

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

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ABSTRACT

The genus *Keetia* E.Phillips has a single representative in the *Flora of southern Africa* region (FSA), namely *K. gueinzii* (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 a *Keetia* for the first time. Differences between the southern African representatives of *Keetia*, *Psydrax* 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. gueinzii*, 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 tolui-

dine 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 *vs*): *Abbott 70* (PRU), *Compton 3155* (PRE), *Hafström & Acocks 1929* (PRE), *Kok 712* (PRU), *Van Wyk & Kok 5888* (PRU); (domatia): *Thompson s.n.* (JRAU), *Tilney 267* (JRAU); (galls): *Tilney 266* (JRAU); (stipules): *Tilney 156, 267* (JRAU).

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

Fruits: *Abbott 70* (PRE), *Hemm 45A* (PRU), *Kluge 25* (PRU), *Kok 712* (PRU), *Van Wyk 2702* (PRU), *Van Wyk & Theron 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 Vanguerieae as currently delimited. The former is partly defined by having two

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+ temporary acronym: Buffelskloof Nature Reserve Herbarium, Lydenburg.

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

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

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

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 *Afrocanthium 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 *Plectroniella* 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

Keetia E. Phillips in *Memoirs of the Botanical Survey of South Africa* No. 10: 587 (1926); E. Phillips: 369 (1927); Bridson: 967 (1986); Bridson: 362 (1998); Retief & Leistner: 487 (2000). Type: *K. transvaalensis* E. Phillips, now included in *K. gueinzii* (Sond.) Bridson.

Canthium sensu Sond.: 16 (1865) p.p., non Lam.; Hiern: 132 (1877) p.p.; Bullock: 360 (1932) p.p.; Phillips: 732 (1951) p.p.; Hepper: 180 (1963) p.p.; Dyer: 618 (1975) p.p.

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 \pm 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 \pm 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, \pm 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 \pm 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 dehiscent 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 ruminant 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 \pm 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.

Keetia gueinzii (Sond.) Bridson in *Kew Bulletin* 41: 970 (1986); Bridson: 911 (1992); Pooley: 478 (1993); Bridson: 363 (1998); Van Wyk & Van Wyk: 280 (1997); Tilney: 37 (2002), 19 (2003a), 28 (2003b); Coates Palgrave: 1101 (2002); Schmidt et al.: 628 (2002). Type: South Africa, Port Natal, *Gueinzium* 576 (P sheet P00551153!, lecto., here designated; sheet P00551152!, iso.).

Note: *Gueinzium* 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, *Gueinzium* 71, could not be traced, unless this is the same as *Gueinzium* 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).

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

K. gueinzii Von Breitenbach: 91 (1985), nom. invalid.

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 (K, lecto. !; PRE, iso.!).

Illustrations: Bullock: t. 3170 (1932a); Gibson: plate 102, 6 (1975); Bridson: 969, fruit (1986); Bridson: 358, fruit (1991); Pooley: 479 (1993); Van Wyk & Van Wyk: 281 (1997); Bridson: 364 (1998); Schmidt et al.: 629 (2002).

Robust climber or scrambling shrub, rarely a small tree \pm 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 \times 28–60 mm but those subtending lat-

eral 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 tanniferous 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 \pm 1.5 mm long, divided into teeth for \pm 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, \pm 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

