

Two new species of *Apodytes* (Icacinaceae) from southern Africa

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Apodytes abbottii Potgieter & Van Wyk and *A. geldenhuysii* Van Wyk & Potgieter, two new species from southern Africa, are described, illustrated and compared with the other African members of the genus. *A. abbottii* is a shrub or small tree endemic to rocky sandstone outcrops in southern Natal and north-eastern Transkei (Pondoland Centre). It is probably allied to the widespread *A. dimidiata* E. Mey. ex Arn. subsp. *dimidiata*, with which its range overlaps. Diagnostic characters of *A. abbottii* include its robust though often stunted habit, thick and rigid blue-green leaves which are rounded, erect terminal inflorescences and glabrous ovaries. *A. geldenhuysii* is a rare multistemmed shrub or small slender tree confined to a small area in the mountains of the south-western Cape. It is a very distinctive species without any close relatives. The few-flowered axillary racemes, unusual pale green and translucent colour of the ripe fruit appendage, intercellular pectic protuberances in the mesophyll of the leaf lamina, and fibres (in addition to sclereids) in the secondary phloem, immediately distinguish it from all other African members of the genus. Other diagnostic characters include the relatively small ovate to ovate-elliptic leaves with retuse apices, blunt-tipped cylindrical flower buds, glabrous ovaries and narrowly oblong off-white petals which are strongly recurved with markedly incurved apices.

Apodytes abbottii Potgieter & Van Wyk en *A. geldenhuysii* Van Wyk & Potgieter, twee nuwe spesies uit Suider-Afrika, word beskryf, geïllustreer en met die ander lede van die genus in Afrika vergelyk. *A. abbottii*, 'n struik of kleinerige boom, is endemies tot rotsagtige sandsteendagsome in Suid-Natal en Noordoos-Transkei (Pondoland-sentrum). Dit is moontlik naverwant aan die wydverspreide *A. dimidiata* E. Mey. ex Arn. subsp. *dimidiata* wat in dieselfde gebied aangetref word. Diagnostiese kenmerke van *A. abbottii* sluit in die robuuste dog dikwels verpotte groeivorm, dik, stewige, geronde blougroen blare, regop eindstandige bloeiwyses en gladde vrugbeginsels. *A. geldenhuysii* is 'n seldsame meerstammige struik of klein slanke boom wat slegs in 'n beperkte gebied in die berge van die Suidwes-Kaap aangetref word. Dit is 'n hoogs kenmerkende spesie sonder enige naverwante. Die min-blommige okselstandige raseme, ongewone liggroen en deurskynende ryp vrugaanhangsels, intersellulêre pektiese uitsteeksels in die mesofil van die blaarlamina, en vesels (bo en behalwe sklereïede) in die sekondêre floëem, onderskei dit van al die ander verteenwoordigers van die genus in Afrika. Ander diagnostiese kenmerke sluit in die relatief klein eieronde tot eierond-elliptiese blare met ingekeepte punte, stomppuntige silindriese blomknoppe, gladde vrugbeginsels en smal-langwerpige witterige kroonblare wat sterk teruggebuig is met opvallende ingekromde punte.

Keywords: *Apodytes*, bird, dispersal, Icacinaceae, phenology, Pondoland Centre, seed, taxonomy.

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Introduction

Apodytes E. Mey. ex Arn. is an Old World genus of forest trees renowned for their excellent timber and peculiar 'pseudo-arillate' drupaceous fruit. Its infrageneric taxonomy, however, is still poorly understood, particularly with regard to Madagascar, Indo-Malesia, Indo-China and China. Owing to an apparent lack of dependable diagnostic characters, the delimitation of taxonomic entities is generally weak and there is uncertainty as to the exact number of species and infraspecific taxa (Sleumer 1969). Depending on the authority, from two to about 17 species may be recognized.

In recent years the trend has been to recognize but one widespread and polymorphic species of the Old World tropics, *A. dimidiata* E. Mey. ex Arn., and two other, less variable and geographically more restricted species, *A. brachystylis* F. Muell., endemic to NE Australia, and *A. clusiifolia* (Baill.) Villiers, endemic to New Caledonia (e.g. Mendes 1963; Sleumer 1969, 1971; Villiers 1980; Guymer 1984). Apparently overlooked by most workers, there are also, besides *A. dimidiata*, at least two distinct species on Madagascar, namely *A. macrocarpa* R. Capuron and *A. thouvenotii* P. Danguy (Capuron 1960, 1970). Thus, in Africa *A. dimidiata* is usually considered the only species, with two subspecies (sometimes treated as varieties, e.g. Lucas 1968; Lebrun & Stork 1992).

The typical subspecies and previously the only member recognized in southern Africa, is characterized by a densely pubescent ovary and sparsely pubescent fruit, whereas in the otherwise very similar, but more northerly distributed subspecies *acutifolia* (Hochst. ex A. Rich.) Cufod., the ovary and fruit are both glabrous.

Lately, certain field botanists have started questioning the validity of formally recognizing only a single variable species of *Apodytes* in southern Africa. Following a multidisciplinary comparative study of the southern African Icacinaceae (Potgieter 1994), we are now convinced that in addition to the variable *A. dimidiata*, at least two other very distinct, but still undescribed species of *Apodytes* occur in the region. In this contribution these two species are described and discussed. Notes are also provided on the infrageneric taxonomy of *Apodytes* in Africa.

Descriptions

1. *Apodytes abbottii* Potgieter & Van Wyk, sp. nov., *A. dimidiatae* subsp. *dimidiatae* affinis, sed habitu robustior; foliis magis rotundatis, glaucis, crassis, rigidis, marginibus planis; inflorescentiis plus minusve erectis; antheris minute papillatis; ovarii glabris.

TYPUS:— Transkei: Bizana District, Hlwlweni River Gorge, near

confluence with Icwaka River, 14 Dec. 1985, *Abbott 2885* (PRU, holotypus; NH, isotypus).

Apodytes sp. nov. A in Potgieter & Van Wyk (1992, 1994); Potgieter (1994).

