



Reinstatement of *Dovyalis revoluta* (Flacourtiaceae, Salicaceae), with an updated key to the species of *Dovyalis* in southern Africa

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Abstract

Dovyalis revoluta, almost since described included in *D. zeyheri*, is reinstated. This restricted-range endemic from South Africa is compared with other southern African members of the genus, in particular *D. zeyheri*. Illustrations, photographs, a distribution map and a revised description are provided. Also included is an updated key to the seven currently accepted members of *Dovyalis* in the *Flora of southern Africa* region. *Dovyalis revoluta* belongs to *Dovyalis* sect. *Dovyalis*, and has only been recorded from a small area in the province of KwaZulu-Natal near the town of Hluhluwe. Most plants are known from the False Bay Park section of the Isimangaliso Wetland Park, a World Heritage Site. *Dovyalis revoluta* is clearly distinguished from other southern African members of the genus by having relatively large (ca. 22–25 mm in diam.), subglobose, orange fruit, with the surface minutely and densely papillate and the calyx lobes (tepals) tightly revolute, but not accrescent, after flowering. Furthermore, the vegetative parts are essentially glabrous and the leaves are usually entire and not distinctly three-veined from the base. Domatia are absent. A preliminary population assessment, including an estimate of the sex ratio, was conducted at False Bay Park. Based on IUCN Red List categories and criteria, a conservation assessment of “Critically Endangered” is recommended for this species.

Keywords: Flacourtiaceae, hybrid, Maputaland Centre of Endemism, narrow endemic, restricted-range, Sand Forest, taxonomy

Introduction

Dovyalis E.Mey. ex Arnott (1841: 251) (Salicaceae tribe Flacourtiaceae) is a genus of about 18 shrub and tree species (Williams 2017, Plants of the World Online 2019). The group is mainly African, with one species occurring in Sri Lanka (Williams 2017). Six species are currently recognised in South Africa, as well as the larger *Flora of southern Africa* (FSA) region, the latter which also includes Namibia, Botswana, Eswatini (formerly Swaziland) and Lesotho (Langenegger 1976, South African National Biodiversity Institute [SANBI] 2016).

While preparing a tree field guide for the eastern region of South Africa in the early 2000s (Boon 2010), one of us (RGCB) encountered trees of a member of *Dovyalis* at False Bay Park near Hluhluwe in the KwaZulu-Natal province, South Africa, that at the time were assigned to *D. zeyheri* (Sonder 1850: 10) Warburg (1893: 44) by local botanists and herbaria. However, these trees differed vegetatively quite noticeably from examples of *D. zeyheri* from the KwaZulu-Natal Drakensberg foothills and savannahs of the midlands of the province. Several follow-up visits to False Bay Park failed to yield any fertile material and the trees at this site were tentatively included in *D. zeyheri* in the field guide (Boon 2010: 372). Since then the plants at False Bay Park have been photographed and collected in flower and fruit and were found to also differ in reproductive features from material of *D. zeyheri* from elsewhere in southern Africa. Further investigation has shown that these trees match the concept and type of *D. revoluta* Thom (1971: 434), a taxon that has subsequent to its description been treated as a synonym of *D. zeyheri*, even by its describing author. The purpose of the present contribution is to make the case for reinstating *D. revoluta* as a species distinct from *D. zeyheri*. We also provide an updated identification key to the currently accepted species of *Dovyalis* in the FSA region.

The earliest known collections of *Dovyalis revoluta* are from 1944 (*Gerstner 4535 & 4735* in PRE). By the time Thom (1970) revised the genus *Dovyalis* in South Africa as part of a master's dissertation, several more collections of this entity were known, all of which were sterile or in fruit. Referred to in her dissertation as a possible new species of *Dovyalis*, Thom (1970) refrained from formally recognizing this entity as a distinct taxon, but decided to provisionally, and pending the collecting of flowering material, treat it as a mere regional variation of *D. zeyheri*. She did, however, suggest that it may well comprise a subspecies, variety or form of *D. zeyheri*, the species considered by her to have been its closest relative.

In 1970 plant ecologist E.J. Moll succeeded in collecting flowering material of this possible new taxon at False Bay Park (*Moll 5112* in PRE, K, S, WAG). This enabled Thom (1971) to formally describe *Dovyalis revoluta*, a new species based on this and several herbarium collections from a relatively small area centred in northeastern KwaZulu-Natal. However, soon after its description, *D. revoluta* was reduced by Sleumer (1972) into synonymy with *D. zeyheri*. Thom (1971: 435) may have prompted the synonymising of *D. revoluta* by stating that the “leaf shape and venation of *D. revoluta* and *D. zeyheri* are very similar and the two species might be confused in the vegetative (sic) state”. Following the approach of Sleumer (1972), Langenegger (1976, née Thom) also included *D. revoluta* in *D. zeyheri* in her account of *Dovyalis* for the *Flora of southern Africa*, a decision that has been followed to the present (for example SANBI 2016, Plants of the World Online 2019, Roskov *et al.* 2019).

Materials and methods

Descriptions and observations in the present paper are based on extensive field work by both authors while studying the tree flora of southern Africa over many years. This was supplemented by a study of the relevant literature and herbarium collections. From 2010 to 2018 a number of field visits were undertaken by one of us (RGCB) to various localities in KwaZulu-Natal (in particular False Bay Park) to study *Dovyalis* species, especially *D. zeyheri* and *D. revoluta*.

Herbarium specimens of *D. zeyheri*, *D. revoluta* and other members of the genus were examined at NH, NU, PCE, PRE, PRU and UDW. Herbarium codes follow Index Herbariorum (Thiers 2019). *Dovyalis revoluta* specimens are listed in the section “Additional collections” using the degree reference system of Edwards & Leistner (1971). Locality names and descriptions were reproduced as stated on the specimen labels. In one instance the spelling of a locality name was corrected and this is included in square brackets.

The distribution map was compiled from specimen data using ArcView 3.1 software. The original base map is based on the GTOPO30 global digital elevation model. The colours were modified in Global Mapper v6.06. Land surface area (hectares) was measured with the polygon tool in Google Earth 7.3.2 (Google Earth 2018). The conservation assessment follows the standard procedures based on IUCN guidelines (IUCN 2012).