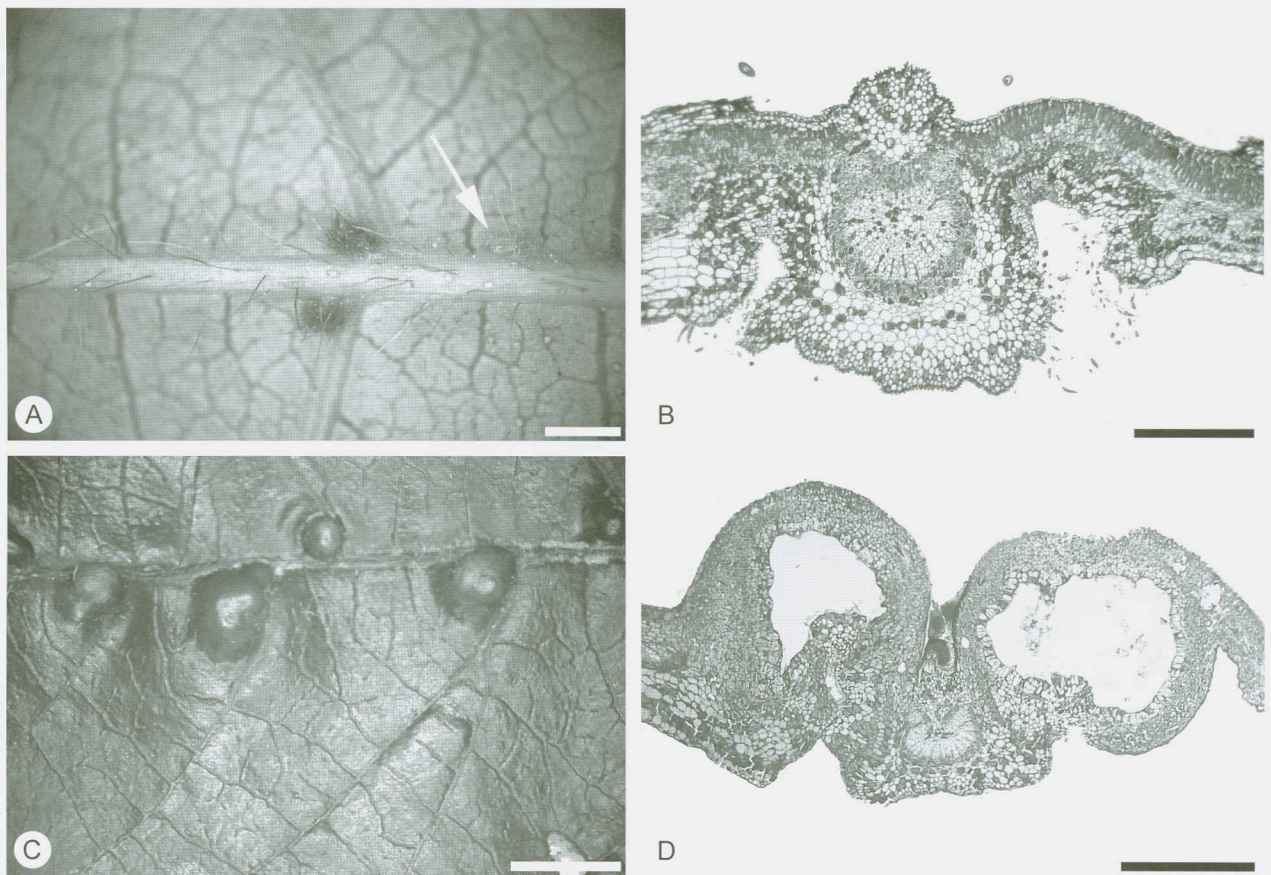


FIGURE 1.—*Keetia gueinzii*. A, hair-tuft domatia with a mite arrowed (*Thompson* s.n.); B, t/s of part of leaf showing domatia and vascular tissue of midrib in form of an arc with invaginated ends (*Tilney* 267). C, D, *Tilney* 266: C, portion of adaxial surface of leaf showing galls; D, t/s of midrib area and two galls. Scale bars: A, 1 mm; B, 400 μ m; C, 4 mm; D, 700 μ m.