Robust evergreen shrub or small tree, 1 – 3(5) m high, usually single-stemmed, occasionally somewhat stunted in growth with a very short main stem, glabrous; bark greyish, smooth to irregularly scaling in old stems, slash pale pink to brownish red. *Branchlets* thick (ultimate ones 3 – 4 mm diam.), sturdy, initially dark pinkish or purplish red to reddish brown to brown, becoming greyish brown to grey when mature. *Leaves* alternate; lamina very thick, stiff and brittle, dark blue-green and dull above, pale blue-green and dull below, elliptic, broadly elliptic, broadly ovate, subrotund or rotund, (20)40 – 65(80) × (20)25 – 54(55) mm, base broadly cuneate to rounded, apex rounded or obtuse, margin entire, plain; midrib (at least basal portion) usually dark red, plane or with basal third sometimes more or less raised above in fresh leaves, plane or raised in dried leaves, raised below in fresh and dried leaves; principal lateral veins alternate or opposite, usually 5 – 8 pairs, obscure on both surfaces or occasionally tending to be translucent below in fresh leaves, slightly raised or obscure in dried leaves; petiole usually 10 – 20 mm long, semi-terete, channelled above in dried leaves, usually dark red; exstipulate. *Inflorescences* panicles, mainly terminal and erect, many-flowered. *Flowers* bisexual, 5-merous, white, sweet-scented; buds elliptic to more or less clavate with apex rounded. *Calyx* 5-fid; lobes broadly deltoid, about 0.25 × 0.5 mm. *Petals* free, spreading, narrowly elliptic with apex shortly and weakly inflexed, about 3.5 × 1.0 mm. *Stamens* free, more or less erect to slightly spreading; filaments subulate, about 2.0 mm long; anthers 2-thecate, linear, about 2.0 × 0.75 mm, base strongly bilobed-sagittate, dorsifixed, versatile, opening lengthwise, surface minutely papillose. *Pistil* about 3.0 mm long; ovary 1-locular, ovoid, glabrous; style excentric; stigma subcapitate; ovules 2, pendulous. *Fruit* essentially a 1-seeded nut with a fleshy lateral appendage, obliquely ovate-reniform or ovate-orbicular, sub-compressed; nut oblong-obovoid, initially pale green, ripening to black; appendage initially small and dark green, considerably enlarging during ripening and sequentially changing through yellow-orange to bright scarlet and opaque (mesocarp bright yellow), eventually black in old fruit (Figure 1).

Reproductive phenology

A mass bloomer/fruiter, with flowering and fruiting phases clearly separate. Flowering time variable, but with a definite peak from October to December. Ripe fruits collected mainly from December to February.

Eponymy

The specific epithet honours Mr A.T.D. Abbott, farmer and amateur botanist from Clearwater, Port Edward. His extensive plant collecting and detailed field observations in the Pondoland Centre have made a major contribution to floristic knowledge of the region. He has, on the basis of field experience, strongly argued for the formal recognition of this new species. We would like to propose the names 'Pondo white pear' and 'Pondo-witpeer' as the English and Afrikaans vernacular names, respectively.

Diagnostic characters and relationships

Although its general morphology suggests a close affinity with *A. dimidiata* subsp. *dimidiata*, with which its range overlaps, *A. abbotii* can easily be distinguished by its robust and often stunted habit, its thick and rigid blue-green leaves which are

more rounded, and its erect terminal inflorescences and glabrous ovaries. In the field the two taxa can readily be distinguished by the following procedure: gently bend the tip of a freshly picked mature leaf upwards and towards the base of the lamina. In the case of *A. abbotii* the thick but brittle lamina snaps audibly into two, whereas that of *A. dimidiata* is flexible and does not break. As the ovaries are always densely pubescent in *A. dimidiata* subsp. *dimidiata*, the glabrous ones of the new species resemble the state in the more northerly *A. dimidiata* subsp. *acutifolia*; it is a particularly reliable diagnostic character to distinguish between the two members of *Apodytes* in the Pondoland Centre.

Despite being sympatric, no evidence of introgression has been observed between the new species and the associated *A. dimidiata* subsp. *dimidiata*. Reproductive isolation is probably partly ensured by a slight, though quite noticeable asynchronous flowering between the two taxa. Within the range of the new species, flowering in *A. dimidiata* subsp. *dimidiata* tends to peak slightly later, namely from December to February, compared with October to December in *A. abbotii*.

Distribution, habitat and conservation status

Apodytes abbotii is endemic to the Pondoland Centre (Figure 2), a regional centre of plant diversity associated with the outcrops of Natal Group sandstone (Msikaba Formation) between Oribi Gorge in southern Natal and Port St. Johns in Transkei (Van Wyk 1990). This region is a frost-free coastal plateau with a mean annual (mainly summer) rainfall of more than 1000 mm in most parts and shallow, acidic soils poor in plant nutrients.

Although plants of the new species also occur on forest margins, they are particularly conspicuous in fire-protected crevices of rocky outcrops in grassland and along the exposed upper cliff margins of forested river gorges. Plants in these exposed habitats are usually stunted in growth and reproductive specimens may be less than 1.0 m high. *A. abbotii* is occasionally found in association with *A. dimidiata*, particularly along forest margins — the morphological difference between the two species then being quite obvious. Unlike *A. dimidiata*, however, the new species does not occur away from the margin inside the forest, nor as a climax high-forest constituent.

In contrast to the scarcity of many other Pondoland Centre endemics, *A. abbotii* is fairly common over the whole region, thus comprising a good indicator species of this remarkable sandstone flora. It is well represented in all the existing conservation areas in the region and is under no immediate threat.

