



New relatives of *Oxalis pes-caprae* (Oxalidaceae) from South Africa

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Key words

new species
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Abstract The genus *Oxalis* in southern Africa contains more than 200 species, with the vast bulk of species in the Greater Cape Floristic Region (GCFR). Recent fieldwork has suggested that many await discovery. Here we investigate the identity of two apparently undescribed *Oxalis* species from Northern Cape, South Africa, using morphological comparisons with closely related taxa. We provide a preliminary phylogenetic placement using DNA sequence-based analyses of the Internal Transcribed Spacer (ITS) region. Both putative new species are distinguished from all known *Oxalis* species based on macro-morphological traits. Molecular data placed both within a clade consisting of the weedy *O. pes-caprae* and its close relatives. *Oxalis hirsutibulba* sp. nov. is characterised by densely hairy bulb tunics, a trait absent from all known members of the *O. pes-caprae* clade. *Oxalis fenestrata* sp. nov. is unique in producing apple green succulent stems and leaflets usually with translucent white markings at their incisions. We also provide the first phylogenetic placement of the GCFR narrow endemic *O. lasiorrhiza* in the *O. pes-caprae* clade. In conjunction with several other recent discoveries, these two new species and the phylogenetic placement of *O. lasiorrhiza* show that the *O. pes-caprae* clade is much more speciose than previously estimated.

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INTRODUCTION

Oxalis contains more than 500 described species (Salter 1944, Lourteig 1994, 2000). South America (c. 250 spp., Lourteig 1994, 2000) and southern Africa (c. 210 spp., Salter 1944, Oliver 1993, Williamson 1999) represent the two major centres of *Oxalis* diversity, with the former being the putative place of origin for the genus (Oberlander et al. 2011). South America also hosts the largest diversity in terms of *Oxalis* growth forms, including shrubs, herbs, annuals, vines and geophytes. Southern African members, in contrast, are all bulbous perennials with above-ground plant parts borne on seasonal rhizomes emergent during the rainy season. The greatest diversity of southern African taxa is confined to Western and Northern Cape in South Africa, corresponding closely to the Greater Cape Floristic Region (GCFR) sensu Born et al. (2007). However, large areas, especially those close to the frontier with Namibia, remain poorly explored for *Oxalis*. This is largely due to their inaccessibility and erratic rainfall.

Increased collecting effort and the use of molecular identification tools has led to the discovery and description of new South African *Oxalis* species at an increasing rate over the past few decades (Oliver 1993, Williamson 1999, Manning & Goldblatt 2008, Dreyer et al. 2009, 2013, 2014, Oberlander et al. 2009, Roets et al. 2013, Suda et al. 2013). The use of molecular techniques for determining phylogenetic relationships in *Oxalis* is especially useful, as many species are morphologically extremely variable, which often leads to misidentifications. This plasticity is evident at all taxonomic levels, as is reflected in the incongruence between morphological (Salter 1944), paly-

nological (Dreyer 1996) and molecular phylogenetic (Oberlander et al. 2011) hypotheses. For example, morphology-based classification divides southern African species into 9 sections (Salter 1944), with sect. *Cernuae* containing all southern African species with pseudo-umbellate inflorescences. However, this character is plesiomorphic for southern African *Oxalis* and molecular phylogenetic analyses have shown this section to be para- or even polyphyletic (Oberlander et al. 2011).

The most recent molecular phylogenetic reconstruction of southern African *Oxalis* divides this group into three major clades: a clade containing the weed *O. pes-caprae* L. and its relatives (the *O. pes-caprae* clade, including members of sect. *Cernuae* subsections *Eu-Cernuae*, *Costatae* and *Purpuratae* sensu Salter (1944)), a clade containing members of sect. *Cernuae* subsect. *Lividae* (sensu Salter 1944), and a large clade containing the majority of southern African taxa (Oberlander et al. 2011). Twelve taxa are currently recognized as members of the *O. pes-caprae* clade: *O. compressa* L.f., *O. copiosa* F.Bolus, *O. knuthiana* T.M.Salter, *O. nivea* Roets, Dreyer & Oberl., *O. pes-caprae*, *O. petricola* Dreyer, Roets & Oberl., *O. pseudo-cernua* R.Knuth, *O. purpurascens* T.M.Salter, *O. purpurata* Jacq., *O. rosettifolia* Roets, Dreyer & Oberl. and *O. rubricallosa* Oberl., Dreyer & Roets (Oberlander et al. 2010, 2011, Dreyer et al. 2013, Roets et al. 2013). All current members of the *O. pes-caprae* clade have trifoliate leaves with cordate leaflets, pseudo-umbellate (rarely reduced to single-flowered) inflorescences and endospermous seeds (Salter 1944). The majority of these species also produce bulbs with longitudinally finely- to coarsely-grooved tunics. However, it should be noted that none of these characters are synapomorphies for this clade, and even this combination of characters is found (although rarely) in other southern African *Oxalis* clades. Based on these characters, the Namibian endemics *O. luederitzii* Schinz and *O. schaeferi* R.Knuth, and the poorly known *O. haedulipes* T.M.Salter and *O. laxicaulis* R.Knuth are probably also members of this clade, this requiring confirmation through future molecular phylogenetic