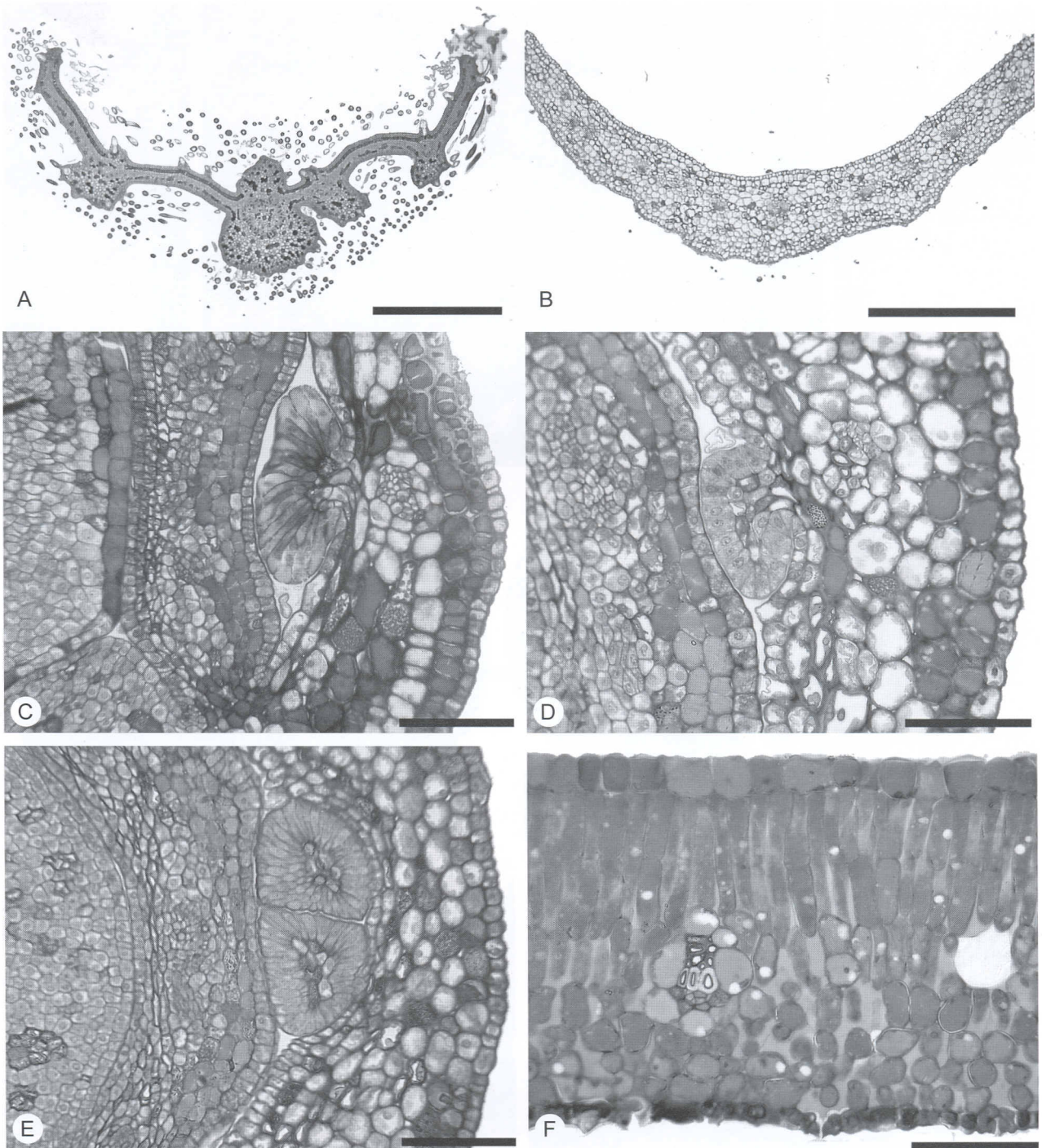


FIGURE 2.—*Keetia gueinzii*. A, *t/s* of very young stipule with abundant hairs on both surfaces (Tilney 156); B, *t/s* of portion of mature stipule showing sparse hairs mainly on abaxial surface (Tilney 267). C–E, Tilney 267: C, *l/s* of portion of bud showing calycine colletelium; D, colleters can clearly be seen to form as emergentia from sepals; E, *t/s* of portion of bud in which two calycine colleters are visible. F, *t/s* of portion of lamina with slime-producing bacteria filling most of intercellular spaces (Van Wyk & Kok 5888). Scale bars: A, B, 700 μ m; C–E, 100 μ m; F, 70 μ m.

inside below throat; lobes spreading, oblong-lanceolate to ovate, 2.3–4 \times 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, \pm erect, 3 \times 1 mm, brown and shriveled at anthesis. *Disc* plane, \pm 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 \times 1.5 mm (Figures 3A, C–F; 4). *Fruit* single or 2-lobed, broadly oblong to roundish, 9–14 \times 7–14 mm, slightly indented, in dense, short-branched clusters, turn-

ing 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 tanniferous intrusions (Figure 5). *Flowering time*: September to November. *Fruiting time*: October to May.

Etymology: the specific epithet commemorates Wilhelm Gueinzus (1814–1874), a German apothecary and naturalist who lived in KwaZulu-Natal from 1841 until his death (Gunn & Codd 1981; Hedge 1993).