Taxonomic treatment

Taxonomic status of Dovyalis revoluta

Based on the number of placentas and ovules in the ovary, two sections are recognized in the most recent worldwide taxonomic revision of *Dovyalis* (Sleumer 1972), namely *D. sect. Dovyalis* and *D. sect. Aberia* (Hochstetter 1844: 2) Sleumer (1972: 66). In the FSA region *sect. Aberia* is represented by only *D. caffra* (Hook.f. & Harv. in Harvey 1862: 584) Warburg (1893: 44). *Dovyalis revoluta* clearly belongs to *sect. Dovyalis*, as do the following five currently accepted species in the region: *D. longispina* (Harvey 1862: 585) Warburg (1893: 44), *D. lucida* Sim (1907: 131), *D. rhamnoides* (Burch. ex De Candolle 1824: 256) Harvey (1860: 69), *D. rotundifolia* (Thunberg 1794: 42) Harvey (1860: 70) and *D. zeyheri*.

Dovyalis revoluta is readily separated in the herbarium and field from other southern African members of the genus, including *D. zeyheri*. Features that can be used to distinguish between *D. revoluta* and *D. zeyheri* are presented in Table 1 and the two species are illustrated in Figs. 1 & 2. Diagnostic characters include shape, size and surface texture of the fruit, calyx size and shape during fruiting, flower size, hairiness of vegetative parts, presence or absence of domatia, and characters of the leaf margin and venation. Vegetatively, *D. revoluta* is more similar to *D. longispina* than *D. zeyheri*, but *D. longispina* tends to have more numerous and larger thorns, and the leaves are often distichously arranged (mainly on young plants and new growth), distinctly 3- to 7-veined at or near the base, with the secondary and tertiary venation on the abaxial leaf surface more conspicuously visible (Fig. 3A).



FIGURE 1. *Dovyalis revoluta*. A. Male flowers; borne in fascicles of up to eight flowers on previous season's growth. B. Female flowers; borne solitary on previous season's growth. C. Branchlets with ripe fruit; note rather rigid erect branches and thorns. Photographs: R.G.C. Boon.

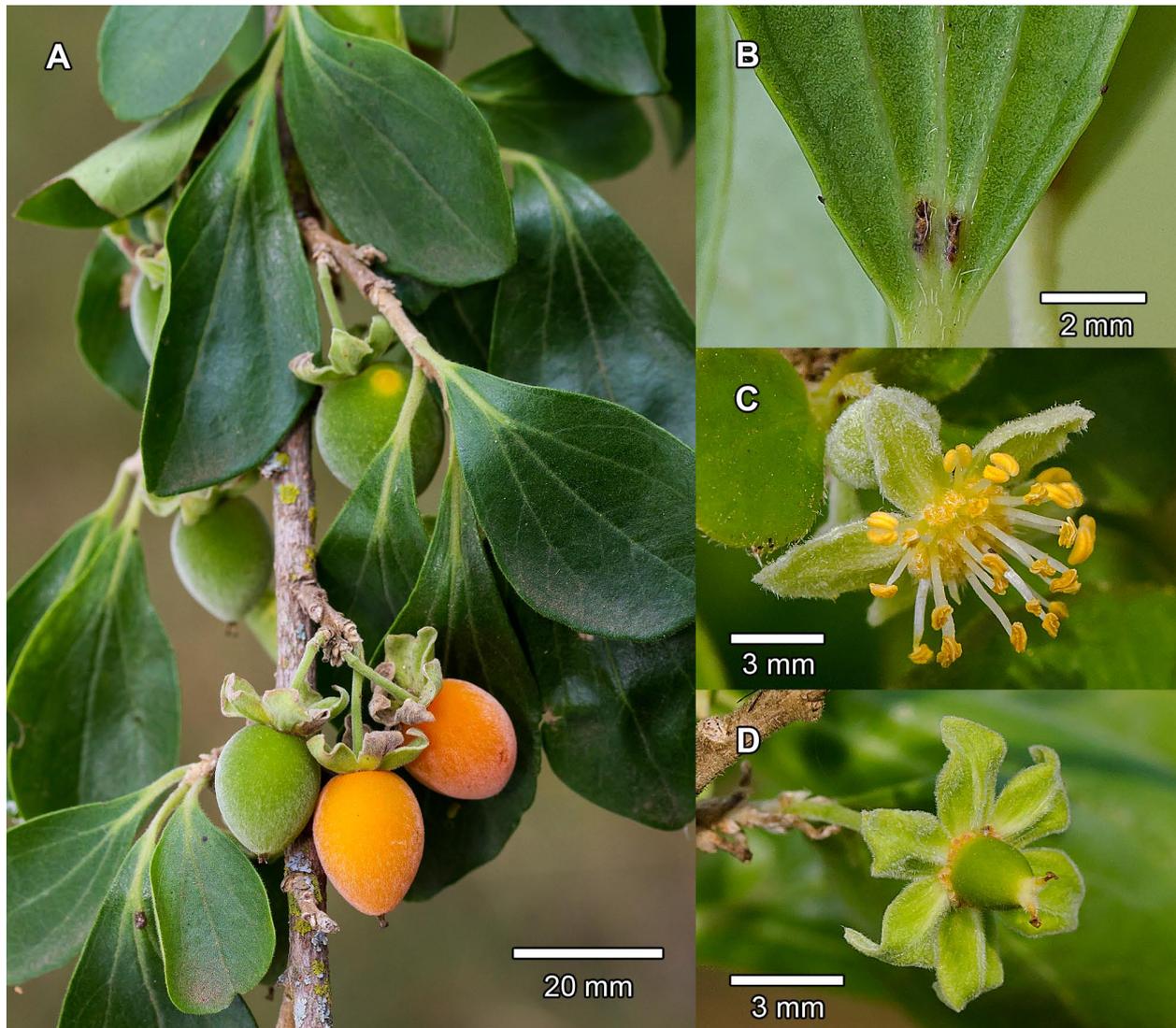


FIGURE 2. *Dovyalis zeyheri*. A. Branchlet with leaves and green and ripe fruit; all more or less pendently orientated. B. Lower side of basal portion of leaf blade showing two pocket domatia (dark-coloured due to accumulated debris) in the axils of the two primary side veins. C. Male flower. D. Female flower. Photographs: R.G.C. Boon.