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analyses. Several morphological characters also suggest the possible membership of the GCFR narrow endemic *O. lasiorrhiza* T.M.Salter within the *O. pes-caprae* clade. Although this species has been placed in sect. *Oppositae* by Salter (1944) due to its single-flowered inflorescences, our fieldwork has indicated that 2–3-flowered inflorescences are not uncommon in the species.

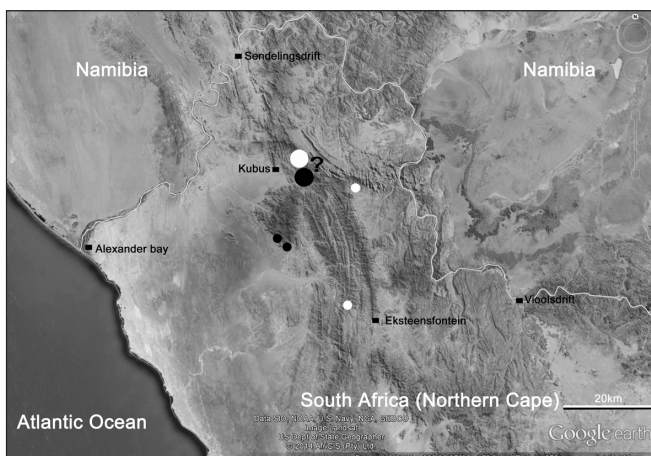
Recent collections of *Oxalis* from Northern Cape revealed the presence of numerous apparently undescribed species (unpubl. data). Two of these produce pseudo-umbellate inflorescences and may therefore also belong in the *O. pes-caprae* clade. Here we evaluate the identity of these through morphological comparisons with all taxa currently included or reasonably expected to be placed in this clade. We further assess the phylogenetic placement of these taxa based on DNA sequence data from the ITS region.

MATERIALS AND METHODS

Field observations

Specimens of the putative new taxa were collected on south- and west-facing hill slopes in the Richtersveld Conservancy (a UNESCO World Heritage site, Fleminger 2008) in Northern Cape, South Africa, and the region bordering it to the south. All collections were made in June 2012, after higher than average rains. Specimens of the first new species (hereafter referred to as *O. hirsutibulba*) were collected from two localities c. 40 km apart (Map 1). At the northern locality, specimens were found growing on a south-facing hillside in Western Gariep desert vegetation (Mucina & Rutherford 2006) on the Richtersberg. At the southern locality, specimens were found on a south-facing rocky hillside in Richtersveld succulent Karoo vegetation (Mucina & Rutherford 2006). Individuals were confined to cooler cracks and crevices in these habitats and were never abundant, with 200–300 individuals encountered at each locality. Specimens of the second taxon (hereafter referred to as *O. fenestrata*) were collected from a granite boulder-dominated hillside at the south-western end of the conservancy. This species is apparently much more localised than the former and consisted of two populations about 1.3 km apart (Map 1). Plants were confined to coarse gravel in the shade of large boulders or of *Ficus ilicina* (Sond.) Miq. At both sites, less than 50 individuals were counted.

During June 2013 we were able to collect herbarium (*Dreyer, Roets & Oberlander MO1555*) and living specimens of *O. lasiorrhiza*, and were therefore able to verify its phylogenetic posi-



Map 1 Google Earth image showing distribution of *O. hirsutibulba* (white dots) and *O. fenestrata* (black dots) in the Northern Cape Province of South Africa. The two localities indicated by larger circles are approximate localities based on herbarium labels.

tion in this study. Specimens were collected from the Nieuwoudtville Wild Flower Reserve, Nieuwoudtville, South Africa, where they were found growing between dolerite boulders on rocky outcrops in Nieuwoudtville Shale Renosterveld (Mucina & Rutherford 2006). This species was described as having single-flowered inflorescences (Salter 1935), but shares the longitudinally grooved bulb character with the *O. pes-caprae* clade. More extensive surveys in April 2014 showed that approximately a third of the populations produced 1–3-flowered inflorescences (<http://www.ispot.org.za/node/254922>, <http://www.ispot.org.za/node/256932>).