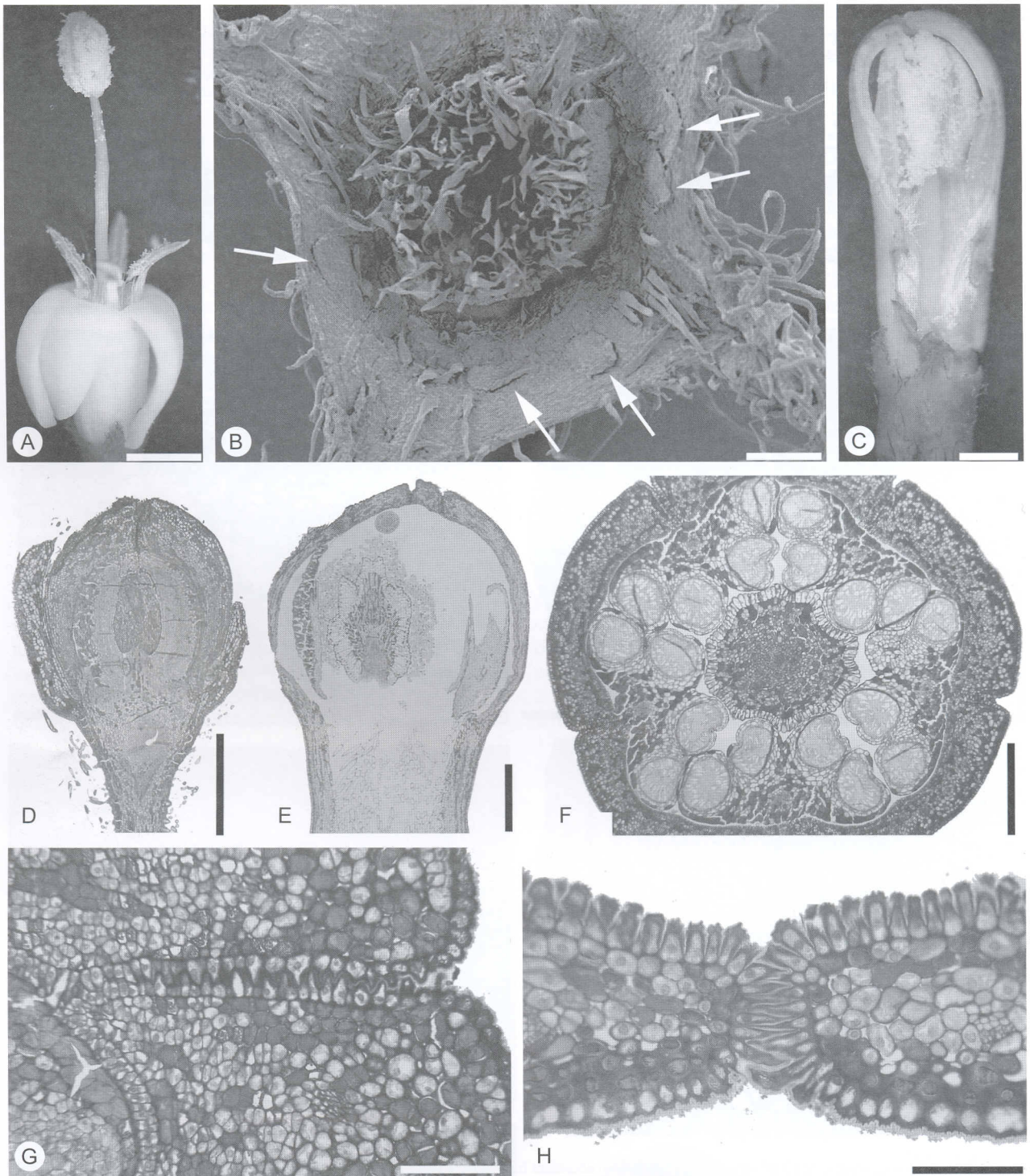


FIGURE 3.—*Keetia gueinzii*. A–C, *Thompson s.n.*: A, flower showing characteristic secondary pollen presentation and hairs concentrated on sepal lobes; B, SEM micrograph showing appearance and position (singly or in pairs) of calyxine colleters (arrowed), and pubescent disc; C, young bud showing pollen already deposited on 'stylar head' complex, closed stigma lobes and downwardly directed hairs in corolla tube. D, *l/s* of young bud showing flower structure and calyxine colleter (*Tilney 267*); E, *l/s* of bud just prior to opening showing rare condition where style is looped such that stigma is near corolla throat (*Thompson s.n.*). F, G, *Tilney 267*: F, *t/s* of bud showing relationship between pollen sacs and furrows of 'stylar head' complex and large number of cells with tanniniferous deposits on dorsal face of anthers; G, *l/s* of portion of corolla lobe showing 'unzipping' appearance where epidermal cells have elongated and formed thickened outer cell walls and cuticle. H, *t/s* of portion of corolla lobe showing how epidermal cells interlock at position where corolla lobes of bud will separate and open (*Burrows 5998*). Scale bars: A, 2 mm; B, 200 μ m; C, E, 1 mm; D, F, 700 μ m; G, H, 70 μ m.

Common names: *rankklipels*, *rankbokdrol* (Afrikaans); climbing turkeyberry, climbing keetia, climbing canthium, monkeyberry (English); *mudanhashoko*, *mudanhanashoko*, *umhlalalelingonyama* (Ndaui); *mokhutswane* (Northern Sotho); *ugcupe*, *sinwati* (Swazi), *muḥambeni* (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-