Mature fruit of *D. revoluta* resembles that of *D. caffra* (Fig. 3B) in being subglobose with a velvety surface texture and in having revolute calyx lobes, but it is orange (not yellow), and although relatively large (22–25 mm in diam.), it is distinctly smaller than in *D. caffra* (30–40 mm in diam.). Furthermore, under magnification it can be seen that the velvety texture of the fruit in *D. revoluta* is due to a surface covered in densely packed, minute papillae, whereas in *D. caffra* it is due to the surface being puberulent with a dense layer of very short hairs. As already pointed out by Thom (1971), *D. lucida* is the only other member of the genus in the FSA region with a papillate fruit surface similar to that of *D. revoluta*. On the other hand, the fruit surface of *D. zeyheri* is quite different from all these species in being puberulous with golden-brown hairs.

Dovyalis rotundifolia stands somewhat apart from the other members of *Dovyalis* in the FSA region in having glabrous seeds. All the other species, including *D. revoluta*, have seeds with a hairy (woolly/villose) testa (Fig. 3C). The origin and development of these seed hairs were studied in *D. caffra* by Steyn *et al.* (2005). Hairs are unicellular and develop from the outer epidermis of the outer integument. They grow perpendicular to the seed surface (instead of becoming depressed) and eventually permeate the space between the seeds and the pericarp. A noteworthy feature of *D. revoluta* is that, at 14 × 9 mm, the species has considerably larger seeds than the other *Dovyalis* species in the FSA and adjacent *Flora Zambesiaca* (FZ) regions (Wild 1960, Langenegger 1976). It also has larger seeds than *D. keniensis* Williams (2017: 1) from East Africa, whose seeds measure 6 × 3 mm (Williams 2017). The next largest *Dovyalis* seeds in the FSA and FZ regions belong to *D. lucida*, which are recorded as 9 mm long in Wild (1960) and 11 mm long in Langenegger (1976), and *D. caffra* with seeds 10 mm long (Langenegger 1976).

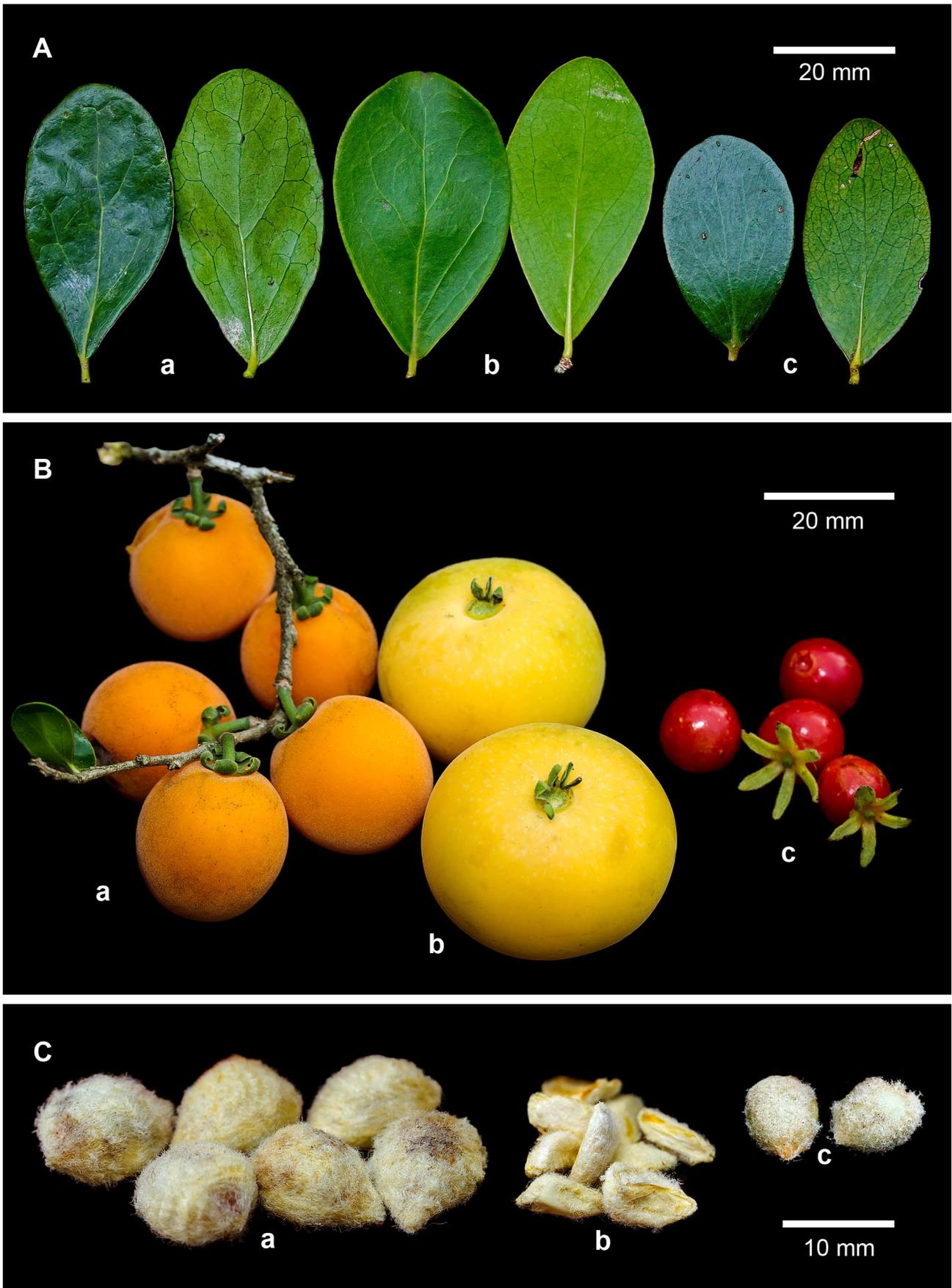


FIGURE 3. *Dovyalis revoluta* (a), compared with *D. caffra* (b) and *D. longispina* (c), the two members of the genus with which its distribution range overlaps at False Bay Park, the location of its largest known population. A. Leaves; adaxial side left, abaxial side right. B. Ripe fruit. C. Seed, removed from pericarp and cleaned to show the hairy surface and variation in size. Photographs: R.G.C. Boon.