Herbarium specimens collected at all sites as well as vouchers of the cultivated material are held in the Stellenbosch University Herbarium (STEU) or the Compton herbarium (NBG). Leaf samples from all populations were preserved in silica gel for use in DNA-based phylogenetic studies.

DNA extraction, amplification and sequencing

Genomic DNA was extracted from dried leaf material following a modified CTAB (Doyle & Doyle 1987) procedure (Oberlander et al. 2004). The ITS region was amplified using the primers AB101 and AB102 (Sun et al. 1994) in PCR reagent mixtures (in 25 µl final volumes) containing 0.5 µM of each primer, 0.2 mM of each dNTP, 0.2 mM 1× Supertherm buffer solution, 2.5 mM MgCl₂, 0.25 U Supertherm Taq polymerase and c. 40 ng template DNA. The PCR protocol (35 cycles) followed was: 94 °C denaturation for 60 s, 60 s annealing at 55 °C, 90 s extension at 72 °C and a final 7 min extension step at 72 °C. PCR products were visualised on a 2 % agarose gel and purified using a Wizard DNA Prep purification kit (Promega, Madison, Wisconsin, USA). Sequencing reactions and base calling were conducted at the Central Analytical Facility (CAF), Stellenbosch University, Stellenbosch, South Africa.

Phylogenetic analyses

All newly-generated sequences were submitted to GenBank (Accession numbers: *Dreyer, Roets & Oberlander MO1519* = KF154266, *MO1521* = KM594528, *MO1527* = KF154263, *MO1532* = KM594527, *MO1555* = KM594529). Based on BLAST searches on GenBank (<http://www.ncbi.nlm.nih.gov/genbank>) (data not shown) using generated ITS sequences, both putative undescribed species and *O. lasiorrhiza* clearly showed the greatest similarity to members of the *O. pes-caprae* clade (Oberlander et al. 2011). Sequences were therefore added to the ITS data matrices of Roets et al. (2013) and Dreyer et al. (2013). The final dataset contained 44 taxa (15 members of the *O. pes-caprae* clade) and 831 characters, and was subjected to Bayesian inference using MrBayes v. 3.2 (Ronquist et al. 2012). We allowed the mcmc chain to visit all time-reversible models across the GTR model space in proportion to their fit to the data. A gamma distribution as well as a proportion of invariant sites parameter was included to model among-site rate variation, as these were strongly favoured by the AIC values calculated in jModeltest v. 0.1.1 (Posada 2008). Two separate analyses of twenty million generations each were performed with a sampling frequency of 5 000 generations. We used the default burnin value of 0.25, and convergence of runs and sufficient sample size were estimated using the standard methods in MrBayes. Clade support was estimated using posterior probability values (PP).

Morphology

No individuals of either putative undescribed species were found in flower in situ as seasonal growth was too young. We potted two accessions of each species from each locality in a 50 : 50 mixture of potting soil and sand and maintained these at the *Oxalis* living collection at the Stellenbosch Botanical

Garden under ambient conditions. Both taxa flowered ± two months after collection and these were used for morphological evaluations. Morphological characters of the two putative new taxa were studied with the aid of a Leica ES2 stereo microscope and compared to all known species of the *O. pes-caprae* clade (Salter 1944, Oberlander et al. 2009, Dreyer et al. 2010, 2013, 2014, Roets et al. 2013) and to material of unidentified *Oxalis* specimens housed in the NBG and BOL herbaria.

