woody climbers or lianas in forest or forest margins where they need to climb over dense vegetation in search of sunlight. It is strongly recommended that all of the taxa mentioned in the above overview be included in future molecular phylogenetic studies.

Molecular phylogeny

Ample leaf and floral morphology (Liben 1968; Exell 1978; Wickens 1973), anatomy (Stace 1965, 1969, 1980; Verhoeven & Van der Schijff 1974; Tilney 2002) and molecular data (Maurin *et al.* 2010) are available for the southern and tropical African species of *Combretum*. Unfortunately, only three species of *Quisqualis*, namely *Q. parviflora* (Africa), *Q. indica* (Asia) and *Q. caudata* (Thailand) have been included in the available molecular studies (Tan *et al.* 2002; Maurin *et al.* 2010). Tan *et al.* (2002) studied the phylogenetic relationships of subfam. Combretoideae (Combretaceae) based on a limited sampling of only two species from each genus. They concluded that *Quisqualis* and *Combretum* are monophyletic sister taxa, but acknowledge that their sampling was insufficient to establish clear generic limits. In subsequent molecular phylogenetic studies based on more comprehensive, though still limited, sampling (Maurin *et al.* 2010), *Quisqualis* as a genus is recovered as a clade embedded within *Combretum* subgen. *Cacoucia*. As a consequence of these results, the third author supports Jongkind (1999), Stace (2007) and Mabberley (2008) in considering *Quisqualis* congeneric with *Combretum*. However, the potentially misleading effects of poor taxon sampling on phylogenetic analyses and their applications should be kept in mind (e.g. Heath *et al.* 2008). To increase the accuracy of phylogenetic estimates in Combretaceae it is strongly recommended that as many as possible of the taxa mentioned in Table 1 be sampled in future studies.

In this paper, however, the first and second authors prefer to retain *Quisqualis* as a separate genus for practical purposes, considering the evolutionary specialization shown by the particular clade. Although there might be intermediate states in the degree of adnation of the style to the upper hypanthium in some species of *Quisqualis* and *Combretum* as noted by Exell & Stace (1966) and Jongkind (1991), there are still enough characters to distinguish between these two genera in East and South Africa and they can easily be keyed out. In *Quisqualis* the upper hypanthium is elongated into a long tube (Figure 1). In *Combretum*, on the other hand, the hypanthium is usually a flattened, short, campanulate, infundibuliform or cupuliform limb above the inferior ovary. In *C. bracteosum* and *C. mossambicense* the upper hypanthium is distally broadly infundibuliform, whereas proximally it is subglobose, the two parts being separated by a slight constriction. Furthermore, in *Quisqualis* the stamens are included or very shortly exerted, whereas in *Combretum* they are always long exerted

(Bredenkamp 2000). The fact that *Combretum* subgen. *Cacoucia* is rendered paraphyletic if *Quisqualis* is maintained as a genus, may be contested by those strictly adhering to Hennigian phylogenetic philosophy, but this is completely acceptable to those prescribing to the more pragmatic evolutionary school of plant classification (Mayr & Bock 2002; Brummitt 2008). Nevertheless, to cater for the alternative point of view, a new combination and new name are provided for *Q. parviflora* below.

Pollination and evolution of adaptive traits in the Combretum–Quisqualis clade

Pollination syndromes have the capacity to predict the types of pollinators of given species based on observations of certain floral traits. To achieve pollination, flowers have evolved suites of convergent floral traits, usually involving flower shape, colour, scent and type of reward (Fenster *et al.* 2004). Stebbins (1970) pointed out that floral diversity has arisen by divergence into different pollination syndromes (evolutionary specialization). In Combretaceae, major adaptations linked to different pollination specializations are evident (Stace 2007). There is, for example, the loss of petals as in *Terminalia*, contrasted with an enlargement of petals in *Quisqualis*. Differences in pollination strategy are most likely responsible for the floral differences between *Combretum* and *Quisqualis*. In the case of *Quisqualis*, the elongation of the hypanthium might represent a modification for pollination by long-proboscid sphingid moths (Stace 2007). This shift towards moth pollination might have occurred independently in different Combretaceae. The white- and yellow-flowered species of *Combretum* with relatively small and reduced petals and with nectaries, suggest pollination by insects with short mouthparts, notably honeybees, whereas those with red flowers and abundant liquid nectar, including the odd-flowered *Quisqualis* (*Campylogene*) *exannulata* are probably bird-pollinated (Faegri & Van der Pijl 1971; Stace 2007). For *Combretum*, this is confirmed by casual observations on the southern African species.