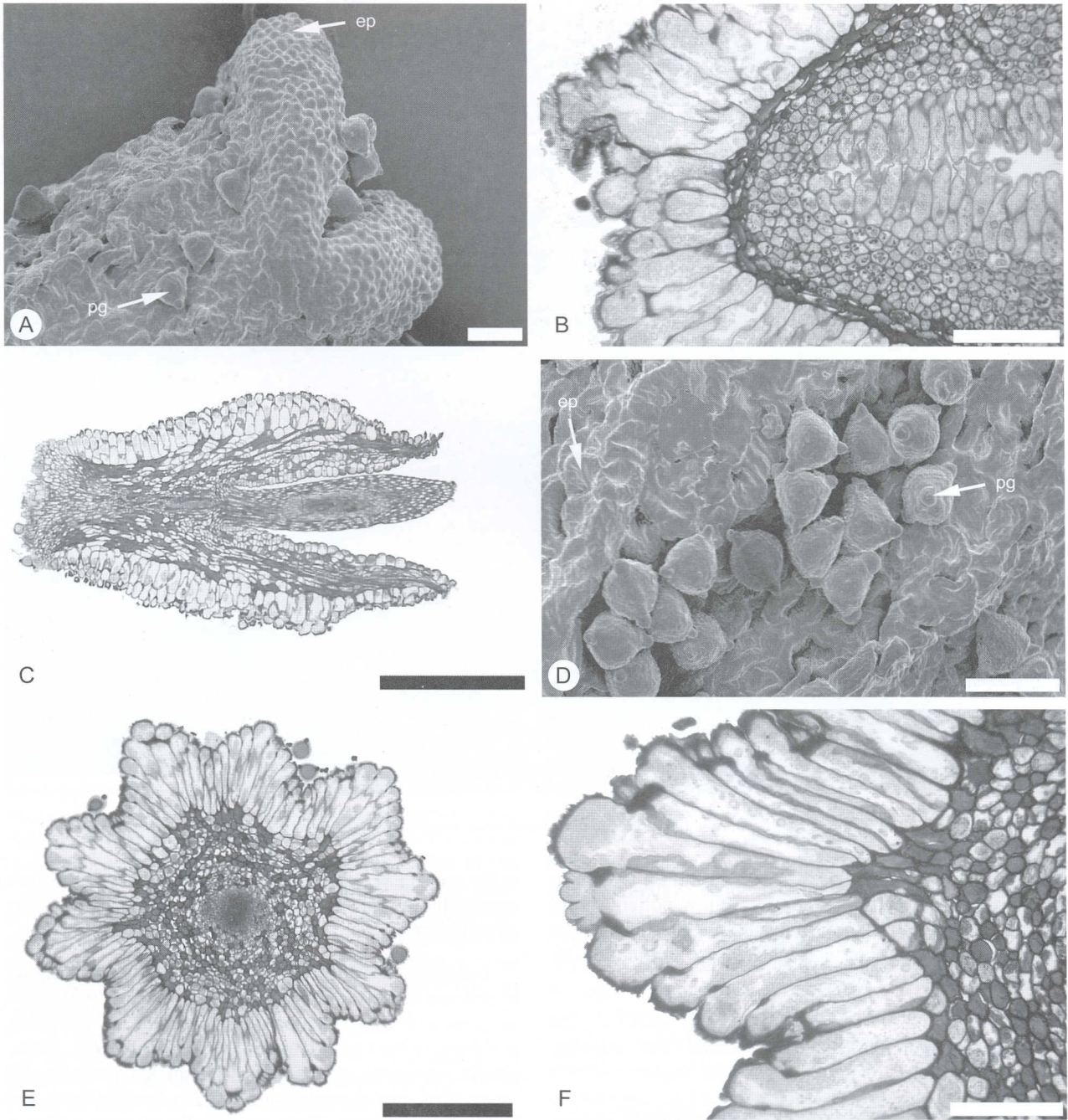


FIGURE 4.—*Keetia gueinzii*, Thompson s.n.: secondary pollen presentation. A, SEM micrograph of upper portion of 'stylar head' complex with two stigmatic lobes; B, t/s of 'stylar head' complex in region of stigma; C, l/s of 'stylar head' complex into which style is recessed; D, SEM micrograph of portion of 'stylar head' complex showing lobed epidermal cells and pollen grains in groove; E, t/s of 'stylar head' complex illustrating ten ridges and grooves, with cells forming ridges being much longer than those of grooves, and numerous tanniniferous subepidermal cells; F, t/s of portion of 'stylar head' complex showing elongated epidermal cells with dense cytoplasm, circular thickenings in more distal parts, and thicker cuticle over ridges than in grooves. ep, epidermal cells; pg, pollen grains. Scale bars: A, D, 50 μ m; B, F, 100 μ m; C, 700 μ m; E, 400 μ m.