RESULTS

Phylogenetic analyses resolved both putative undescribed taxa and *O. lasiorrhiza* as embedded within the *O. pes-caprae* clade with strong support (Fig. 1). *Oxalis lasiorrhiza* is closely related to the species *O. pes-caprae* and *O. compressa* based on ITS sequence data. One of the other taxa (*O. hirsutibulba*) resolved strongly as sister to a clade containing *O. cf. copiosa*, *O. cf. haedulipes*, *O. nivea* and *O. rosettifolia*. This fairly iso-

lated position is reflected in a suite of morphological traits that differentiate *O. hirsutibulba* from these and other taxa in the *O. pes-caprae* clade (Table 1). Most noteworthy is the finely but densely hairy nature of the entire plant body (including the bulb) (Fig. 2). Herbarium specimens indicate that this species was collected as early as 1975 by Bayer (*Bayer 1507*, NBG) and 1977 by Thomson and Le Roux (*Thomson & Le Roux 101*, NBG), but was not subsequently described. According to the data labels, some specimens collected by Bayer (*Bayer 1497*, NBG) were from roughly the same locality as our southern accession ('Skouerfontein W Eksteensfontein'). Unlike our specimens, he found the plants in flower in late September. This coincides with flowering in our living collections. In addition to our recorded localities, both Thomson and Le Roux (*Thomson & Le Roux 101*) and Bayer (*Bayer 1507*) collected specimens from the top of Helskloof pass in the conservancy. The precise locality is unknown, but is believed to be close to Kubus in the north of the conservancy, as the collection