Combretum displays different floral traits indicative of different pollination syndromes and separate evolutionary diversification, patterns supported by molecular (Maurin *et al.* 2010) and morphological data. Some evolutionary trends most probably developed independently within the *Combretum–Quisqualis* clade. In *Combretum* subgen. *Combretum* the leaves all have glandular scales, the flowers have long-exserted stamens, short styles, the colour varies from whitish, yellow or green, the upper hypanthium is short, either little developed and flattened (*C. imberbe* Wawra), campanulate, infundibuliform or cupuliform, all indicative of pollination by insects (Faegri & Van der Pijl 1971).

All species of *Combretum* subgen. *Cacoucia* lack scales on their leaves but have a great diversity in other leaf characters and floral traits. In sect. *Poivreia* the leaves have abundant, subepidermal, crystalliferous idioblasts, stalked glands and flowers with campanulate upper hypanthiums, exserted stamens, pinkish to bright red. In *C.* sect. *Conniventia* the flowers are bright red, with long-exserted stamens and short hypanthiums, suggesting bird pollination. Their leaves lack scales and glands. In sections *Megalantherum* (*C. wattii* Exell) and

Oxystachya (*C. oxystachyum* Welw. ex M.A. Lawson), both endemic to the Kaokoveld (northwestern Namibia and southwestern Angola), the flowers are white or grey-green with a pinkish or reddish tinge and a well-developed nectariferous disc; the leaves are densely pubescent with dark brown stalked glands. The stamens and style are exserted beyond the petals and the upper hypanthium is short.

The flowers of *Quisqualis* in West Central Africa (excluding *Q. hensii* and *Q. exannulata*), East and South Africa as well as India, Asia and Malesia are pendent, ± zygomorphic, white, yellowish to greenish turning red with age; have narrowly tubular hypanthiums slightly widening at the tip, petals and calyx lobes bent backwards; no nectar guides; included styles which are straight and adnate for some distance to the hypanthium; and stamens inserted in two rows with versatile anthers, the latter included or very slightly exserted. This syndrome suggests pollination by long-proboscid insects such as sphingid moths (Exell 1954; Faegri & Van der Pijl 1971). Exell (1954) also noted that the petals in *Quisqualis* are rather large in the family, much exceeding the calyx lobes and enlarging during anthesis.

Distribution of Quisqualis parviflora

Quisqualis parviflora is endemic to South Africa (Bredenkamp 2000; Jordaan 2003, 2006). Van der Schijff & Schoonraad (1971), Carr (1986) and Bredenkamp (2000) give the distribution of *Q. parviflora* as occurring in Mpumalanga (Mariepskop and Graskop), KwaZulu-Natal and Eastern Cape. Subsequently, all the specimens claimed to be *Q. parviflora* in Mpumalanga, were shown to be *Combretum edwardsii* (Verhoeven & Van der Schijff 1975; McClelland 2002). Sterile material collected from more inland localities in KwaZulu-Natal and previously named *Q. parviflora* also belongs to *C. edwardsii* and/or probably an undescribed species of *Combretum*. Therefore, *Q. parviflora* only grows with certainty as a woody climber in mainly coastal forest from Ndumu Game Reserve in the north, through most of KwaZulu-Natal to the Eastern Cape (Port St Johns) in the south (Figure 3). Although no records have been found in Mozambique, it may well occur there, at least in the far south where it borders KwaZulu-Natal (Carr 1986).

Taxonomy of Quisqualis parviflora

Quisqualis has microscopic stalked glands similar to those in *Combretum* subgen. *Cacoucia*, and the scales so characteristic of *Combretum* subgen. *Combretum* are absent (Exell & Stace 1966; Wickens 1973). Flowers are 5-merous and the fruit of *Quisqualis* are generally 5-winged. The petals are well developed in *Quisqualis*: white, pink or red in *Q. indica* (rangoon creeper), a decorative species originally from Asia and commonly cultivated in gardens, and green in the South African *Q. parviflora*. Specimens seen on the Aluka Library website, <http://www.jstor.org/> (accessed December 2010), are distinguished by the code e! in the citations below. Gerrard gave the material he collected with McKen at Umhloti in KwaZulu-Natal the manuscript name, *Quisqualis natalensis* (now the type of *Quisqualis parviflora*). Sonder (1862) changed the epithet 'natalensis' to 'parviflora' and validly published the name *Quis-*

qualis parviflora for the species. Engler & Diels (1900) recorded the name *Quisqualis natalensis*.

