Taxonomy of the genus *Keetia* (Rubiaceae—subfam. Ixoroideae—tribe Vanguerieae) in southern Africa, with notes on bacterial symbiosis as well as the structure of colleters and the ‘stylar head’ complex

P.M. TILNEY* and A.E. VAN WYK**

**H.G.W.J. Schweickerdt Herbarium. Department of Plant Science, University of Pretoria, (KMI 2 Pretoria.**

Keywords: Afrocanthium (Bridson) Lantz & B.Bremer, anatomy, bacteria, Canthium Lam., colleters, Keetia E.Phillips, Psydrex Gaertn., Rubiaceae, taxonomy, Vanguerieae

**ABSTRACT**

The genus *Keetia* E.Phillips has a single representative in the Flora of southern Africa region (FSA), namely *K. guieizii* (Sond.) Bridson. The genus and this species are discussed, the distribution mapped and traditional uses indicated. The structures of the calycine colleters, and the ‘stylar head’ complex which is involved in secondary pollen presentation, are elucidated and compared with existing descriptions. Intercellular, non-nodulating, slime-producing bacteria are reported in leaves of *Keetia* for the first time. Differences between the Southern African representatives of *Keetia*, *Psyderax* Gaertn., Afrocanthium (Bridson) Lantz & B.Bremer, and *Canthium* s.str., which for many years were included in *Canthium* s.l., are given.

**INTRODUCTION**

This paper is the first in a planned series on the classification of the *Canthium* s.l. group of the tribe Vanguerieae in southern Africa. This tribe of the Rubiaceae is notorious for the difficulties in resolving generic boundaries. For most of the 20th century the name *Canthium* Lam. was applied in a broad generic sense to a heterogeneous assemblage of taxa in southern Africa (Phillips 1951; Dyer 1975). Pioneering work initiated by Bridson (1985) was followed by several subsequent contributions advocating the recognition of various segregate genera. Evidence in support of the subdivision of *Canthium* s.l. has been forthcoming, amongst others, from anatomy and morphology (Tilney 1986), palynology (Tilney & Van Wyk 1997) as well as comparative molecular studies (Lantz & Bremer 2004). In this contribution we briefly review the generic treatment of *Canthium* s.l., followed by a taxonomic treatment of the genus *Keetia* E.Phillips for the Flora of southern Africa (FSA) region. Notes are also provided on the morphology and anatomy of the calycine colleters and ‘stylar head’ complex in *K. guieizii*, as well as a first report on slime-producing bacteria in the leaves.

**MATERIAL AND METHODS**

Leaves, flowers in various stages of maturity, and fruits were selected for study (see below for voucher specimens). Fresh material was preserved in FAA; dried material was first rehydrated in distilled water and then placed in FAA. Transverse sections of fruits and lamina portions (of healthy leaves including portions with domatia, and of gall-infected leaves), as well as transverse and longitudinal sections of flowers, were prepared by embedding in GMA, sectioning with an ultramicrotome and staining according to the periodic acid–Schiff reaction, with toluidine blue as counterstain (Feder & O’Brien 1968). Slides are housed at JRAU. For scanning electron microscopy, material was examined with a Jeol JSM 5600 scanning electron microscope after being coated with gold. Some sections of the ‘stylar head’ complex were treated with Sudan black and Sudan III to reveal any cutinization.

Voucher specimens (acronyms of herbaria as in Holmgren et al. 1990) are as follows:

Leaves: (lamina structure in t/s): Abbott 70 (PRU), Compton 3155 (PRE), Hafström & Acocks 1929 (PRE), Kok 712 (PRU), Van Wyk & Kok 3888 (PRU); (domatia): Thompson s.n. (JRAU), Tilney 267 (JRAU); (galls): Tilney 266 (JRAU), (stipules): Tilney 156, 267 (JRAU).

Flowers: (light microscopy): Barrows 9558 (BNRH+), Thompson s.n. (JRAU), Tilney 162, 267 (JRAU); (scanning electron microscopy): Thompson s.n. (JRAU).