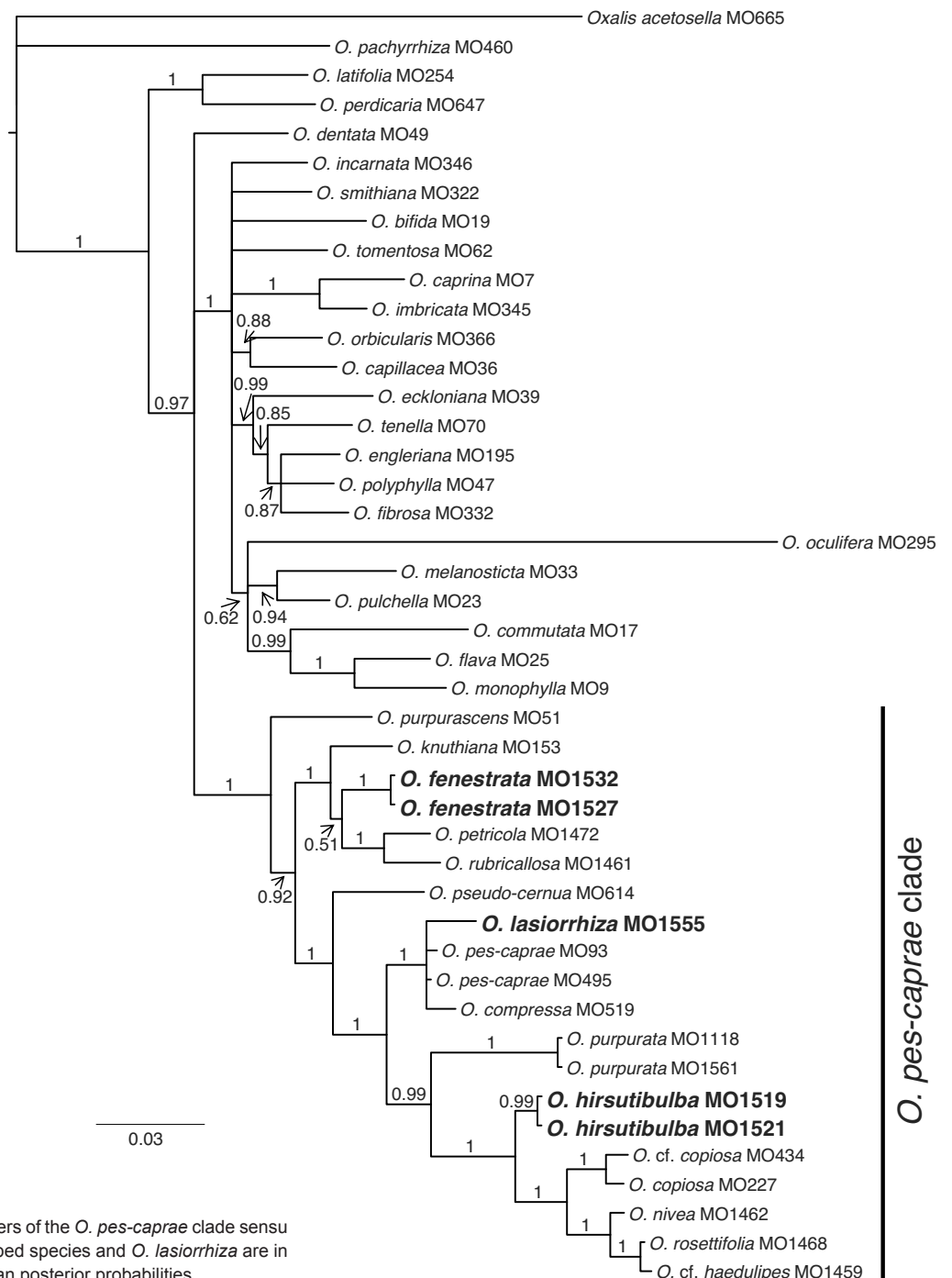


Fig. 1 ITS-based phylogeny of members of the *O. pes-caprae* clade sensu Oberlander et al. (2011). Newly described species and *O. lasiorrhiza* are in bold. Values at nodes indicate Bayesian posterior probabilities.

Table 1 Morphological comparisons of confirmed and potential members of the *Oxalis pes-caprae* clade (sensu Oberlander et al. (2011)) collected in the present study (bold) and described previously (Salter 1944, Dreyer et al. 2013, Roets et al. 2013). Size measurements indicate maximum size of each character and were taken either from the literature or from specimens in the Stellenbosch University Herbarium.

Species	Character									
	Bulb	Bulb tunics	Rhizome	Stem	Leaves	Leaflets	Flowers *	Sepals		
<i>O. compressa</i>	Oblong ovoid, 3 cm	Brown, ridged	Glabrous, 7 cm	Acaulescent	10–30	Cuneate-obovate, pilose underneath	2–6, yellow	Lanceolate, pubescent, ecallose		
<i>O. copiosa</i>	Oblong-ovoid, 2 cm	Pale brown, prominently ridged	Glabrous, 7 cm	Acaulescent	Numerous, apically congested	Boadly-obcordate, glabrous	1–2, yellow	Lanceolate to oblong-lanceolate, glabrous, callose		
<i>O. fenestrata</i>	Ovoid, 5 cm	Dark brown, splitting, prominent veins	Glabrous, 25 cm	Bright apple green, branched, succulent, glabrous, 20 cm	Numerous, alternate or apically congested	Obcordate, glabrous, usually with translucent regions	1–6, white	Lanceolate, glabrous, ecallose		
<i>O. haedulipes</i>	Narrow-ovoid, 3.5 cm	Pale brown, prominently ridged	Glabrous, 7 cm	Green, single, non-succulent, glabrous or sparsely pubescent, 10 cm	Numerous, apically congested	Cuneate-obcordate, glabrous	1–6, yellow	Lanceolate, sparsely pubescent, callose		
<i>O. hirsutibulba</i>	Oblong-ovoid, 6 cm	Light brown, finely grooved, pubescent	Densely hairy, 20 cm	Bright green, single, non-succulent, pubescent, 4 cm	3–8, apically congested	Obcordate, pubescent	1–7, white	Linear-lanceolate, pubescent, ecallose		
<i>O. knuthiana</i>	Ovoid to cylindrical, 7 cm	Blackish brown, splitting	Glabrous, 15 cm	Glaucous green, branched, semi-succulent, glabrous, 30 cm (can reach 70 cm in shade)	Numerous, alternate	Cuneate-obcordate, pubescent below	3–7, yellow	Ovale-lanceolate, glabrous, ecallose		
<i>O. lasiorrhiza</i>	Ovoid, beaked, 2 cm	Pale brown, with prominent longitudinal nerves	Pubescent, 30 cm	Acaulescent	< 30, apically congested	Broadly cuneate-obcordate to obdelto-obcordate, hairy	1–3, yellow	Broadly lanceolate, hairy, ecallose		
<i>O. luederitzii</i>	Narrow-ovoid, 6 cm	Dark brown with 3 conspicuous ridges	18 cm	Acaulescent	8–20	Reniform, glabrous	2–5, yellow (or white?)	Lanceolate, glabrous, ecallose		
<i>O. nivea</i>	Ovate to ovoid, 3.5 cm	Dark brown to blackish, longitudinally ridged and finely reticulate	7 cm	Green, single, semi-succulent, glabrous, 10 cm	10–20, apically congested	Obcordate, sparsely hairy	6–11, white	Linear-lanceolate, sparsely hairy, callose		
<i>O. pes-caprae</i>	Ovate-oblong, 2.5 cm	Pale brown, finely longitudinally ridged	18 cm	Usually acaulescent	1–40, apically congested	Cuneate-obcordate, hairy above (usually)	3–20, yellow (rarely cream)	Lanceolate to oblong-lanceolate, glabrous, callose		
<i>O. petricola</i>	Narrow-ovoid to ovoid, 7 cm	Dark brown to black, longitudinally ridged, gummy	10 cm	Glaucous green, semi-succulent, branched, glabrous, 20 cm	Numerous, alternate or apically congested, upper in pseudo-whorls	Cuneate-obcordate to cordate, glabrous	2–6, white with light pink margin	Lanceolate, glabrous, ecallose		
<i>O. pseudo-cernua</i>	Elongate, 5 cm	Brown, prominently longitudinally ridged	10 cm	Acaulescent (rarely single, 1 cm)	Numerous, apically congested	Cuneate-obcordate, sparsely pubescent below	3–5, white	Lanceolate, glabrous, callose		
<i>O. purpurascens</i>	Narrow-ovoid, 7 cm	Chestnut brown, prominently longitudinally ridged	10 cm	Acaulescent (rarely single)	≤ 20, basal, rarely apically congested	Obcordate, glabrous?	3–5, pink	Lanceolate, glabrous, callose		
<i>O. purpurea</i>	Ovoid, 1.5 cm	Chestnut brown, smooth	30 cm, many runners	Acaulescent	3–5, apically congested	Cuneate-obcordate, pilose below	2–7, pale pink	Lanceolate, pubescent, ecallose		
<i>O. roseifolia</i>	Irregularly, ovoid, 5 cm	Pale to blackish brown, prominently ridged	4 cm	Acaulescent	Numerous, apically congested	Obcordate, glabrous with sparse hairs on main veins	2–5, yellow or cream	Lanceolate, sparsely hairy, callose		
<i>O. rubricalosa</i>	Narrow-oblong, 8 cm	Dark brown, prominently veined	50 cm	Apple green, branched, semi-succulent, glabrous, 50 cm	Numerous, alternate or apically congested, upper in whorls	Obcordate, glabrous when mature	2–7, pink	Oblong, glabrous, callose		
<i>O. schaeferi</i>	Unknown	Unknown	Unknown	Green, branched, semi-succulent, glabrous, 18 cm	Numerous, apically congested	Cuneate-obcordate, glabrous	3–7, yellow	Broadly-lanceolate, glabrous, ecallose		