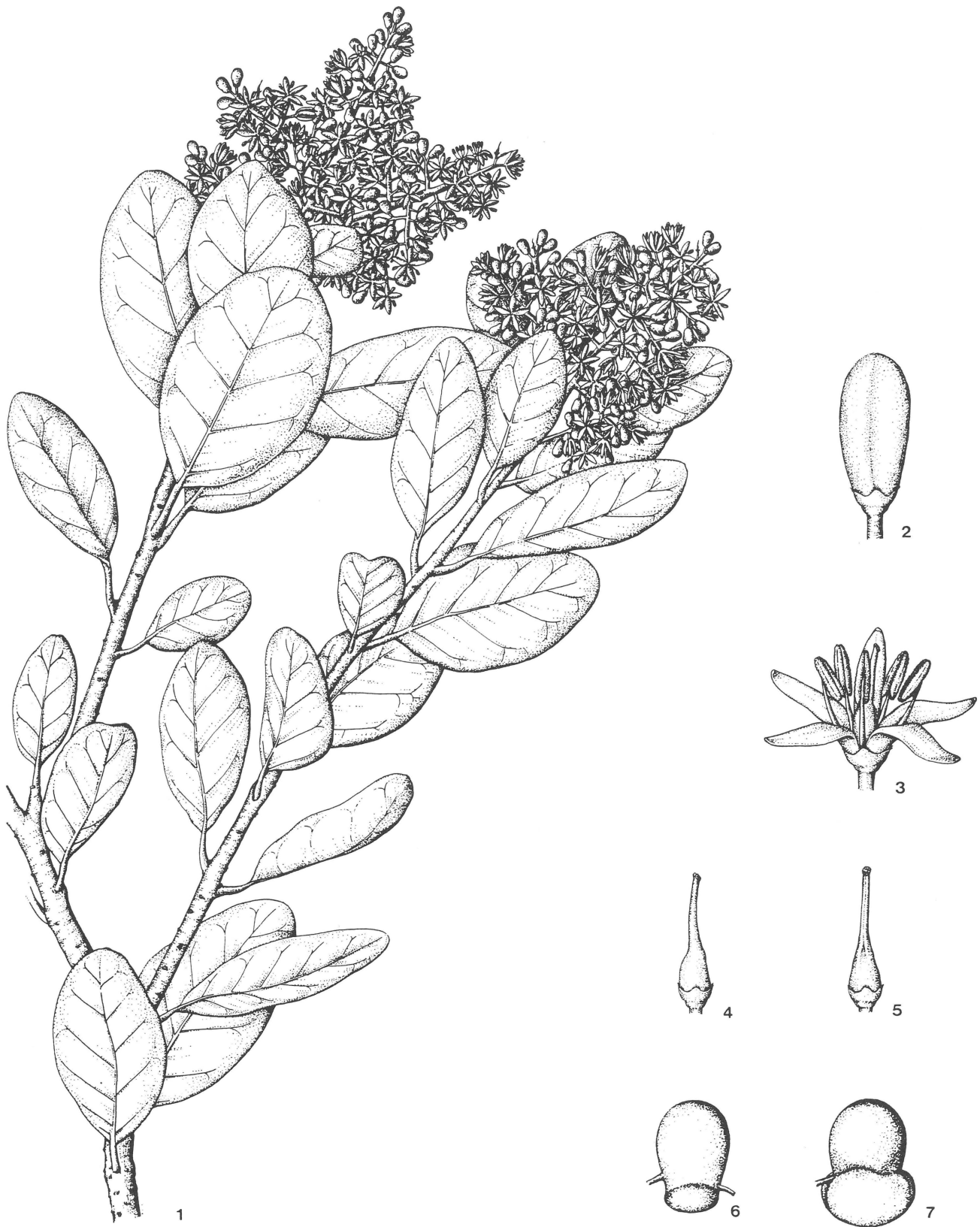
Specimens examined

—**3030** (Port Shepstone): Oribi Gorge (–CB), *Dodds 92* (NU); Oribi Gorge, Fair Acres Estate (–CB), *Van Wyk 10470* (PRU); Umtamvuna Nature Reserve [UNR], Beacon Hill (–CC), *Nicholson 337* (Herb. Nich.), *Strey 6408* (NH), *Van Wyk 2332* (PRU); UNR, Gonioma Heights (–CC), *Abbott 4387* (PRU); UNR, Outeniqua Trail (–CC), *Abbott 2265* (PRE, PRU); UNR, Smedmore Forest (–CC), *Van Wyk & Lowrey 6822, 6835* (NH, PRU); UNR, Plot No. 12 (–CC), *Abbott 2230* (NH, PRU); UNR, without precise locality, *Potgieter 66* (PRU); Hlolweni River Gorge, near confluence with Icwaka River (–CC), *Abbott 2885* (NH, PRU, holo.); Icwaka River Gorge (–CC), *Van Wyk 7181* (KEI, NH, PRU); Izotsha Kloof (–CD), *Strey 7437* (NH); St Michaels on Sea, about 2 miles inland (–CD), *Nicholson 414* (NH); Uvongo Nature Reserve (–CD), *Nicholson 262* (NH), *Van Wyk 7154* (NH, PRU), *7155* (PRE, PRU).

—**3129** (Port St. Johns): Lusikisiki District, Magwa Falls (–BC), *Van Wyk & Matthews 7628* (PRE, PRU), *7629* (NH, PRE, PRU); Ntsubane Area, Fraser's Gorge, Cutweni side (–BC), *Van Wyk &*

Mathews 7700 (K, NH, PRE, PRU); Ntsubane Area, between Magwa Tea Estate and Fraser's Gorge (-BC), *Potgieter 67* (PRU); Ntsubane Area, Fraser's Gorge (-BC), *Hilliard 1088* (NU); Isicezula Forest, bordering Mazizi Tea Estate, along southern

tributary of Mlambomkulu River (-BC), *Van Wyk & Matthews 7867* (KEI, NH, PRU); Mkambati Game Reserve (-BD), *Jordaan 1082* (NH), *Nicholas & Smook 2445* (NH), *Van Wyk & Matthews 7987* (NH, PRU); Lusikisiki District, Lupatana (-BD), *Van Wyk &*



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Figure 1 *Apodytes abbottii*. 1. Flowering branchlet, $\times 1$. 2. Flower bud, $\times 5$. 3. Flower, $\times 5$. 4 & 5. Pistil, lateral views, $\times 5$. 6. Fruit (pedicel left, persistent style right), immature, with fleshy appendage not yet enlarged, $\times 2$. 7. Fruit, ripe, $\times 2$. (1 - 5 from *Van Wyk 9913*, 6 & 7 from *Van Wyk 7155*.)