TABLE 1. Selected features distinguishing between *Dovyalis revoluta* and *D. zeyheri*.

	<i>D. revoluta</i>	<i>D. zeyheri</i>
Habit	Small tree with erect branchlets. Known specimens reach about 7 m, but are more typically 3–4 m high. Genets unknown. Trunk to 150 mm diameter	Small tree to 11 m, often with arching to pendent branchlets. May form genets. Trunk to 300 mm diameter
Bark	Pale or dark; most faintly fissured, cracking into blocks on oldest stems, but not as distinctly as in <i>D. zeyheri</i>	Pale with fairly deep longitudinal fissures and cracking into irregular, rectangular blocks
Vestiture	Mature vegetative parts at False Bay Park glabrous. Coppice pubescent. Plants at KwaKhangela Royal Palace puberulous	Ultimate branchlets, thorns and leaves usually pubescent, rarely glabrous
Leaf arrangement	Well-spaced	Well spaced or clustered on slender brachyblasts
Leaf blade texture	Coriaceous	Thin and soft, rarely coriaceous
Leaf venation	Veins essentially flush with leaf blade. Blade usually not distinctly 3-veined from base; on occasion obscurely so. Domatia absent	Primary veins raised on abaxial surface. Blade usually prominently 3-veined from near base with pocket domatia usually present in axils of principal lateral veins
Leaf blade margin	Usually entire, occasionally faintly serrate in apical half	Often crenate in apical half. Well-spaced gland-tipped serrations may be present on basal half. Occasionally entire
Flower size and calyx lobes (tepals)	Relatively smaller. Male calyx (tepals) to 3 × 2 mm. Female calyx (tepals) to 4 × 2 mm, not accrescent, usually tightly revolute in fruit	Relatively larger. Calyx (tepals) 4–5 × 2–2.5 mm, accrescent, spreading or somewhat recurved, but not tightly so; not revolute in fruit
Nectaries (male flowers)	Glabrous	Densely setulose-ciliate
Style and stigma	Styles 2. Stigma bilobed	Styles 2 or 3. Stigma bilobed
Fruit	Subglobose, ca. 22–25 mm in diameter. Velvety to touch due to dense, minute papillae	Ellipsoid ca. 20 × 13 mm. Velvety puberulous with golden-brown hairs
Seeds	Ca. 14 mm long, villose	Ca. 7 mm long, villose

Distribution and habitat

Dovyalis revoluta is near-endemic to the Maputaland Centre of Endemism, a biogeographical region rich in restricted-range plants and animals, the core area of which is centred in northeastern KwaZulu-Natal (South Africa) and southern Mozambique (Van Wyk 1996, Van Wyk & Smith 2001). The Maputaland Centre is at the northern end and forms part of the Maputaland-Pondoland-Albany Hotspot, one of 36 global biodiversity hotspots (Steenkamp *et al.* 2004). The distribution of the species based on herbarium records is shown in Fig. 4, along with that of *D. zeyheri* in the FSA region.

Reference to correctly identified herbarium specimens and field experience shows that *D. zeyheri* does not occur in at least the KwaZulu-Natal part of Maputaland and the ranges of the two species are mutually exclusive. The lowest elevation from which a specimen of *D. zeyheri* has been taken in KwaZulu-Natal is to the north of Nongoma at approximately 480 m (*Acocks 13020* in PRE). The species has also been collected inland of the Umtamvuna Nature Reserve at an elevation of 550 m (*Abbott 7018* in NH, PRU). On the contrary, most *D. revoluta* specimens have been collected at False Bay Park where trees grow near the Lake *St Lucia* at 20–50 m above sea level.

Three species of *Dovyalis* occur in the forest and forest margins at False Bay Park, namely *D. longispina*, *D. revoluta* and *D. caffra* (Fig. 3). Although this forest is classified and mapped as Northern Coastal Forest (FOz 7) in Mucina & Rutherford (2006), it has strong affinities with Sand Forest (FOz 8), a vegetation type near endemic to the Maputaland Centre (Van Wyk & Smith 2001). Forty-one mature specimens of *D. revoluta* are known in an area of

about 55 ha (measured with the polygon tool in Google Earth 7.3.2) between Lister and Sandy Points, False Bay Park. An approximate central point of this polygon is 27°58'20.77"S, 32°22'13.34"E. The forest has not been systematically searched for the species and much apparently suitable habitat remains to be surveyed. Elsewhere in False Bay Park the species has also been observed just over 3 km south of Sandy Point at the Dukandlovu camp. No specimens of *D. revoluta* were found during a visit to the nearby Nibela Peninsula (27°59'18.58"S, 32°25'20.34"E), nor does the species occur (RGCB, pers. obs.) in the remnant Sand Forest at the nearby Sand Forest Lodge (27°58'24.85"S, 32°19'48.43"E) or on a smallholding (27°58'47.77"S, 32°21'11.31"E) immediately west of the protected area (F. du Randt, pers. comm.). The species also appears to be absent from accessible forest at the Bonamanzi Nature Reserve (28°3'56.46"S, 32°18'36.41"E) near the town of Hluhluwe.