* numbers indicate number of flowers per peduncle, colour indicates petal lobe colour

locality on both refers to the 2816BD quarter degree grid square (near Kubus), and the area directly to the east of Kubus has similar vegetation and terrain to where we found our specimens (Mucina & Rutherford 2006).

The other taxon (*O. fenestrata*) grouped within a clade containing species with branched above-ground plant bodies (*O. knuthiana*, *O. rubricallosa* and *O. petricola*) (Salter 1944, Roets et al. 2013). *Oxalis fenestrata* shares this branching character, but can easily be distinguished from the former species by usually having clear white markings just below the apical incision of the leaflets (Table 1, Fig. 3). A single herbarium accession of this species is known to us. It was collected in 1980 by P. Drijhout (Drijhout 2916, NBG) on the Vandenster Mountain near Kubus. These specimens do not seem to have the translucent markings on the leaves as our accessions, but these may be less obvious due to the age of the specimens.

Based on molecular phylogenetic reconstructions (Fig. 1) and morphological comparisons (Table 1), the two undescribed taxa group with other members of the *O. pes-caprae* clade, but are clearly distinct from all currently known taxa. They therefore represent two new species, which we formally describe here.

TAXONOMIC TREATMENT

1. *Oxalis hirsutibulba* Dreyer, Roets & Oberl., *sp. nov.* — Fig. 2

Type. Bayer 1497 (NBG), South Africa, Northern Cape, Richtersveld Conservancy, west of Eksteensfontein, 2817CC, Sept. 1978, flowering.