Fruits: Abbott 70 (PRE), Hemm 454 (PRU), Kluge 25 (PRU), Kok 712 (PRU), Van Wyk 2702 (PRU), Van Wyk & Therom 4568 (PRU).

**GENERIC CONCEPTS**

The tribe Vanguerieae consists of about 600 species largely restricted to sub-Saharan Africa and Madagascar, but some are also found in southern Asia, the Pacific Ocean islands and Australia. Amongst the principal characters shared by members of the Vanguerieae are axillary inflorescences, flowers with corolla lobes valvate and thickened, stamens inserted on the rim of the corolla tube, single pendulous ovules in each locule of the ovary and fruit a drupe with one or more pyrenes. Most notable, however, are the anthers in the bud which are in close contact with a modified portion of the upper style, a so-called ‘stylar head’ complex (Igersheim 1993), where the pollen is deposited and which serves in secondary pollen presentation.

*Canthium* and *Vangueria* Comm. ex Juss. are among the oldest generic names in the Vangueriaceae as currently delimited. The former is partly defined by having two
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locules and the latter five (Lantz et al. 2002). According to Bridson (1985), *Canthium s.l.* was a very heterogeneous group of species and she re-instated the genera *Psydrax* Gaertn. and *Keetia* (Bridson 1986) to accommodate several of the members. The distinctiveness of the leaf and young stem anatomy, pollen morphology and fruit structure of *Keetia gueinzii* (Sond.) Bridson from other southern African species of *Canthium s.l.* was shown by Tilney (1986). Using sequence data from the Internal Transcribed Spacer (ITS) region in the nuclear ribosomal DNA, Lantz et al. (2002) confirmed the separate generic status of *Keetia*. Their study also provided evidence that *Keetia* is one of the best-delimited genera in the Vanguerieae. In further studies, Lantz & Bremer (2004) added *trnT-F* sequences from the chloroplast genome and morphological characters. *Keetia* was again shown to be monophyletic with strong support. Morphologically, *Keetia* species are climbers or scandent shrubs, rarely small trees, have a lid-like area on the pyrenes and, at least in the species examined, smooth retrorse hairs in the corolla tube.

The genus *Psydrax* is weakly supported as monophyletic in a molecular study (Lantz & Bremer 2004), but the species share a number of morphological (Lantz & Bremer 2004) and anatomical (Tilney 1986) synapomorphies. *Psydrax*, the most widely distributed genus of the tribe, is thought to be related to *Keetia* (Bridson 1985, 1986). The southern African representatives of

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**TABLE 1.—Distinguishing characters in southern African species of Keetia, Afrocanthium, Canthium s. str and Psydrax**