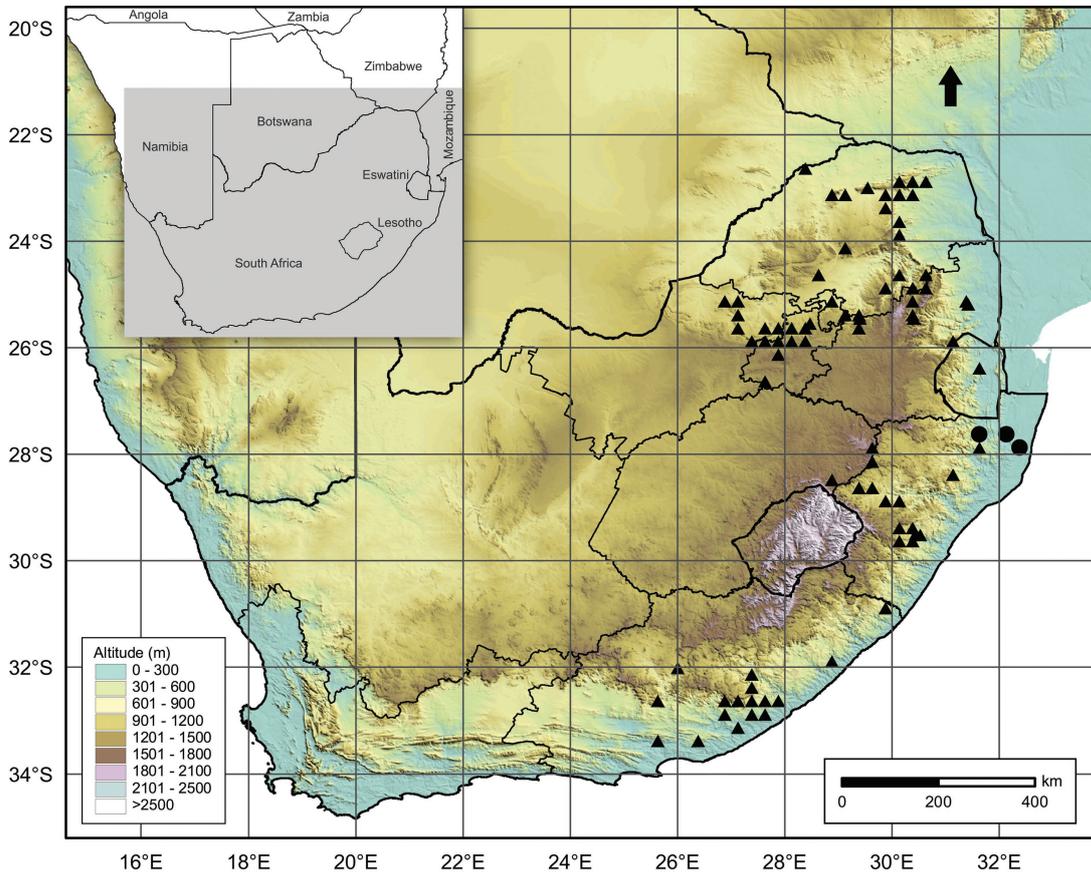


FIGURE 4. Topographical map showing the known distribution (black dots) of *Dovyalis revoluta* in northeastern KwaZulu-Natal, South Africa. Also depicted is the known distribution of *D. zeyheri* (black triangles) in the *Flora of southern Africa* region, with the arrow denoting that it is also found further north in Africa. The insert shows a map of southern Africa with names of countries; the grey rectangle indicates the area depicted by the topographical map.

All herbarium specimens seen, barring the recently collected *Boon 126* and *Gerstner 4535* taken in 1944, are from False Bay Park. The *Gerstner* specimen is sterile and, although it was cited as a paratype for *D. revoluta* by Thom (1970), annotations on the specimen indicate that it had at times also been identified as *D. caffra* and *D. rhamnoides*. Initially False Bay Park was the only locality at which one of us (RGCB) had observed *D. revoluta* and the identification of *Gerstner 4535* had been problematic, hence it was thought that *D. revoluta* may be confined to False Bay Park. However, in the course of preparing the aforementioned field guide (Boon 2010), the first author was given photographs taken at the KwaKhangela Royal Palace near Nongoma by S. Louw of a *Dovyalis* species in fruit resembling *D. revoluta*. This site is approximately 70 km inland from False Bay Park. The locality was visited by one of us (RGCB) on 30 April 2018 and four trees were found in short, closed savannah on a rocky, southeast-facing, moderately-sloping hillside at an elevation of 400 m above sea level. Although the plants were sterile, they were very similar to those at False Bay Park and are here assigned to *D. revoluta*. No other *Dovyalis* species were seen at the Palace. Upon confirming that *D. revoluta* is not confined to False Bay Park, *Gerstner 4535* was re-examined closely and it too seems to be a good match for *D. revoluta*, a conclusion which is in agreement with Thom's identification in 1970.

With regard to the distribution of *D. revoluta*, specific mention of the collection *Ward 4781* is necessary. The original, in UDW, is labelled “*Dovyalis sp. nov.*” and was collected on 18 October 1963 at False Bay Park. Duplicates of this collection are housed at NH, NU and PRE. The collector’s number and notes for the duplicates match the original, but the locality recorded for the duplicates is Hluhluwe Game Reserve, the date 17 October 1963 and the elevation is given as “c. 300 feet”. C.J. (Roddy) Ward’s notes and collector’s books were consulted and according to his notes on 17 October 1963 he was in the Hluhluwe Game Reserve and collected various herbarium specimens, none of which were *Dovyalis* species. The following day (18 October 1963) he was at False Bay Park and collected specimens from three *Dovyalis* species. He then moved on to the Umfolozi River floodplain and Richard’s Bay. Notably, on 18 October 1963 *Edwards 3199* (in NU, PRE) was also collected at False Bay Park. The *Ward 4781* and *Edwards 3199* specimens and accompanying notes are sufficiently similar to suggest that the two botanists collected together on that day. Thus the labels on the *Ward 4781* duplicates have almost certainly been incorrectly transcribed from the original and these collections cannot be taken as evidence that the species occurs in the Hluhluwe Game Reserve.

Phenology and sex ratio

Dovyalis revoluta usually flowers in September and October and the fruiting period is from October to January. Later flowering was observed on some plants in December 2018 and December 2019 (G. Lang, pers. comm.) and may have been triggered by good rainfall received earlier in the month.

From 2003 to 2015 the first author made many visits to False Bay Park in search of flowering and fruiting plants of *D. revoluta*, but without success. It thus seems likely that the trees do not flower or fruit every year. Fortunately a local resident (G. Lang) agreed to keep known trees under observation and in late December 2016 and early January 2017 he found six plants heavily laden with fruit. These were photographed by the first author. Then in September 2018, at the beginning of the following growing season, G. Lang advised that the plants were beginning to flower. The first author travelled to False Bay Park on the 21 and 22 September 2018 and 29 and 30 September 2018 to obtain photographs and herbarium specimens. During those visits, 22 individuals out of 41 known trees were in flower, of which only one was female. The female tree was one of the six specimens that fruited during the previous growing season. This specimen bore very few flowers and young fruit in September 2018, while in the previous growing season it fruited well. The male plants, on the contrary, flowered prolifically in September 2018. It is surmised that the female plants had reduced reserves following the previous season’s successful fruiting and this impacted on flowering in the spring of 2018. The sex of 27 of the 41 plants is known, namely 21 male and six female trees, suggesting a male-biased sex ratio. However, if all 14 plants that did not flower in September 2018 are female, the sex ratio would be almost 1:1.