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-

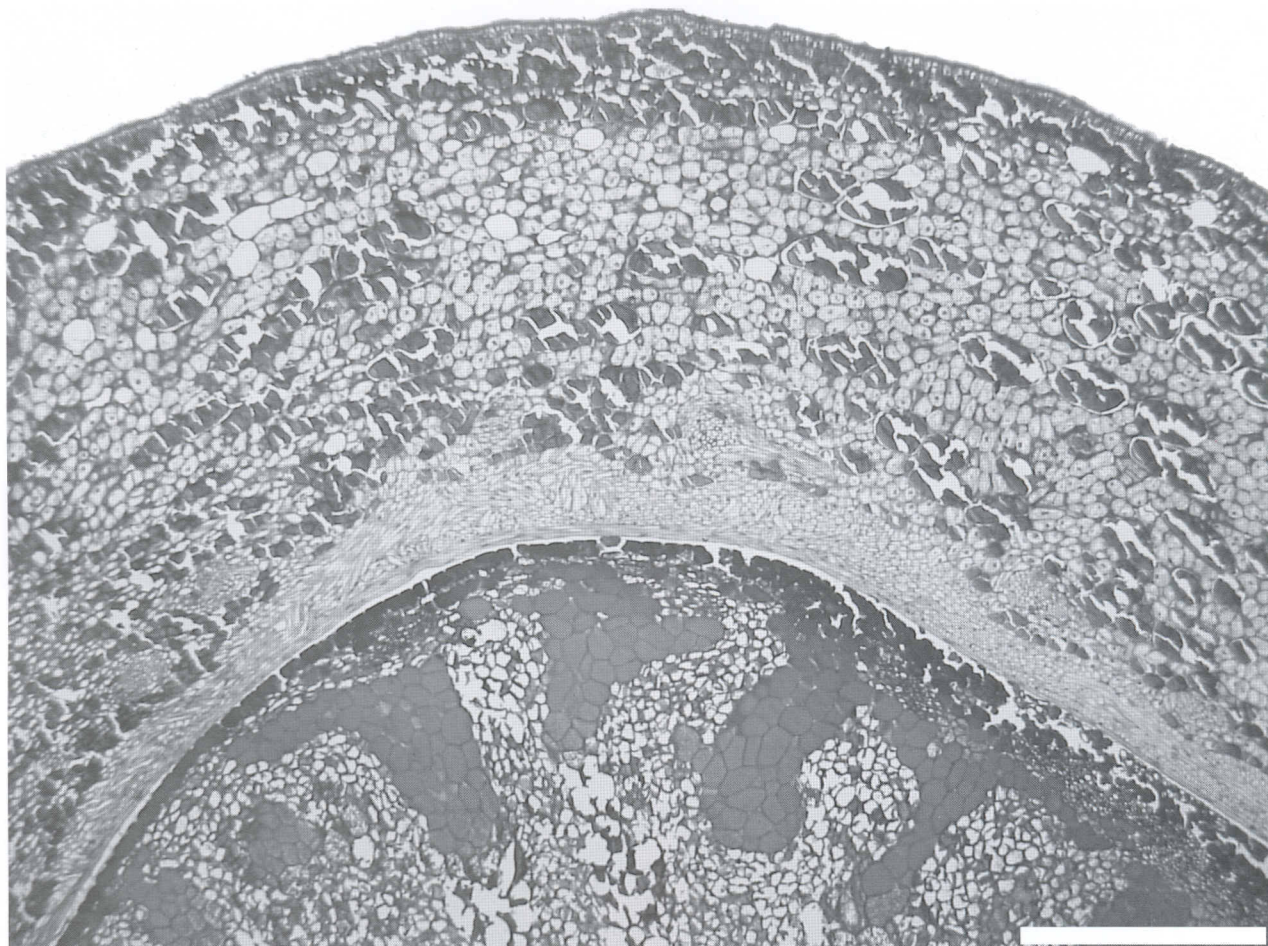


FIGURE 5.—*Keetia gueinzii*, Kok 712. Portion of pericarp and seed with endosperm showing tanniniferous intrusions. Scale bar: 400 μ m.

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 l/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 cornelia* (Cham. & Schldtl.) 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 rubiaceaceous genera *Pachystigma* Hochst. and *Fadogia* Schweinf. (Van Wyk *et al.* 1990), both belonging to the Vanguerieae. 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 2E). 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 rubiaceaceous 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 Vanguerieae. 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 $S = \pm 2x N$, tectum thickness of 0.6–0.8 μm , nexine thickness of 0.5–1.2 μm , and the columellae 2 μm in height. Lens *et al.* (2000) also noted that the margin of the ecto-aperture is not obviously demarcated, and is circular, the sexine semitectate, the lumina elongated, the columellae long ($\pm 2.7 \mu\text{m}$) and widely separated. Apertures of fresh grains have prominent protruding onci—or so-called 'pollen buds' of some authors (Tilney & Van Wyk 1997; Dessein *et al.* 2005).