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>Habitat</td>
<td>On forest margins</td>
<td>On rocky ridges, may also occur in forest; often in small groups</td>
<td>Variety of habitats although individual species may have restricted distribution</td>
<td>In bushveld or other regions with some individual species having a restricted distribution</td>
</tr>
<tr>
<td>Growth form</td>
<td>Robust climber or scrambling shrub</td>
<td>Tree or shrub</td>
<td>Tree or shrub</td>
<td>Tree or shrub</td>
</tr>
<tr>
<td>Duration</td>
<td>Evergreen</td>
<td>Usually deciduous</td>
<td>Usually deciduous</td>
<td>Usually evergreen</td>
</tr>
<tr>
<td>Spines</td>
<td>Absent</td>
<td>Absent</td>
<td>Present but may be mainly associated with coppice growth</td>
<td>Absent</td>
</tr>
<tr>
<td>Young plant parts</td>
<td>Covered in ginger-brown hairs</td>
<td>With whitish hairs</td>
<td>Glabrous</td>
<td>Glabrous or with whitish hairs</td>
</tr>
<tr>
<td>Side branches</td>
<td>Often subtended by smaller rotund leaves</td>
<td>Not subtended by smaller rotund leaves</td>
<td>Not subtended by smaller rotund leaves</td>
<td>Not subtended by smaller rotund leaves</td>
</tr>
<tr>
<td>Leaves</td>
<td>length of blade</td>
<td>At least 70 mm but usually considerably more</td>
<td>Considerably less than 70 mm</td>
<td>Considerably less than 70 mm</td>
</tr>
<tr>
<td></td>
<td>texture</td>
<td>Thinely textured, ± leathery</td>
<td>Soft and easily wilting</td>
<td>Generally stiff and leathery</td>
</tr>
<tr>
<td></td>
<td>base</td>
<td>Usually subcorolate to corolate</td>
<td>Frequently tapering</td>
<td>Frequently tapering</td>
</tr>
<tr>
<td></td>
<td>stipules</td>
<td>Not keeled; without hair tufts inside</td>
<td>Usually slightly keeled; without hair tufts inside</td>
<td>Keeled, usually strongly so; without hair tufts inside</td>
</tr>
<tr>
<td></td>
<td>Domatia</td>
<td>Tufts</td>
<td>Tufts, or pits sometimes with small hairs</td>
<td>Pits, pockets or domes with opening at top, sometimes with hairs</td>
</tr>
<tr>
<td>Flowers</td>
<td>In dense shortly-pedunculate clusters in leaf axils</td>
<td>Usually in small shortly-pedunculate clusters, rarely in dense clusters in leaf axils</td>
<td>Solitary or in small shortly-pedunculate clusters, occasionally in dense clusters in leaf axils</td>
<td>Usually in small shortly-pedunculate clusters, occasionally in dense clusters in leaf axils</td>
</tr>
<tr>
<td>Anthers</td>
<td>Fully exerted but rarely reflexed</td>
<td>Partially to fully exerted but never reflexed</td>
<td>Often only partially exerted and not reflexed</td>
<td>Exserted and usually reflexed</td>
</tr>
<tr>
<td>Style</td>
<td>length</td>
<td>At least twice length of corolla tube</td>
<td>Slightly longer than corolla tube</td>
<td>Usually somewhat longer than corolla tube (in <em>C. kuntzeanum</em> ± as long)</td>
</tr>
<tr>
<td></td>
<td>head</td>
<td>Distinctly longer than wide</td>
<td>Usually ± as long as wide</td>
<td>Usually wider than long</td>
</tr>
<tr>
<td></td>
<td>Fruit</td>
<td>Globose</td>
<td>± globose, but remiform when single-seeded</td>
<td>± globose</td>
</tr>
<tr>
<td></td>
<td>size</td>
<td>Relatively large</td>
<td>Relatively small</td>
<td>Varies from relatively small to relatively large</td>
</tr>
<tr>
<td></td>
<td>pyrene</td>
<td>With clear lid-like area across apex</td>
<td>Without clear lid-like area across apex</td>
<td>Without clear lid-like area across apex</td>
</tr>
<tr>
<td></td>
<td>apical indentation</td>
<td>2-seeded fruit strongly or slightly indented</td>
<td>2-seeded fruit strongly or slightly indented</td>
<td>2-seeded fruit not or scarcely indented</td>
</tr>
<tr>
<td></td>
<td>Seed: endosperm</td>
<td>Streaked with resinous granules</td>
<td>Not streaked with resinous granules</td>
<td>Not streaked with resinous granules</td>
</tr>
</tbody>
</table>

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Psydrax and other taxa, at one time called ‘Canthium’, will be discussed in future contributions. The genera Psydrax and Keetia are compared in Table 1.