Conservation

Dovyalis revoluta occurs at False Bay Park where 41 trees have been recorded. Four trees occur at the KwaKhangela Royal Palace near Nongoma and a single old collection is from between Ubombo and Mkuze towns. In all, less than 50 trees are known and, given the paucity of collections outside of False Bay Park, the species may be rare and highly localised. Most known specimens are protected in the Isimangaliso Wetland Park and this sub-population is well conserved. Taxa with total populations of less than 50 mature individuals are categorised as Critically Endangered (CE D) according to the IUCN Red List Category and Criteria (IUCN 2012), the status here awarded to the species in the light of current knowledge. However, it seems probable that there are more mature individuals at False Bay Park, but site knowledge suggests it is unlikely that this sub-population exceeds 200 individuals. As the total population is predicted to be less than 250 mature individuals, the species is likely to be categorised as Endangered (EN D) should more plants indeed be discovered in future.

Etymology and common names

The specific epithet refers to the calyx lobes that are tightly revolute in fruit. The proposed English common names are Zulu wild-apricot or Zulu Kei-apple and *zuluwildeappelkoos* is suggested as the Afrikaans common name. The isiZulu name is unknown, but is likely to be *umnyazuma* in common with most other *Dovyalis* species.

Notes

Given that *D. caffra* and *D. longispina* grow sympatrically with *D. revoluta* and flower more or less simultaneously, it is possible that *D. revoluta* could have originated as a fertile and now stable hybrid of these two species. Shared features and differences are discussed briefly above. However, the ranges of the former two species also overlap elsewhere in coastal KwaZulu-Natal and no putative hybrids have ever been recorded between these two species. Hybridization is also considered unlikely because the two species belong to different sections.

The Maputaland Centre is known for what appears to be many neo-endemics and speciation is still active considering the many endemic taxa differentiated from close relatives at infraspecific level (Van Wyk 1996, Van Wyk & Smith 2001, Matthews 2005). The outlier plants near Nongoma (where *D. longispina* does not occur) may have been established through long-distance dispersal, including by anthropogenic means considering the edibility of the fruit. Honey bees and several other smaller bee species were observed visiting male flowers at False Bay Park. However, the main pollinators have not yet been established, but are almost certainly insects considering the relatively small size of the flowers and the fact that both male and female flowers produce ample nectar.

The ripe fruit is edible and the flesh is pleasantly sweet, but sour near the seeds. Although the seeds are suspected to be primarily bird-dispersed, no fruit-eating birds were seen visiting the plants. However, other fruit eaters such as the vervet monkey, *Chlorocebus pygerythrus pygerythrus* (Cuvier 1821: 2), may also play a role. Collector's notes (Gerstner 4735) state that the fruit are enjoyed by nyala antelope, *Tragelaphus angasii* (Angas 1849: 89). Much fruit may abort when green and fall to the ground.

Dovyalis revoluta grows easily and rapidly from cleaned and freshly sown seed. Some specimens planted in January 2018 had attained a height of 1.5 m by March 2019 (G. Lang, pers. comm.). The seeds are suspected to be recalcitrant.

Key to the species of *Dovyalis* in the Flora of southern Africa region

We here present an updated identification key to the, now seven, accepted species of *Dovyalis* in the *Flora of southern Africa* region. Based on the key of Langenegger (1976), we have made several amendments in the new key in an attempt to improve its practicability. It is often difficult to identify members of *Dovyalis* to species level when only vegetative material is available, and then a combination of several characters is nearly always required. The most reliable diagnostic characters are provided by the fruit and seeds. Unfortunately fruit are often not readily available because plants are dioecious, fruiting tends to be erratic and the fruiting period brief. Ripe fruit are also quickly removed by fruit eaters. Of particular taxonomic significance are the size, shape, colour and surface texture of the ripe fruit, the number of seeds per fruit and whether the seeds are glabrous or hairy. It is species-specific whether the exocarp is glabrous or velvety. Fruit with a velvety feel may have the surface puberulent, puberulous, or minutely papillate (papillulose), character states that are constant for a species. Magnification is required to correctly identify these three states, in particular to distinguish between puberulent and papillate. In the key to the species, the more important diagnostic characters are introduced first in the leads, followed by often more readily available albeit less reliable characters. Characters are best used in combination for positive identifications. The broad geographical range is supplied for each species as it can be helpful when attempting to identify plants in the field.