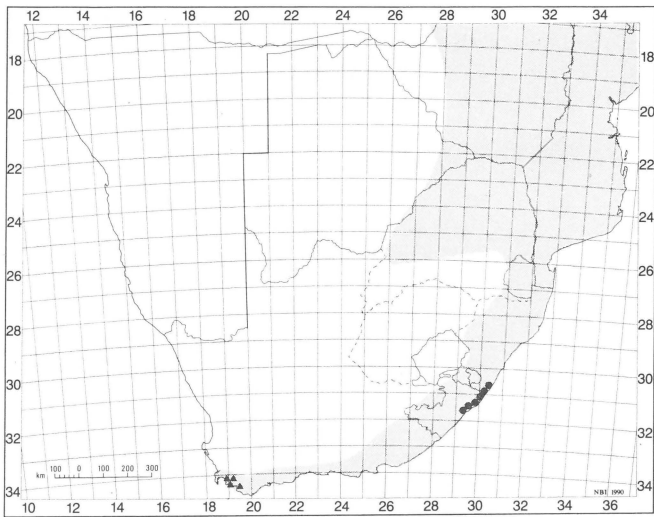


Figure 2 The known geographical distribution of *Apodytes abbotii* (●) and *A. geldenhuysii* (▲). Distribution range of *A. dimidiata* subsp. *dimidiata* is shaded.

Matthews 7919, 7940 (NH, PRU); Cutweni, along Myekani River (–BD), Van Wyk 8454 (PRU); Stream just south of Mkwani River Mouth (–BD), Van Wyk 8483 (PRU); Port St. Johns, Mt. Theisiger (–DA), Van Wyk 8380 (PRU).

—3130 (Port Edward): Umtamvuna Nature Reserve [UNR], Clearwater (–AA), Abbott 2219 (PRE, PRU); Port Edward (–AA), Sirey 6408 (NH); Port Edward, S.A. Police Holiday Resort, sandstone outcrop near chalet No. 90 (–AA), Van Wyk 9913 (PRU); Port Edward, Clearwater Farm (–AA), Abbott 851 (NH, PRU); Port Edward, UNR, on edge of gorge (–AA), Bayer 1344 (NU), Cooper 108 (NH); about 4 km from Port Edward to Izingolweni (–AA), Botha & Coetzee 1612 (PRU, PUC); Sikuba River Gorge, tributary of Mzamba River (–AA), Van Wyk 7401 (PRU); Mnyameni River Gorge (–AA), Abbott 4135, Van Wyk 8026 (PRU).

2. *Apodytes geldenhuysii* Van Wyk & Potgieter, sp. nov., a speciebus nobis notis bene distincta habitu fruticoso; foliis parvis, praecipue ovatis et apicibus retusis; inflorescentiis constantibus ex racemis paucifloribus axillaribus, alabastris cylindricis; floribus albidis; ovarii glabri; fructuum appendicibus carnosus in maturitate pallide viridibus translucidis.

TYPUS:— Cape: Hermanus, Vogelgat Private Nature Reserve, along stream in vicinity of Druids' Wall, 28 Jan. 1984, *Geldenhuys* 750 (PRU, holotypus; PRE, isotypus).

Apodytes sp. nov. B in Potgieter & Van Wyk (1992, 1994); Potgieter (1994).

Evergreen, leafy, multistemmed shrub, occasionally a small slender tree up to 3(5) m high, glabrous; bark greyish, more or less smooth in old stems, slash whitish to pale brownish white. *Branchlets* slender (ultimate ones 1 – 2 mm diam.), initially dark pinkish red to maroon, becoming greyish brown to brown when mature. *Leaves* alternate; lamina relatively thin, flexible and subcoriaceous, dark green and shiny above, pale green and dull below, ovate to elliptic-ovate, on mature growth (20)25 – 40(55) × (8)10 – 15(25) mm, up to 70 × 40 mm in coppice shoots after fire, base broadly cuneate to rounded, apex retuse or acute, margin entire, often slightly undulate; midrib slightly raised or plane above in fresh leaves, slightly channelled above in dried leaves, slightly raised below in fresh and dried leaves; principal lateral veins alternate or opposite, usually 3 – 5 pairs, obscure on both surfaces in fresh and dried leaves, occasionally tending to be translucent below in fresh leaves; petiole on

mature growth 3 – 5(8) mm long, up to 10 mm in coppice shoots, semi-terete, channelled above in dried leaves; exstipulate. *Inflorescences* racemes, mainly axillary, (3)4 – 6(8)-flowered. *Flowers* bisexual, 5-merous, off-white, sweet-scented; buds more or less cylindrical with apex blunt and indented. *Calyx* 5-fid; lobes narrowly deltoid, about 0.50 × 0.25 mm. *Petals* free, strongly recurved, narrowly oblong with apex thickened and markedly incurved (almost cucullate), about 5.0 × 1.0 mm. *Stamens* free, more or less erect to slightly spreading; filaments subulate, about 3.0 mm long; anthers 2-thecate, linear, about 3.0 × 0.5 mm, base bilobed-sagittate, dorsifixed, versatile, opening lengthwise, surface smooth. *Pistil* about 4.0 mm long; ovary 1-locular, ovoid, glabrous; style excentric; stigma subcapitate; ovules 2(3), pendulous. *Fruit* essentially a 1-seeded nut with a fleshy lateral appendage, obliquely ovate-reniform, subcompressed; nut broadly ellipsoidal, initially pale green, ripening through dark maroon to black; appendage initially small and dark green, considerably enlarging during ripening and becoming green, then pale green and translucent, eventually black and opaque in old fruit (Figure 3).

Reproductive phenology

An extended bloomer/fruiter. Flowering and fruiting specimens have been collected throughout the year. A plant usually bears flowers and fruits (all stages of ripening) at the same time. Asynchronous blooming of individuals also results in extended blooming at the population level.

Eponymy

We have pleasure in naming this plant in honour of Dr C.J. Geldenhuys, forest ecologist, who first suggested to us its possible distinctness. We pay tribute to the substantial contribution he has made towards our knowledge of the phytogeography, ecology and sustainable management of the indigenous forests in South Africa. As English and Afrikaans vernacular names, we propose 'dwarf white pear' and 'dwerfwitpeer', respectively.