***Quisqualis parviflora* Sond.** in *Flora capensis* 2: 512 (1862); Dummer: 232 (1913); Bews: 147 (1921); J.D.Carr: t. 1925 (1986); Pooley: 362 (1993); M.Coates Palgrave: 809 (2002); Boon: 410 (2010). Type: South Africa, Natal [KwaZulu-Natal], 'Nototi' [Umhloti], *Gerrard & McKen s.n.* (TCD, holo. e!; K, iso. e!).

Q. natalensis Gerrard ex Engl. & Diels (1900), nom. nud.

For description see Carr (1986).

Selected specimens examined

KWAZULU-NATAL.—2632 (Bella Vista): Ndumu Game Reserve, Khondo Sand Forest, (–CD), 03-1968, *P. de Moor* 35 (PRE). 2732 (Ubombo): Mkuzi Station, from Ubombo Magistracy to uGaza Mtn, (–CA), 26-04-1944, *J. Gerstner* 4552 (PRE); Hlabisa Dist., False Bay, lower Mzinene River, (–CD), 26-10-1944, *J. Gerstner* 4963 (PRE). 2831 (Nkandla): Eshowe, Memorial Hill, (–CD), 15-05-1951, *J.G. Lawn* 1974 (PRE); Ngoye Forest Reserve, (–DC), 19-11-1993, *R. Williams* 1106 (NH, PRE). 2930 (Pietermaritzburg): Durban, Burman Bush, (–DD), 11-07-1970, *R.G. Strey* 9839 (NH, PRE), Isipingo, Jeffels Hill South, (–DD), 16-02-1966, *C.J. Ward* 5313 (PRE). 2931 (Stanger): Stanger Dist., 4 miles [6.4 km] from Mapumulo to Kranskop, (–AA), 20-01-1966, *E.J. Moll* 2958 (PRE); Mtunzini Forest, (–BA), 17-02-1961, *M. Wells & D. Edwards* 22 (PRE); Inanda Dist., 5 miles [8 km], W of Verulam, (–CA), 15-09-1965, *E.J. Moll* 2083 (PRE). 3030 (Port Shepstone): Vernon Crookes Nature Reserve, (–BC), 15-03-1986, *C.J. Ward* 9831 (PRE); Port Shepstone, Farm Tigerhole, (–CB), 08-08-1965, *R.G. Strey* 5927 (PRE). 3130 (Port Edward): Umtamvuna Nature Reserve, Bululu River, (–AA), 09-04-1981, *H.B. Nicholson* 2171 (PRE).

EASTERN CAPE.—3129 (Port St Johns): Lotana Forest near Ntafufu, (–DA), 11-04-1991, *K.H. Cooper* 283 (NH, PRE); Port St Johns, on road to Agate terrace, (–DA), 10-03-2001, *P.M. Gavhi, P.J.H. Hurter & E. van Wyk* 39 (PRE).

Alternative taxonomic treatment

If *Quisqualis* is sunk under *Combretum*, a new combination and name is required for *Q. parviflora*. The specific epithet 'parviflorum' cannot be used in *Combretum* since it was already used by Reichenbach (1825). Exell (1953) pointed out that *Index kewensis* incorrectly attributes *C. parviflorum* to De Candolle (1828), where it was cited as a synonym of *C. micranthum* Don, a mistake still reflected in The International Plant Name Index (IPNI), accessed January 2011. The name *C. parviflorum* was validly published three years earlier by Reichenbach (1825), thus invalidating *C. parviflorum* Eichler (1867). The latter name was proposed for a species from Brazil, but because it is a later homonym, this species is now known by the new name *C. vernicosum* Rusby (1927).

***Combretum sylvicola* O.Maurin**, comb. et nom. nov.

Quisqualis parviflora Sond.: 512 (1862), non *Combretum parviflorum* Rchb.: 46, t. 62 (1825), nec *C. parviflorum* Eichl.: 114 (1867), nom. illegit. Type: South Africa, Natal [KwaZulu-Natal], 'Nototi' [Umhloti], *Gerrard & McKen s.n.* (TCD, holo. e!; K, iso. e!).

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