1. Ovary with 5–7 placentas, each placenta with 2 ovules, styles 5–7; fruit yellow, velvety puberulent, 30–40 mm in diam.; seeds ca. 12; leaves clustered on cushion-like or short, relatively thick (3–4 mm in diam.) brachyblasts (but alternate on young shoots); South Africa (eastern and northern parts), Eswatini, southern Mozambique and Zimbabwe *D. caffra*
- Ovary with 2 or 3 placentas, each placenta with 1 ovule; styles 2 or 3; fruit red, orange-red or orange, glabrous, puberulous or minutely and densely papillate, 6–25 mm in diam.; seeds 1–3; leaves alternate, sometimes fasciculate, but then borne on short, relatively thin (1.5–2.5 mm) brachyblasts 2
2. Fruit glabrous, red to orange-red; plants heavily armed with thorns, the latter usually up to ca. 60–80 mm long 3
- Fruit velvety puberulous or densely minutely papillate, but appearing velvety puberulous to the naked eye, orange to orange-red; plants without thorns, or sparsely to heavily armed, with thorns if present usually tending to be shorter, up to ca. 30–40 mm long, but up to 60 mm in some cases 5
3. Fruit red, without whitish spots; calyx (tepals) usually fringed with stipitate or sessile glands, noticeably accrescent in fruit; leaves distichously arranged in young and mature growth; lamina ovate to elliptic-ovate, base cordate to truncate, mid-green, thinly-textured, glabrous or puberulous on the veins, margin entire to crenate, 3(–5)-veined from or near the base, secondary veins along the main vein tending to spread towards the leaf margin; shrub or small, slender tree to 7 m; South Africa (Eastern Cape to Mpumalanga) and Eswatini *D. rhamnoides*
- Fruit red to orange-red, with whitish spots; calyx (tepals) entire, or sometimes with a few sessile glands in the distal half, not accrescent, or slightly so; leaves spiraled on mature growth, sometimes distichously arranged on young growth; lamina sub-orbicular, obovate to rhomboid-elliptic, base cuneate, dark green, coriaceous, glabrous when mature, margin entire, usually 5-veined from near the base, secondary veins tending to ascend towards the leaf tip; shrubs or medium-sized trees to 15 m; South Africa (Eastern Cape and KwaZulu-Natal) to Eswatini and southern Mozambique, usually at or near the coast, especially on coastal sand dunes 4
4. Seed with testa hairy (villose); female flowers with calyx (tepal) lobes 3–5 mm long, slightly accrescent to about 6 mm; fruit red to orange-red, to 15 mm in diameter; leaves obovate to rhomboid-elliptic, rarely orbicular; medium-sized tree to 15 m, at low elevations and often on coastal dunes in South Africa (KwaZulu-Natal), Eswatini and southern Mozambique *D. longispina*
- Seed with testa glabrous; female flowers with calyx (tepal) lobes 1–2 mm long, not accrescent; fruit red, to 10 mm in diameter; leaves sub-orbicular to obovate; shrub or small tree to 7 m; confined to a small area in South Africa's Eastern Cape (coastal dunes from just north of East London to just west of Port Elizabeth) *D. rotundifolia*

5. Fruit velvety puberulous (hairs golden-brown), orange; leaves and branchlets usually hairy; lamina distinctly 3-veined from or near the base, pair of pocket domatia usually present abaxially in axils of the two primary side veins; female flowers with calyx (tepal) lobes 4–6 mm long in anthesis, accrescent; South Africa (widespread in eastern and northern parts), Eswatini, southern Mozambique and Zimbabwe *D. zeyheri*
- Fruit densely and minutely papillate (velvety to the touch), orange or orange-red; leaves and branchlets usually glabrous or essentially so; lamina not distinctly 3-veined from or near the base, domatia absent; female flowers with calyx (tepal) lobes 1.5–4.0 mm long in anthesis, not accrescent 6
6. Fruit ellipsoid, to 15 mm in diameter, orange-red; female flowers with calyx (tepal) lobes 1.5–2.0 mm long in anthesis; trees of temperate forest or forest margins; thorns absent or sparse; leaves entire or with widely scattered, distinct serrations in coppice and young plants; South Africa (eastern and northern parts), Eswatini, eastern Zimbabwe and adjacent parts of Mozambique *D. lucida*
- Fruit subglobose, to 25 mm in diameter, orange; female flowers with calyx (tepal) lobes 4 mm long in anthesis; trees of subtropical/tropical forest or forest margins and savannah; thorns present; leaves usually entire, occasionally with a few indistinct serrations at the leaf apex; South Africa, confined to a small area centered on False Bay Park, northeastern KwaZulu-Natal *D. revoluta*

Amplified description of Dovyalis revoluta

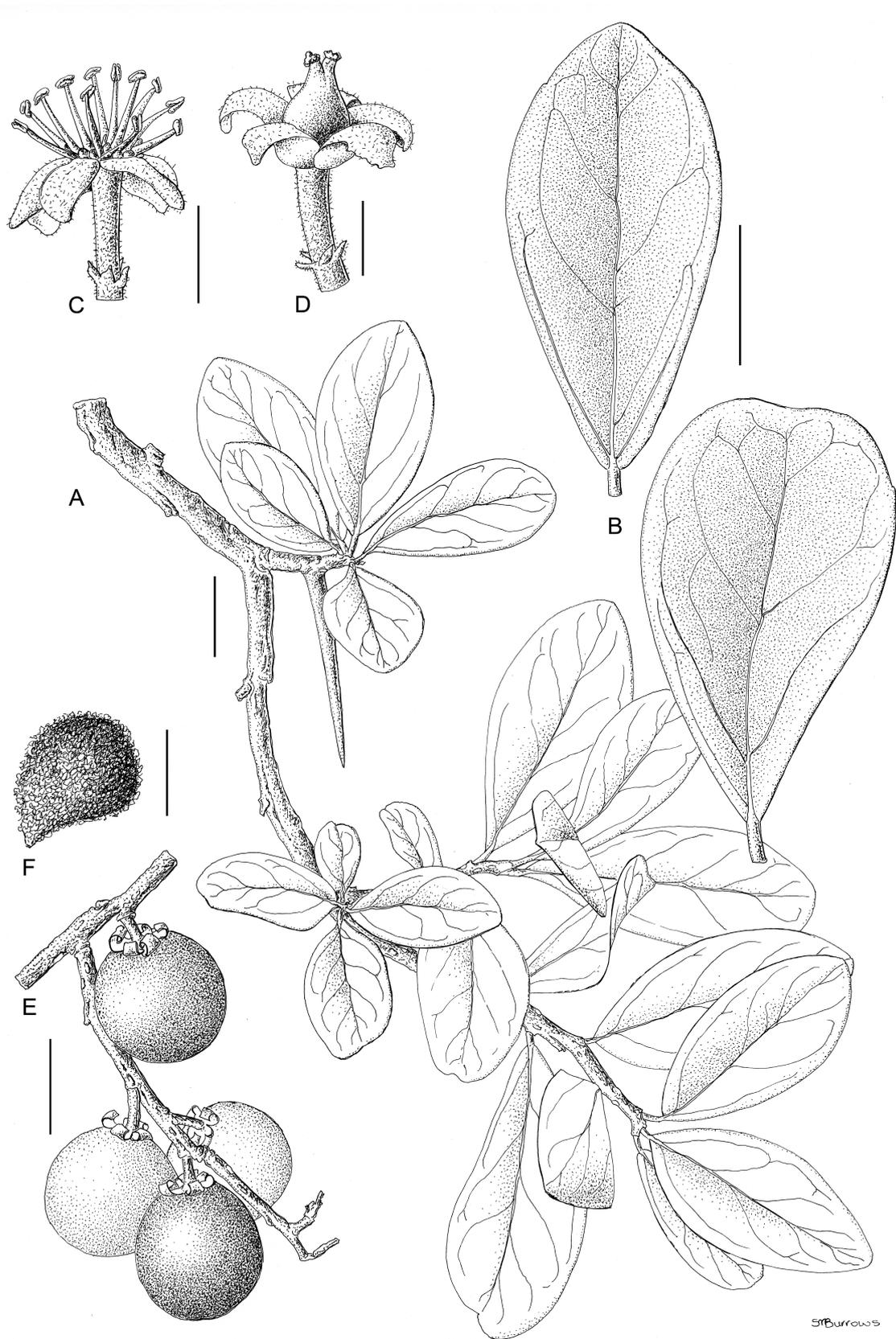
Dovyalis revoluta Thom (1971: 434) (Figs. 1, 3a & 5)