Diagnostic characters and relationships

The few-flowered axillary racemes and unusual pale green and translucent colour of the ripe fruit appendage immediately distinguish *A. geldenhuysii* from all other African members of the genus. The flowers are also distinctive in their blunt-tipped cylindrical buds, glabrous ovaries and narrowly oblong off-white petals which are strongly recurved with markedly incurved apices. Diagnostic anatomical characters include the presence of fibres (in addition to sclereids) in the secondary phloem and intercellular pectic protuberances in the mesophyll of the leaves (Potgieter & Van Wyk 1992, 1994).

Apodytes geldenhuysii appears to be an isolated species without any obvious close relatives. Although its distribution range (almost?) overlaps with that of *A. dimidiata* subsp. *dimidiata*, confusion between the two is unlikely, even in the case of non-reproductive specimens. In addition to its diminutive habit, foliage leaves of *A. geldenhuysii* are usually smaller and more ovate than those of *A. dimidiata* subsp. *dimidiata*, with retuse apices. Moreover, the latter is uncommon (if not absent) within the range of *A. geldenhuysii* and the two taxa are apparently mutually exclusive. *A. dimidiata* subsp. *dimidiata* is known from coastal forests at Stanford, east of Hermanus, and from the Cape Peninsula, but has not yet been recorded from the nearby mountain ranges where *A. geldenhuysii* occurs.

Distribution, habitat and conservation status

Apodytes geldenhuysii occurs in the south-western Cape where



Figure 3 *Apodytes geldenhuysii*. 1. Flowering branchlet, $\times 1$. 2. Flower bud, $\times 5$. 3. Flower, $\times 5$. 4 & 5. Pistil, lateral views, $\times 5$. 6. Fruit (pedicel left, persistent style right), immature, with fleshy appendage not yet enlarged — note characteristic curvature of style, $\times 2$. 7. Fruit, ripe, $\times 2$. (1 – 5 from *Van Wyk 9925*, 6 & 7 from *Geldenhuys 750*.)

it has a restricted distribution extending from the Hottentots Holland Mountains, Groenland Mountains and Kogelberg east to the Klein River Mountains (Figure 2). This is the most species-rich part of the Cape Floristic Kingdom and coincides with the South-Western Phytogeographical Centre of Oliver *et al.* (1983). A mediterranean-type climate prevails with mean annual rainfall in this mountainous region ranging from 700 to 3600 mm, mainly in the form of winter rains, but on the higher peaks also derived from summer clouds. Most herbarium

records are from the vicinity of Jonkershoek, Betty's Bay, Kleinmond and Hermanus.

Apodytes geldenhuysii grows in rocky, often humus-rich soils derived mainly from Cape Supergroup sandstone and at elevations from near sea-level to about 1300 m, generally along streams and in moist places sheltered from fire and wind, such as along drainage lines, boulder screes, rocky outcrops and at the base of cliffs. Plants are often associated with relictual patches of Afromontane Forest, or forest precursors

Table 1 Summary of salient differences between the African members of *Apodytes*. Characters regarded as most significant are marked with an asterisk

	<i>A. dimidiata</i> subsp. <i>dimidiata</i>	<i>A. dimidiata</i> subsp. <i>acutifolia</i>	<i>A. abbottii</i>	<i>A. geldenhuysii</i>
* Geographical distribution	widespread in southern and eastern Africa; also extra-African	widespread in eastern, central and north-eastern Africa	endemic to a small area in southern Natal and northern Transkei (Pondoland Centre)	endemic to a small area in the south-western Cape
Habitat	associated with various forest types (particularly Afromontane), often a canopy tree in climax forest, rarely in savannah		exposed sandstone outcrops and forest margins	rocky outcrops in mountain fynbos or riverine forest (usually on margins)
* Habit	tree up to 25(35) m high; larger trees with fluted trunks		stunted single-stemmed shrub or small sturdy tree up to 3(5) m high	multistemmed leafy shrub or small slender tree up to 3(5) m high
Stems (young)	slender, green, sometimes flushed with reddish purple, becoming grey to greyish brown and lenticellate when mature		thick, sturdy, dark pinkish or purplish red to reddish brown to brown, becoming greyish brown to grey when mature	slender, dark pinkish red to maroon when young, becoming greyish brown to grey when mature
Bark (mature)				
Surface pattern	± smooth		± scaling	± smooth
* Sclerenchyma type	sclereids			fibres and sclereids
Leaves (mature and fresh)				
* Shape	usually ovate-elliptic or broadly elliptic		usually elliptic, subrotund or rotund	ovate to elliptic-ovate
Apex	obtuse, acute, shortly acuminate, rarely retuse		rounded or obtuse	retuse or acute
Size (lamina)	(30)50—80(150) x (15)25—40(80) mm		(20)40—65(80) x (20)25—54(55) mm	(20)25—40(55) x (8)10—15(25) mm
* Colour (adaxial)	dark green, shiny		blue-green, dull	dark green, shiny
* Texture (lamina)	subcoriaceous, flexible		thick, stiff and brittle	subcoriaceous, flexible
Margin	± wavy, rarely plane		plane	± wavy, rarely plane
Midrib (adaxial)	whitish or yellowish green, rarely pale pinkish; ± flush with lamina surface or slightly submerged		often red; lower third ± raised above lamina surface	whitish or yellowish green, rarely pale pinkish; ± flush with lamina surface
* Mesophyll	intercellular pectic protuberances absent			intercellular pectic protuberances present
Inflorescences				
* Type	panicle			raceme
* Position	mainly terminal			mainly axillary
* Flowers (number)	numerous (usually > 100)			(3)4—6(8)
Direction	usually ± pendulous		± erect	variable