Bridson (1987) divided the African Canthium species into four subgenera, one of which is Canthium subgenus Afrocanthium Bridson (Bridson 1987, 1992). The molecular studies of Lantz & Bremer (2004) also support Canthium subgenus Afrocanthium as being monophyletic and this subgenus was therefore given generic rank. Although Keetia and Afrocanthium (Bridson) Lantz & B.Bremer were strongly supported as sister taxa in these studies, the authors point out that the morphology gives little indication of this relationship—apart from a lack of white silky hairs inside the stipules of both K. gueinzii and Canthium mundianum (Lantz & Bremer 2004: 274), but this character is shared with many other Vanguerieae genera (Bridson 1998). In characterizing Afrocanthium, Lantz & Bremer (2004) point out that it is geographically restricted to eastern and southern Africa (see Bridson 1992, Map 3). As a genus, Afrocanthium is further distinguished by the absence of a dark connective on the stamens, inflorescences borne at nodes from which the leaves have fallen, lenticels usually visible, and very short calyx limb tubes (Lantz & Bremer 2004). A comparison between southern African species of Afrocanthium and Keetia incorporating other characters is given in Table 1.

The elevation of Canthium subgenus Afrocanthium to generic level as Afrocanthium has assisted in lessening the heterogeneity of the remaining Canthium s.l. species, at least in southern Africa, but the latter still remains polyphyletic (Lantz & Bremer 2004). These researchers suggested that the genus Canthium s. str. should essentially be restricted to thorny members, i.e. those having paired, usually supra-axillary thorns. Also included in their concept of Canthium s. str. is the genus Plectronia Robyns, a segregate based on the southern African P. armata (K.Schum.) Robyns, a species with the ovary plurilocular (the other taxa are bilocular). Since thorns are erratically present in some southern African members of the group, e.g. C. inerme (L.f.) Kuntze and C. suberosum Codd, this diagnostic character is more accurately expressed as having the potential to produce thorns. In the last-mentioned two species, thorns are either absent in some plants, or produced in juvenile plants or sucker shoots only. This is the sense in which Canthium s. str. has been used in Table 1. Note, however, that these spiny southern African species were kept as Canthium s.l. by Bridson (1992), as in her opinion they did not fully accord with the type of Canthium, namely C. coromandelicum (Burm.f.) Alston, from India.

**TAXONOMIC TREATMENT**


Plectronia sensu auctt. div., non L.

The generic description below is for the genus as a whole and is largely based on Bridson (1986, 1998).

Climbers or scrambling shrubs, rarely small trees, evergreen; stems glabrous or frequently pubescent. Leaves not confined to new growth at ends of branchlets, petiolate, opposite, simple, margin entire; lamina chartaceous or occasionally coriaceous; those leaves subtending lateral branchlets often smaller and broader than main ones; stipules interpetiolar, lanceolate to ovate or triangular at base, not keeled, usually without white silky hairs inside. Inflorescences axillary, pedunculate and usually distinctly branched cymes; bracts and bracteoles often conspicuous. Flowers bisexual, 4–6-merous. Calyx with segments ± equal to or sometimes longer than tube. Corolla whitish or yellow, cylindrical, tube with a ring of deflexed hairs, throat often pubescent or bearded, lobes usually ± same length as tube, curving well backwards, often thickened towards apex. Stamens 5, attached in corolla throat; filaments moderately well developed; anthers partly or fully exerted, usually not reflexed, narrowly ovate or oblong. Disc nearly always puberulous to pubescent. Ovary 2-locular, with single ovule per locule, attached above middle of septum; style slender, ± twice length of corolla tube; stigmatic knob (‘stylar head’ complex) cylindrical, conspicuously longer than wide, hollow to mid-point or to just below apex, apex slightly bifid at maturity. Fruit a 2-seeded drupe or often 1-seeded by abortion and asymmetric, slightly to strongly 2-lobed, somewhat laterally flattened, variously indented at apex, dark when mature; pyrenes woody or less often cartilaginous, usually ± ovoid with ventral face flattened, somewhat colliculose, point of attachment either on ventral face shortly above centre or near apex; lid-like area completely or incompletely defined (but more clearly apparent from inside), either lying along ventral face above point of attachment, or across apex, provided with a central crest, presumably deliscent around circumference on germination. Seed ovoid, shaped at apex according to position of lid-like area in pyrene, convoluted; endosperm streaked with patches of resinous granules (resembling a ruminate endosperm except that testa is never invaginated), or less often with resinous granules evenly dispersed or absent; testa thin, very finely reticulate; embryo straight with radicle erect, and small cotyledons lying parallel to ventral face of seed.