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

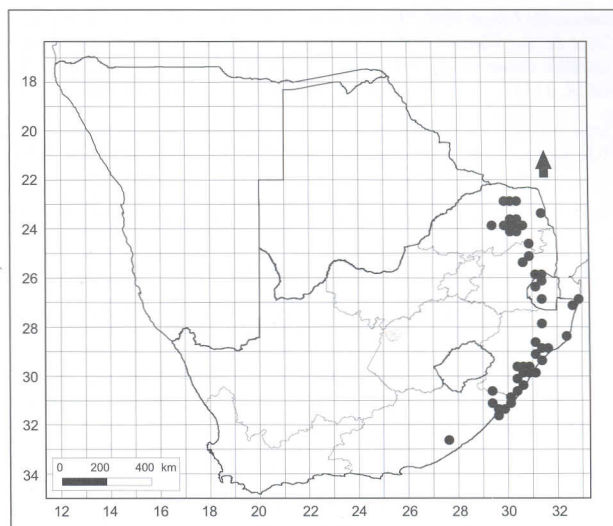


FIGURE 6.—Known distribution of *Keetia gueinzii* in the Flora of southern Africa region. Arrow indicates that its distribution extends further north into tropical Africa.

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 Luvale 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 Luvale 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 tenuis* Hansf., *B. velutina* (Berk. & M.A.Curtis) Höhn., *Balladynocallia glabra* (Hansf.) Bat. (= *Balladynastrum glabrum* Hansf.) (all Parodiopsisidae) and *Meliola littoralis* Syd. (Meliolaceae).

SPECIMENS EXAMINED (FSA region only)

Abbott 70 PRE, PRU; 3799, FSA?7251 PRU. Acocks 10957, 11805 PRE.

Balkwill & Cadman 2016 PRE. Barnard & Mogg 17424 PRE. Borchards 55 PRE. Botha 2949, 3470, s.n. herb. No. 6071 PRE. Bower 9212 PRE. Brand, Bosch, Logie, Venter 342 PRE. Bredenkamp 1369 PRE, PRU. Buthelezi 301, 619 PRE.