Table 1 Continued

	<i>A. dimidiata</i> subsp. <i>dimidiata</i>	<i>A. dimidiata</i> subsp. <i>acutifolia</i>	<i>A. abbottii</i>	<i>A. geldenhuysii</i>
Flowers				
* Buds (shape)	broadly elliptic to \pm clavate, apex rounded			\pm cylindrical, apex blunt and indented
Colour	white			off-white
Calyx-lobes (shape)	broadly deltate, \pm 0,25 x 0,5 mm			narrowly deltate, \pm 0,50 x 0.25 mm
Petals (shape)	narrowly elliptic, \pm 3,5 x 1,0 mm			narrowly oblong, \pm 5,0 x 1,0 mm
Petals (apices)	slightly thickened and weakly inflexed			markedly thickened and strongly inflexed
* Petals (orientation)	recurved or spreading; if recurved, apices not conspicuously incurved		spreading	strongly recurved with apices conspicuously incurved
Anthers (size)	\pm 2,0 x 0,75 mm			\pm 3,0 x 0,5 mm
Anthers (surface)	\pm smooth or weakly papillate		strongly papillate	\pm smooth
Pistil (length)	\pm 3 mm long			\pm 4 mm long
* Ovary (surface)	densely pubescent	glabrous		
Fruit colour	ripening from dull green through brownish green to black			ripening from dull green through dark maroon to black
Nut (dry) portion				
* Fleshy appendage	sequentially changing from dark green through yellow-orange to bright scarlet and opaque (mesocarp bright yellow) when ripe; eventually black in old (spent) fruit [directly from dark green to black in Maputaland form of <i>A. dimidiata</i> subsp. <i>dimidiata</i>]			sequentially changing from dark green through green to pale green and translucent when ripe; eventually black and opaque in old (spent) fruit
* Reproductive phenology	mass bloomer/fruiter			extended bloomer/fruiter

mixed with woody riparian Cape elements, and occur mainly in more open vegetation, along forest margins or stream banks, occasionally as a forest understorey constituent. In its ecotonal setting at the interface between forest and fire-prone fynbos, or amongst rocks in mountain fynbos, *A. geldenhuysii* is frequently subjected to fire which usually completely destroys above-ground growth. Burned plants take some time to recover, with vigorous coppice shoots sprouting from a woody rootstock. Unlike some typical resprouting fynbos shrubs, however, it does not flower promptly after fire, and its blooming is not dependent upon the stimulus of fire.

Owing to its restricted geographical distribution, *A. geldenhuysii* should be considered vulnerable. For a woody species in a well-botanized area, it has relatively seldom been collected, perhaps because the plants are fairly inconspicuous, both when in flower and in fruit, but more likely because they are uncommon and restricted to isolated sites. Fortunately, most known populations are within conservation areas, notably the Hottentots Holland, Vogelgat and Maanskynekop nature reserves. Habitat destruction by invasive Australian species of *Acacia* Mill. probably poses the major threat. Populations of the new species have, for example, been wiped out almost completely by alien vegetation along the lower Palmiet River near the main-road bridge at Kleinmond.

Specimens examined

—3418 (Simonstown): Jonkershoek, Second Waterfall (–BB),

Geldenhuys 1212 (PRE), *Thompson 613* (PRE, STE), *Van Wyk 12186a, 12187a, 12188a* (PRU); Nuweberg, between hut and Landdroskloofnek (–BB), *Taylor 10347* (PRE, STE); Hottentots Holland Mountains [HHM], slopes of Somerset-Sneeukop (–BB), *Goldblatt 1634* (MO, NBG, PRE); HHM, Diepgat Ravine above Lourensford (–BB), *Esterhuysen 8247* (BOL); HHM, Landdros Kloof (–BB), *Esterhuysen 32151* (BOL); HHM, between the Triplets and Guardian (–BB), *Esterhuysen 9793* (BOL); HHM, Roos Kraal near Elgin (–BB), *Hubbard 438* (BOL); Betty's Bay (–BD), *Levyms 10392* (BOL); Betty's Bay, Cascades (–BD), *Parker 4735* (BOL, NBG); Betty's Bay, Luipaards Kloof (–BD), *Van Wyk 12192a, 12193a* (PRU); Betty's Bay, slopes of Voorberg (–BD), *Taylor 7063* (PRE, STE), *Van Jaarsveld 2339* (NBG, PRE); Caledon District, Hangklip Gorge (–BD), *Compton 13612* (NBG); Hangklip Estates, waterfall above old toll gate (–BD), *Levyms 10419* (BOL); Caledon District, Kogelberg (–BD), *Compton 16458* (NBG), *Leighton 758* (BOL); Kogelberg Forest Reserve, Buffelstalberg, ridge near second highest peak (–BD), *Boucher 345* (PRE); Kogelberg Forest Reserve, Wynand Louw's Bos (–BD), *Boucher 359* (PRE, STE); Kleinmond Nature Reserve [KNR], Forest above Fairy Glen on E side of Palmiet River (–BD), *Hanekom 293* (PRU); KNR, along Palmiet River, just above weir at bridge between Betty's Bay and Kleinmond (–BD), *Van Wyk 9925* (PRU).

—3419 (Caledon): Franschhoek Mountains, Eensbedrogen (–AA), *Viviers 990* (PRE, STE); Hermanus, Maanskynekop Nature Reserve [MNR], along Maanskynekop (–AD), *Williams 3828* (NBG,

PRU); MNR, scree slope below Raven Ridge (-AD), *Hanekom 301* (PRU), *Williams 3842* (PRU); MNR, Rooiels Rest (-AD), *Hanekom 302* (PRU); Hermanus, Vogelgat Private Nature Reserve [VPNR], vicinity of Druids' Wall (-AD), *Geldenhuis 750* (PRE, PRU, holo.), *Williams 3557, 3586* (PRU); VPNR, near Washington Bridge (-AD), *De Lange s.n.* (10-05-1985) (PRE, PRU); VPNR, Cathedral Forest (-AD), *Williams 3864* (NBG, PRE, PRU); VPNR, without precise locality, *Geldenhuis 847* (PRU).

Discussion and miscellaneous notes on *Apodytes* in Africa

The description of the two new species has brought to four the number of African taxa currently recognized in *Apodytes*. These are listed in Table 1, together with some of the characters employed to distinguish between them. Pressed material of all these taxa share the peculiarity that the leaves, flowers and fruits tend to dry dark brown to black, thus imparting to the specimens some superficial similarity. Because of the uncritical acceptance of the convenient blanket notion of polymorphism, herbarium material of *A. abbotii* and *A. geldenhuisii* has hitherto been placed almost without exception under *A. dimidiata* subsp. *dimidiata*.