A genus of ± 40 species, occurring in southern and throughout tropical Africa. Named after J.D.M. Keet (1882–1976), a South African forester and plant collector (Gunn & Codd 1981). Represented by Keetia gueinzii in the FSA region, a species common and widespread in Africa. K. venosa (Oliv.) Bridson is the only other species in southern Africa; it has been reported from Zimbabwe and Mozambique.

Note: Gueinzius 71.576, as cited in Sonder (1850), is a typographical error; the full stop should be a comma, thus indicating two different gatherings. The other syntype, Gueinzius 71, could not be traced, unless this is the same as Gueinzius s.n. cited by Bridson (1986) as holotype, but considering the aforementioned comment, it should be a syntype.

Canthium gueinzii Sond. 54 (1850); Sond.: 16 (1865); Moore 40: 89 (1911); Bullock: t. 3170 (1932a); Bullock: 368 (1932b); Henkel: 147 (1934); Dale & Greenway: 428 (1961); White: 403 (1962); Palmer & Pitman: 2093 (1972); Compton: 580 (1976); Coates Palgrave: 881 (1977).

Plectronia gueinzii (Sond.) Sim: 241 (1907); Eyles: 493 (1916); Bews: 198 (1921).


K. transvaalensis E.Phillips: 369 (1927), p.p., excluding syntypes Schlechter 12290 [PRE!], K. venosa (Oliv.) Bridson] and Borle 293 [PRE!]; K. zanzibarica (Klotzsch) Bridson subsp. cornelioides (De Wild.) Bridson. Type: South Africa, Transvaal, Barberton, woody ravines, Galpin 519 (lecto:!, PRE, iso.!).


Robust climber or scrambling shrub, rarely a small tree ± 3 m high; main stem faintly 4-angled, becoming dark brown to almost black, smooth to finely rough; branches long and trailing, with slender branchlets almost at right angles and sometimes slightly bending backwards, sparsely to densely covered with fine, brownish hairs; unarmed. Leaves oblong-lanceolate to ovate, 40–135 × 28–60 mm but those subtending lateral branches much smaller and often almost round, rather thinly textured, glossy dark green, usually drying brown, glabrous or very sparsely hairy adaxially, abaxially somewhat paler with sparse or dense rough hairs particularly on 6–9 pairs of lateral veins, with fine net-veining and hair-tuft domatia (Figure 1A, B); apex attenuate; base usually subcordate to cordate or sometimes rounded to truncate; margin slightly rolled under; petiole 3–13 mm long, hairy; stipules conspicuous, lanceolate to ovate, tapering to a point, 9–13 mm long, up to 6 mm wide at base, densely hairy on both surfaces but particularly on midrib where hairs longer and with tanniniferous substances when very young, becoming more sparsely hairy with most hairs confined to abaxial midrib when mature (Figure 2A, B), yellowish, falling early. Inflorescence in dense 20–50-flowered, branched axillary cymes; peduncle 5–15 mm long, at least initially pubescent; pedicels 3–7 mm long, pubescent to densely pubescent; bracteoles, linear-lanceolate to lanceolate, 3–6 mm long, hairy. Flowers usually produced in profusion, sweetly scented. 5-merous. Calyx with tube campanulate, 1–2 mm long, usually pilose below, glabrous above; calyx-limb obtuse, up to ± 1.5 mm long, divided into teeth for ± half its length, usually sparsely pilose to glabrescent and ciliate at apex; colleters present on adaxial surface, usually between calyx lobes, singly or in pairs, ± squashed (Figure 2C–E). Corolla white at anthesis, fading to cream-coloured or pale yellow; tube 2.2–5.0 mm long, gradually widening upwards, glabrous without, with erect hairs at throat and deflexed hairs.