Canson & Irvine 95B PRE. Cloete 1913, 2085 NH. Codd 3056 PRE. Codd & De Winter 3087 PRE. Codd & Dyer 4516 PRE. Coleman 406 NH. Compton 2873d, 24756, 28200 NBG; 28218, 29120, 29476, 30658, 31551, 31719 NBG, PRE; 28734 PRE. Cooper 80 PRE.

Davis 86 NH. De Winter 8255 PRE. De Winter & Vahrmeijer 8599 PRE. Dlamini s.n. PRE; s.n. NH; 38301, 43743, 49529, 57029 NBG. Doidge 6070 PRE.

Eastwood 1284 PRE. Edwards 1308, 1381 PRE. Elan-Puttick 94, 142 PRE.

Felton & Thornhill FSA347 PRU. Fitzsimons & Dam 26276 PRE.

Galpin 519, 9397 PRE. Gerstner 4507, 5412 PRE; s.n. NH. Gordon 352 NH.

Hafström & Acocks 1929 PRE. Hahn FSA327, 386 PRU. Heath 294, 518 PRE. Hemm 45, 45A PRE, PRU. Hobson 2054 PRE. Hutchings 3084 NH.

Jacobsen 5305 PRE. Jordaan 3120 PRE. Junod 4152 PRE.

Keet 1181, 1335 PRE; US15255 NBG. Kemp 1116 PRE. Kirkman 3057 PRE. Kluge 25, 1585 PRE. Korsten s.n. PRE. Krige 136 PRE.

Law 70 NBG. Lawn s.n., 170 NH. Leighton 2982 PRE. Leistner, Thom & Gillham 3282 PRE. Lubke FSA262 PRU, NH.

MacDevette 1542 PRE. Marloth 4095 PRE. McCallum s.n., 708 PRE. Meeuse 9394 PRE. Miller 8497, S/151 PRE. Mills 394 PRE. Moffet 1480 PRE. Mogg & Nicholson 37974 PRE. Moll 2196, 2298, 2722 PRE.

Nel 350 PRE, NBG. Nicholson 102 NH.

Obermeyer 859 PRE; TM30111.

Pegler 2002 SAM. Plath s.n. PRE. Pole-Evans 3750 PRE. Pott TM13528. Poynton & Brent For. Herb. 11601. Prior 390 PRE.

Rael 541 PRE. Rodin 4102 PRE. Rogers TM13870, TM18904, TM24016?, TM24426?.

Sanderson 846 NH. Scheepers 362 PRE, PRU; 813 PRE. Scheepers & Haasbroek s.n. PRE. Schlechter 12290 SAM. Schmidt 28 NH. Sidey 3004 PRE. Sim s.n., 20215, 2392 PRE; 2393 SAM. Skott 1661 PRE. Smook 1267 PRE. Smuts & Gillett 3184 PRE. Stalmans 264, 593, 1117 PRE. Strey 6881 PRE, NH; 7152, 8510 PRE. Swynnerton 49 NH; 170 SAM, PRE.

Thorncroft 372 PRE; 898 NH. Tilney 156, 162 JRAU, PRE, PRU.

Vahrmeijer 510, 1476 PRE. Vahrmeijer & Tölken 927 PRE. Van der Schijff 4373, 4560, 6168 PRE, PRU; 4792 PRU. Van Jaarsveld 519 NBG, PRE. Van Jaarsveld, Van der Walt & Crous 32 PRE. P.van Wyk BSA349, BSA616 PRU. P.van Wyk & Hahn BSA838 PRU. Van Wyk 1640 PRE; FSA10424, FSA12215 PRU; 2174, 2702, 2966 PRE, PRU. Van Wyk & Kok 5888 PRE, PRU. Van Wyk & Theron 4568, 4569, 4872 PRE, PRU. Venter 89, 1858, 12661 PRE; 272, 438 NH. Victoria College (Stellenbosch) Herbarium US15254 NBG.

Wager 23009 PRE. Ward 1086, CJ1525, CJ5243, CJ9888 PRE; 1647, MC1549 NH. Wells & Edwards 28 PRE. Wood s.n., 10378, 11392, 12773 PRE; 23853 PRU; 305, 11356 NH; 5477 PRE, SAM. Whyte Herb. Musei Austro-Africani 16033 SAM. Wylie 8550 NH.

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