Despite the recognition of the two new species, *A. dimidiata* subsp. *dimidiata* still remains a variable taxon, particularly as to habit, leaf size and shape, although less so than in the past. As can be seen from Table 1, the characters on which the two new species are based, are far more marked and convincing than those that have been proposed for the distinction of the two currently recognized subspecies/varieties of *A. dimidiata* in Africa. We believe that in *Apodytes* infraspecific ranks are best suited to accommodate some of the many geographical forms of *A. dimidiata* s.l. These forms differ in only one or a few morphological characters, but intermediates are often present in boundary zones.

At least two morphological entities of *A. dimidiata* in southern Africa may deserve formal recognition at the infraspecific level. The most conspicuous of these is a form with extremely hairy leaves from the Natal Midlands. The other is the prevailing form in coastal northern Natal and southern Mozambique (Maputaland). During ripening the fleshy fruit appendage in the Maputaland plants usually skips the orange-yellow and bright scarlet stages and turns directly from green to a shiny black. Besides these differences, both forms are morphologically essentially identical to *A. dimidiata* subsp. *dimidiata*, although there are indications that the Maputaland plants behave ecologically quite differently from their counterparts in the southern Cape (*Geldenhuis*, pers. commun.). For example, Maputaland plants have a bushy, multistemmed growth form, flower and fruit from an early age and occur in abundance on forest margins and in early stages of bushclumps. Southern Cape plants, on the other hand, rarely occur on forest margins, but are prominent in mature forest, have a single-stemmed growth form and take long to flower, even when grown outside the forest. Formal recognition of these forms, like many others throughout the extensive range of *A. dimidiata* s.l., is clearly desirable, but should preferably form part of a monographic treatment of the genus. Therefore, at the present state of our knowledge and pending further study, it is considered best to still include these two southern African entities in a heterogeneous subsp. *dimidiata*.

The two new species can immediately be distinguished from *A. dimidiata* subsp. *dimidiata* by their glabrous ovaries. In southern Africa the ovaries in the latter subspecies are always densely pubescent (appearing sericeous in pressed specimens) and no intermediates occur. However, as one moves northwards in Africa, the form with pubescent ovaries (subsp./var.

dimidiata) is replaced by a form with glabrous ovaries (subsp./var. *acutifolia*), until in Ethiopia only the latter form is found (Lucas 1968). Malesian forms of *Apodytes dimidiata* s.l., as well as *A. macrocarpa* and *A. thouvenotii*, have pubescent ovaries (Capuron 1960, 1970; Sleumer 1971), whereas those of *A. brachystylis* and *A. clusiifolia* are glabrous (Villiers 1980, Guymier 1984). Glabrous/pubescent ovaries have apparently developed independently several times in the genus.

Based on inflorescence position and style length, Sleumer (1940) established two subgenera in *Apodytes*: subgenus *Euapodytes* (type species: *A. dimidiata*) with terminal panicles and an elongated, slender style, and the monotypic subgenus *Pseudapodytes* (type species *A. brachystylis*) with reduced axillary panicles and a short, thick style. *A. geldenhuisii*, with reduced axillary racemes and an elongated slender style does not fit neatly into one of these two subgenera which, in any case, are probably artificial categories.

The sequential colour changes and red-black fruit displays in *A. abbotii* and most forms of *A. dimidiata* signify bird dispersal. Despite Von Breitenbach's (1965) claim that the fruits of *A. dimidiata* subsp. *dimidiata* are unpalatable and not taken by birds and mammals, bulbuls (several species) do eat the fruit and seem to be the most important dispersers of the seed in this taxon. However, many other frugivorous birds are also involved, notably bush and rameron pigeons as well as various starlings and white-eyes (Palmer & Pitman 1973), even mammals such as bushpigs (Breytenbach & Skinner 1982). Frost (1980) recorded no less than 18 species of birds eating fruits in the Maputaland form of *A. dimidiata* subsp. *dimidiata*, the majority being opportunists and less specialized frugivores. By far the majority of fruits were removed by the yellow-bellied bulbul [*Chlorocichla flaviventris* (Smith)], with the blackbellied starling [*Lamprotornis corruscus* Nordmann] in second place. Unfortunately, most available evidence on seed dispersal in *Apodytes* is scanty and usually based on casual observations. It is, for example, not yet clear whether the fleshy fruit appendage is consumed and the hard seed-containing nut merely dropped at the site of feeding, or whether the nuts, if ingested, are subsequently regurgitated or passed through the alimentary canal. It would be informative to establish whether the peculiar fruit colour in *A. geldenhuisii* and the different fruit colour variants in *A. dimidiata* could be linked to an association with specific primary avian or other dispersal agents.

With its asynchronous and extended blooming/fruitletting (both at the individual and population levels), the reproductive phenology of *A. geldenhuisii* is markedly different from the more or less synchronous mass blooming/fruitletting displayed by the other African members of *Apodytes*. *A. geldenhuisii* also complies with the observation that in general the longer the blooming period of a species, the smaller the number of flowers that are produced per day. Blooming and fruitletting over a long period of time, as in this species, may allow better control of the relative investment in flowers and fruits than mass blooming. It should, for example, entail less risk of reproductive failure resulting from a lack of pollinators and/or seed dispersers (Bawa 1983). In this regard the mountainous region in which *A. geldenhuisii* occurs has a very low incidence of fruit-eating birds. There are, in fact, no fruit-eating birds permanently resident in mountain fynbos (Siegfried 1983). A detailed comparative study on the reproductive ecology of *A. geldenhuisii* and some of the other African species of *Apodytes* (see, e.g., Phillips 1926, 1927), is likely to yield informative results.