FIGURE 1.—Keetia gueinzii. A, hair-tuft domatia with a mite arrowed (Thompson s.n.); B, t/s of part of leaf showing domatia and vascular tissue of midrib in form of an arc with invaginated ends (Tilney 267); C, D, Tilney 266; C, portion of adaxial surface of leaf showing galls; D, t/s of midrib area and two galls. Scale bars: A, 1 mm; B, 400 μm; C, 4 mm; D, 700 μm.
inside below throat; lobes spreading, oblong-lanceolate to ovate, 2.3-4 × 1.2-2.3 mm, apex acute and thickened. Stamens adnate to corolla throat; filaments erect, 1.5-2.0 mm long; anthers fully exserted, ± erect, 3 × 1 mm, brown and shriveled at anthesis. Disc plane, ± 0.5 mm wide, pubescent. Ovary with style linear, gradually tapering upwards, 5-10 mm long, pale green, glabrous; pollen presenter pale green, covered with yellow pollen, 1.8-2.3 × 1.5 mm (Figures 3A, C–F; 4). Fruit single or 2-lobed, broadly oblong to roundish, 9-14 × 7-14 mm, slightly indented, in dense, short-branched clusters, turning blackish, nearly always pubescent when immature becoming glabrous or very rarely possessing few hairs largely restricted to base in vicinity of pedicel; pyrene with lid-like area across apex. Seed with cotyledons orientated parallel to ventral face of seed; endosperm with tanniniferous intrusions (Figure 5). Flowering time: September to November. Fruiting time: October to May.

Etymology: the specific epithet commemorates Wilhelm Gueinzius (1814–1874), a German apothecary and naturalist who lived in KwaZulu-Natal from 1841 until his death (Gunn & Codd 1981; Hedge 1993).
Common names: rankklipels, rankhokdrol (Afrikaans); climbing turkeyberry, climbing keetia, climbing canthium, monkeyberry (English); mudanhashoko, mudanhanashoko, umhlalalelingonyama (Ndau); mokhutswane (Northern Sotho); ugupe, sinwati (Swazi), muthambeni (Venda); umnyushulube (Xhosa); ibinda, ugupe, umnyisi (Zulu).

Diagnostic features: in southern Africa this species has ginger-brown trichomes on the young plant parts, and also on the midrib and smaller veins on the abaxial sides of mature leaves, and petioles, pedicels and calyx lobes. The leaves are oblong-lanceolate to ovate with usually subcordate to cordate bases. The lamina is fre-
quently at least 70 mm long, being glossy and glabrous adaxially. Stipules are conspicuous, lanceolate to ovate and sharply pointed. Hair-tuft domatia (Figure 1A, B) are associated with the axils of most major secondary veins.

**Pollination syndrome:** although secondary pollen presentation is a rather common phenomenon in the Rubiaceae, the presentation of pollen by a 'stylar head' complex (Igersheim 1993) to a pollinator is a unique characteristic of the tribe Vanguerieae (Lantz et al. 2002). Skottsberg in 1945 described the general anatomy of this 'style-head'. The structure consists not only of stylar tissue but also of the stigmatic lobes and forms a swollen globose to cylindrical structure at the apex of the style into which the style is recessed (Figures 3A; 4C). In buds of *Keetia gueinzii*, the 'stylar head' complex forms ridges which fit into grooves between the two thecae of each anther and between adjacent anthers; there are thus ten ridges and ten grooves (Figure 3F). Just prior to the bud opening, the style elongates considerably, even rarely forming a loop so that the stigmatic surfaces are in close proximity to the corolla throat (Fig-
ure 3E). The style and 'stylar head' complex is pale to bright green, the latter covered by yellow pollen. Floral structure suggests pollination by night-flying moths, but this needs confirmation, especially since pollination by beetles has also been suggested.