Type:—SOUTH AFRICA. KwaZulu-Natal: False Bay Park, 1 mile from gate, degraded sand forest, 100 ft [30 m], 2732CD, 18 October 1970, *E.J. Moll 5112* (holotype PRE0299971-0!; isotypes K000231236!, S10-11937!, WAG0001386!).

Illustration: Boon (2010: 373, as “*Dovyalis zeyheri*—Nongoma”).

Tardily deciduous tree, dioecious or rarely polygamous [sensu Thom (1971); all plants observed by the first author at False Bay Park apparently dioecious], 5(–7) m high. *Crown* open to roundish, usually not well formed. *Trunk* single- or multi-stemmed with 2–6 stems, mostly crooked and leaning, up to 100(–150) mm in diam.; bark pale grey-brown, sometimes almost black when covered in lichen, shallow fissures form irregular blocks on some specimens. *Branchlets* often more or less erect, lenticellate, red-brown when young. *Thorns* to 30(–60) mm long. *Leaves* alternate, arranged in erect, open, spiralled clusters, exstipulate, blade shiny, mid to dark green above, distinctly paler green below, glabrous at False Bay Park, coppice leaves densely velvety, mature leaves somewhat hairy near Nongoma, obovate, to about 50 × 25(–30) mm, apex obtuse to rounded, base cuneate, midrib and secondary veins paler than the adaxial surface, midrib raised below, secondary veins in 3 or 4 pairs, brochidodromous, sometimes indistinctly 3-veined from the base, domatia absent, secondary and tertiary veins dark green and distinct on abaxial surface, blade coriaceous, margin light green, drying distinctly pale, wavy and rolled under, entire or occasionally with very fine, gland-tipped serrations on the upper half; petiole glabrous, 3–4 mm long. *Inflorescence* axillary, sessile; male inflorescence glomerate, in fascicles of up to 8 flowers, borne on previous season’s growth, pedicels pubescent, 3–4 mm long, surrounded at the base by triangular, hairy, brown bracts about 1 mm long, corolla 0, calyx (tepals) 4- to 6-lobed, lobes to 3 × 2 mm, yellowish green, ovate-elliptic, pubescent, hairs white, stamens 15–25, filaments white, 3 mm long, surrounded at the base by glabrous nectaries forming a honeycomb structure, anthers bilocular, dehiscing by means of longitudinal slits, pollen yellow; female flowers pedicellate, solitary, borne on previous season’s growth, yellowish green, pedicels pubescent, 4–7 mm long, surrounded at the base by small pubescent scale-like bracts, calyx (tepals) 5- to 7-lobed, lobes oblong, to 4 × 2 mm, pubescent, hairs white, apex acute, revolute, not accrescent in fruit, ovary superior, green, with two parietal placentas, each placenta with one ovule, unilocular, surrounded at the base by a glutinous, sparsely hairy, lobed annulus; styles 2, channelled. *Fruit* a subglobose berry, 22–25 mm in diameter, densely and minute papillate (velvety to the touch), initially green ripening through greenish yellow to bright orange. *Seeds* 2(or 3), 14 × 9 mm, densely woolly, embedded in fleshy pulp.

Additional specimens examined:—SOUTH AFRICA. KwaZulu-Natal: Khangela Royal Palace, (2731DA), 30 April 2018, *R. Boon 126* (NH!); On the way from Ubombo Magistracy to uGaza Mountain Mkuzi [Mkuze] Station (2732CA), 26 April 1944, *F.J. Gerstner 4535* (PRE!); Bushveld Reserve of False Bay, Hlabisa District, near Mr Redman’s Camp in the birds’ sanctuary, (2732CD), 27 July 1944, *F.J. Gerstner 4735* (paratype PRE!); False Bay, (2732CD), 18 October 1963, *D. Edwards 3199* (paratypes NU!, PRE!); False Bay Park, 18 October 1963, *C.J. Ward 4781* (paratypes NH!, PRE!, NU!, UDW!); 8 miles from Hluhluwe–False Bay, (2732CD), 29 November 1965, *E.J. Moll 2823* (paratypes NH!, NU!, PRE!); False Bay, sand forest, (2732CD), January 1982, *D. Lawson 33* (NH!); False Bay Park, (2732CD), 4 October 1982, *D. Lawson 433* (NH!); False Bay Park, on the roadside near Lister Point, (2732CD), 30 March 2014, *R.G.C. Boon 66* (NH!); False Bay Park, road to Lister Point, at intersection of road and cutting for powerline, (2732CD), 29 September 2018, *R.G.C. Boon & B. Church 147* (NH!); False Bay Park, track between Rocky and Sandy Points, (2732CD), 29 September 2018, *R.G.C. Boon & B. Church 148* (NH!).



SBurrows

FIGURE 5. *Dovyalis revoluta*. A. Leafy branchlet. B. Leaves. C. Male flower. D. Female flower. E. Fruiting twig. F. Seed. Scale bar = 10 mm (A & B), 4 mm (C & D), 20 mm (E), or 8 mm (F). A & B based on photographs, *Edwards 3119*, *Moll 5199* and *Boon & Church 147*; C from photograph, *Moll 5199* and *Boon & Church 147*; D from photograph and *Moll 5122*; E from photograph and *Edwards 3199*; F from photograph. Artist: Sandie Burrows.

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