One interpretation of sclerophyllous leaves is that they may be a response to low levels of soil nutrients, particularly phosphorus and nitrogen (e.g. Loveless 1962; Seddon 1974;

Sobrado & Medina 1980). The thick and rigid leaves in *A. abbotii*, compared to the thinner and flexible ones in its widely distributed (though sympatric) sister taxon, *A. dimidiata* subsp. *dimidiata*, may reflect one type of adaptation to the particular edaphic conditions associated with the sandstone-derived soils in the Pondoland Centre [PC]. What appears to be a convergent trend has been noted in members of at least three other woody genera in the latter region. The PC endemics *Canthium vanwykii* Tilney & Kok (1987), *Grewia pondoense* Burret (Wild 1984) and *Eugenia umtamvunensis* Van Wyk (1982), are all characterized by more thickly textured leaves, compared to those of their closely related and more widespread counterparts, *C. ciliatum* (Eckl. & Zeyh.) Kuntze, *G. occidentalis* L. and *E. natalitia* Sond.

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References

- BAWA, K.S. 1983. Patterns of flowering in tropical plants. In: Handbook of experimental pollination biology, eds. C.E. Jones & R.J. Little, pp. 394 – 410. Van Nostrand Reinhold, New York.
- BREYTENBACH, G.J. & SKINNER, J.D. 1982. Diet, feeding and habitat utilization by bushpigs *Potamochoerus porcus* Linnaeus. *S. Afr. J. Wildl. Res.* 12: 1 – 7.
- CAPURON, R. 1960. Contributions a l'étude de la flore forestière de Madagascar. *Notul. syst.* 16: 60 – 80.
- CAPURON, R. 1970. Notes sur les Icacinacées. *Adansonia* ser. 2, 10: 507 – 510.
- FROST, P.G.H. 1980. Fruit–frugivore interactions in a South African coastal dune forest. In: Acta XVII Congressus Internationalis Ornithologici, ed. R. Nohring, Vol. 2, pp. 1179 – 1184. Berlin.
- GUYMER, G.P. 1984. Icacinaceae. In: Flora of Australia, ed. A.S. George, Vol. 22, pp. 204 – 212. Australian Government Publishing Service, Canberra.
- LEBRUN, J.-P. & STORK, A.L. 1992. Énumération des plantes à fleurs d'Afrique tropicale, Vol. 2. Conservatoire et Jardin Botaniques, Geneva.
- LOVELESS, A.R. 1962. Further evidence to support a nutritional interpretation of sclerophylly. *Ann. Bot.* 26: 551 – 561.
- LUCAS, G.L. 1968. Icacinaceae. In: Flora of tropical East Africa, eds. A. Milne-Redhead & R.M. Polhill, pp. 1 – 17. Crown Agents for Oversea Governments and Administrations, London.
- MENDES, E.J. 1963. Icacinaceae. In: Flora Zambesiaca, eds. A.W. Exell, A. Fernandes & H. Wild, Vol. 2(2), pp. 340 – 352. Crown Agents for Oversea Governments and Administrations, London.
- OLIVER, E.G.H., LINDER, H.P. & ROURKE, J.P. 1983. Geographical distribution of present-day Cape taxa and their phyto-geographical significance. *Bothalia* 14: 427 – 440.
- PALMER, E. & PITMAN, N. 1973. Trees of Southern Africa, Vol. 2. A.A. Balkema, Cape Town.
- PHILLIPS, J. 1927. Mortality in the flowers, fruits and young regeneration of trees in the Knysna forests of South Africa. *Ecology* 8: 435 – 444.
- PHILLIPS, J.F.V. 1926. General biology of the flowers, fruits, and young regeneration of the more important species of the Knysna forest. *S. Afr. J. Sci.* 23: 366 – 417.
- POTGIETER, M.J. 1994. Contributions to the systematics of southern African Icacinaceae. M.Sc. thesis, University of Pretoria, Pretoria.
- POTGIETER, M.J. & VAN WYK, A.E. 1992. Intercellular pectic protuberances in plants: their structure and taxonomic significance. *Bot. Bull. Acad. Sin.* 33: 295 – 316.
- POTGIETER, M.J. & VAN WYK, A.E. 1994. Bark structure of the southern African Icacinaceae. *IAWA J.* 15: 161 – 170.
- SEDDON, G. 1974. Xerophytes, xeromorphs and sclerophylls: the history of some concepts in ecology. *Biol. J. Linn. Soc.* 6: 65 – 87.
- SIEGFRIED, W.R. 1983. Trophic structure of some communities of fynbos birds. *Jl S. Afr. Bot.* 49: 1 – 43.
- SLEUMER, H. 1940. Beiträge zur Kenntnis der Icacinaceen und Pteripterygiaceen. *Notizbl. bot. Gart. Mus. Berl.* 15: 228 – 257.
- SLEUMER, H. 1969. Materials towards the knowledge of the Icacinaceae of Asia, Malesia, and adjacent areas. *Blumea* 17: 181 – 264.
- SLEUMER, H. 1971. Icacinaceae. In: Flora Malesiana, ed. C.G.G.J. van Steenis, Vol. 7, pp. 1 – 87. Noordhoff International Publishing, Leyden.
- SOBRADO, M.A. & MEDINA, E. 1980. General morphology, anatomical structure, and nutrient content of sclerophyllous leaves of the 'bana' vegetation of Amazonas. *Oecologia* 45: 341 – 345.
- TILNEY, P.M. & KOK, P.D.F. 1987. A new species of *Canthium* (Rubiaceae) from southern Natal and Pondoland. *S. Afr. J. Bot.* 53: 98 – 102.
- VAN WYK, A.E. 1982. A new species of *Eugenia* L. (Myrtaceae) from southern Natal. *S. Afr. J. Bot.* 1: 158 – 163.
- VAN WYK, A.E. 1990. The sandstone regions of Natal and Pondoland: remarkable centres of endemism. In: Palaeoecology of Africa, ed. K. Heine, Vol. 21, pp. 243 – 257. A.A. Balkema, Rotterdam.
- VON BREITENBACH, 1965. The indigenous trees of southern Africa. Government Printer, Pretoria.
- VILLIERS, J.-F. 1980. Icacinaceae. In: Flore de la Nouvelle-Calédonie et Dépendances 9: 159 – 174.
- WILD, H. 1984. Tiliaceae. In: Flora of Southern Africa, ed. O.A. Leistner, Vol. 21(1). Botanical Research Institute, Pretoria.