The 'stylar head' complex of *Keetia gueinzii* was studied using light (in t/s and 1/s sections) and scanning electron microscopy (Figures 3; 4). The anatomy of this structure in *K. gueinzii* resembles that of *K. zanzibarica* (Klotzsch) Bridson subsp. *zanzibarica* and three species of *Vangueria* (Igersheim 1993) in the unusual elongated epidermal cells of the 'receptaculum pollinis' with circular thickenings towards the outer tangential walls, abundant tanniniferous cells and conspicuous transmitting tissue in the style (Figure 3F; 4E). However, the lobed nature of the outer tangential portions of many of the elongated epidermal cells (Figure 4D, F) is a conspicuous feature not commented on previously, but visible in published photographs of longitudinal sections of *K. zanzibarica* subsp. *zanzibarica* (Igersheim 1993). In *K. gueinzii*, these elongated epidermal cells are densely cytoplasmic, especially distally, and droplet-like structures were frequently observed (Figure 4F). These cells are likely to produce a secretion to enable pollen grains to adhere to them. Sections were tested with Sudan black and Sudan III and the outer walls were found to be cutinized. A thicker cuticle was observed over the ridges than in the grooves. In transverse section, it can be seen that those cells forming the longitudinal ridges of the 'stylar head' complex are longer than those in the grooves (Figure 4E, F). The circular thickenings are responsible for the bicellular appearance of many of the cells (Figure 4E, F).

**Anatomy**: detailed descriptions of the leaf (petiole, midrib and lamina) and stem anatomy, together with comparisons with other members of *Canthium s.l.*, are given in Tilney (1986) and Tilney et al. (1988, 1990). Hairs, present on leaves, young stems, peduncles, pedicels and calyx lobes, are characteristically long, multicellular and highly tanniniferous. They are usually inserted within a raised cluster of small epidermal cells. Hair-tuft domatia in which these hairs extend into the cavity of the domatium are shown in transverse section (Figure 1B). Different species of mites, of which one is shown in Figure 1A, were readily observed associated with them. In the petiole and midrib, the main vascular bundle is a distinctive arc with invaginated ends (Figure 1B). The first-formed periderm in stems originates cortically and in segments. Wood anatomy of some species, including *Keetia corneliana* (Cham. & Schltdl.) Bridson, *K. cf. gueinzii* (Sond.) Bridson and *K. cf. hispida* (Benth.) Bridson, is covered by Lens et al. (2000). All the features of the wood anatomy of these three taxa correspond with those of other members of the tribe Vanguerieae. The secondary xylem has been found to be homogeneous in this tribe.

Intercellular spaces in the mesophyll of healthy mature leaves may contain abundant non-nodulating, slime-producing bacteria (Figure 2F), here reported in
a member of *Keetia* for the first time. Hitherto this particular form of bacterial symbiosis was known only in the rubiaceous genera *Pachystigma* Hochst. and *Fadogia* Schweinf. (Van Wyk et al. 1990), both belonging to the Vangueriaceae. The presence of these seemingly nonpathological bacteria, the functional significance of which remains a mystery, is easily overlooked in anatomical studies and their presence should be checked in other Rubiaceae.

Colleters are present, usually singly or in pairs (the so-called ‘alternate’ pattern of Simões et al. 2006), on the adaxial surface of the calyx usually between the calyx lobes (Figures 2C–E; 3B, D). They form as emergentia from the calyx lobes (Figure 2F). The main body (termed a ‘head’ by Thomas 1991) is undivided and is attached by means of a short stalk. Colleters are of the ‘standard’ type of Lersten (1974a, b), being composed of columnar epidermal cells not separated from each other and having a central parenchymatous axis. Epidermal cells have dark-staining materials adjacent to the cell walls (Figure 2C). During maturation of the colleters, the epidermal cells become more densely cytoplasmic and columnar. Colleters were not observed on the stipules. These secretory structures occur in a large number of rubiaceous species where they are usually associated with the stipules. They are believed to protect the developing shoot apex although other functions have been ascribed to them (e.g. Klein et al. 2004).

As mentioned above, valvate aestivation of the corolla lobes is a character of the tribe Vangueriaceae. Furthermore, the margins of the lobes are thickened and usually thicker towards the apex. During development of the buds of *Keetia gueinzii* it was observed that the future epidermal cells, in the position where separation of the corolla lobes will take place at anthesis, initially elongate and interlock (Figure 3G, H). The outer periclinal cell walls of these cells gradually become thickened and striate, and a cuticle is deposited. Both these processes appear to facilitate the separation of the cells giving an ‘unzipping’ appearance.

**Palynology:** pollen is a pale yellow. SEM and TEM studies of southern African specimens (Tilney 1986; Tilney & Van Wyk 1997) revealed the following taxonomically significant characteristics of the pollen grains: a length (P) of (36-)40-45 μm, diameter (E) of 40-50 μm, suboblate to spheroidal shape, circular apertures, coarsely reticulate exine 2.6-4.2 μm thick with a sexine: nexine (S:N) of S = ± 2× N, tectum thickness of 0.6-0.8 μm, suboblate to spheroidal shape, circular apertures, and columnar. Colleters were not observed on the stipules. These secretory structures occur in a large number of rubiaceous species where they are usually associated with the stipules. They are believed to protect the developing shoot apex although other functions have been ascribed to them (e.g. Klein et al. 2004).

**Distribution and habitat:** occurs in Limpopo, Mpumalanga, Swaziland, KwaZulu-Natal and Eastern Cape (Figure 6), also northwards in Africa to Cameroon and Ethiopia. With *Keetia venosa,* it shares the distinction of being one of the most widespread species of *Keetia* in Africa. It is often locally common, occurring at the margins of and in evergreen forest and thickets, and in swamp forest.

**Ecological significance and ethnobotany:** used as knob-sticks in Swaziland (Dlamini 1981). Fruits are edible but astringent (Coates Palgrave 2002) and specifically eaten by the Luvalve people (Watt & Breyer-Brandwijk 1962). Peters et al. (1992) also quote reports of fruits being eaten by baboons and chimpanzees as well as leaves and cambium by the latter. The Luvalve use this species medicinally but no details are available (Watt & Breyer-Brandwijk 1962). The Swazi use the root medicinally (Dlamini 1981). Neuwinger (2000) refers to authors reporting that the leaves are pounded in a little water and the liquid drunk for epilepsy. Also, for hydrocele, a leaf infusion is drunk and used as a wash and, for colic, abdominal pain and nausea especially during pregnancy, and intestinal parasites, a leaf decoction is drunk. An extract of *Keetia hispida* (Benth.) Bridson has shown strong activity against Gram +ve bacteria (Koné et al. 2004).

A population heavily infested with galls has been recorded and a portion of a leaf showing these structures macroscopically and in transverse section is shown in Figure 1C, D respectively. In southern Africa the following ascomycete fungal pathogens have been recorded on *Keetia gueinzii* (Doidge 1950): *Balladyna temus* Hansf., *B. velutina* (Berk. & M.A.Curtis) Höhnh., *Balladynocallia glabra* (Hansf.) Bat. (= *Balladynastrum glabrum* Hansf.) (all Parodiopsidaceae) and *Meliola littoralis* Syd. (Meliolaceae).

**SPECIMENS EXAMINED**
(FS4 region only)

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Herbarium</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abbott 70 PRE</td>
<td>37°9′, 34°7′25′</td>
<td>PRU. Acocks 10957, 11805 PRE.</td>
</tr>
<tr>
<td>Balkwill &amp; Cadman 2016 PRE</td>
<td>Barnard &amp; Mogg 17424 PRE.</td>
<td>Borchards 55 PRE. Bortha 2949, 3470, s.n. herb. No. 6071 PRE. Bower 9212 PRE. Brand, Bosch, Logie, Venter 342 PRE. Bredenkamp 1369 PRE.</td>
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