Geophyte up to 20 cm tall, bright green, densely but finely hairy. *Bulb* shallow, up to 6 cm long, teardrop-shaped, distinct elongated upper portion between a third and half of bulb length (apical beak), tunics hard, densely hairy, distinctly longitudinally grooved, light brown, often with contractile root. *Rhizome* brown, up to 20 cm long, hairy to densely hairy, with light brown alternating scales up to 4 mm long. *Above-ground stem* up to 4 cm long, green, hairy, with 1–2 large (up to 8 mm long) semi-amplexicaul, membranous scales. *Leaves* 3–14, bright green, loosely apically congested, hairy; petioles up to 14 cm long, dilated below basal articulation, hairy; leaflets 3, cuneate-obcordate to obcordate, up to 3 × 3.5 cm broad, finely hairy on both sides and along margin, distinctly petiolulate, adaxial side glossy along margin. *Peduncles* 1–7-flowered, densely hairy, as long as to 2.5 times longer than and as thick as petioles. *Bracts* 2–6, linear, erect, up to 7 mm long, densely hairy, without calli. *Pedicels* slender, up to 25 mm long. *Sepals* 5, linear-lanceolate, acute, densely hairy, without calli. *Corolla* up to 25 mm long, glabrous to sparsely hairy, white, with broad funnel-shaped yellow tube. *Petals* 5, lobes white, tube yellow, funnel-shaped, densely hairy. *Stamens* 10, in 3 whorls; 2 whorls per plant, lower whorl 2.5–4 mm long, middle whorl c. 5 mm long, longest whorl c. 9 mm long; filaments hairy; anthers oval, yellow. *Ovary* narrowly ovoid, c. 5 mm long, 5-loculed, yellow, densely hairy, up to 13 ovules per locule; styles 5, separate, reciprocally herkogamous with two stamen whorls, short-whorled styles curving outwards between filaments, mid- and long-whorled styles erect, densely hairy. *Stigmas* green, fimbriate. *Fruit* capsule cylindrical, hairy, twice as long as sepals. *Seed* endospermous.

Diagnostic characters — Geophyte with densely hairy vegetative plant body. Bulb tunics light brown, finely grooved, densely hairy and with apical beak. Corolla lobes white, tube yellow. Both morphological characters and DNA evidence distinguish *O. hirsutibulba* from all known *Oxalis* species with umbellate inflorescences. It prefers cool, south-facing cliffs, where it grows in loose soil in cracks. *Oxalis hirsutibulba* flowers from August to September.

Distribution — Only known from three localities in the Northern Cape Province of South Africa. One locality is situated on

the southern slopes of the Richtersberg range, another is west of Eksteensfontein, while a third population is known from near Kubus.

Additional specimens examined. SOUTH AFRICA, Northern Cape, Richtersveld Conservancy, southern slopes of Richtersberg, 2817CA, June 2012, sterile, Dreyer, Roets & Oberlander MO1519 (NBG, STEU); Northern Cape Province, Richtersveld Conservancy, west of Eksteensfontein, 2817CC, June 2012, sterile, Dreyer, Roets & Oberlander MO1521a (STEU); Stellenbosch Botanical Garden, Aug. 2012, cultivated from Dreyer, Roets & Oberlander MO1521a, origin Northern Cape, Richtersveld Conservancy, west of Eksteensfontein, 2817CC, June 2012, flowering, Dreyer, Roets & Oberlander MO1521b (STEU); Northern Cape Province, Richtersveld Conservancy, Top of Helskloof pass, 2816BD, June 1977, Thomson & Le Roux 101 (NBG); Northern Cape Province, Richtersveld Conservancy, Top of Helskloof pass, 2816BD, Sept. 1975, flowering; Bayer 1507 (NBG).

2. *Oxalis fenestrata* Dreyer, Roets & Oberl., *sp. nov.* — Fig. 3

Type. Dreyer, Roets & Oberlander MO1527b (STEU), cultivated from Dreyer, Roets & Oberlander MO1527a, originally from South Africa, Northern Cape, Richtersveld Conservancy, Tierhoek camping site, 2816DD, June 2012, flowering.

Geophyte with thick succulent stem, up to 40 cm tall, bright apple green, nearly entirely glabrous. *Bulb* up to 30 cm deep, large, ovoid, 2–7.5 cm long, with numerous, dark brown, rumpled and splitting tunics with prominent veins. *Rhizome* white, up to 25 cm long, glabrous, with large (c. 5 mm long) semi-amplexicaul, light brown, membranous, alternating scales. *Arial stem* well-developed, thick and succulent, distinctly tapering towards the tip, often branching, bright apple green, glabrous. *Leaves* alternate along stem or loosely apically congested in groups of 3–5, often on short side stems, glabrous; leaf base semi-amplexicaul, winged below articulation with petiole; petioles slender, up to 9 cm long, glabrous; leaflets 3, obcordate to broadly obcordate, adaxially glabrous, abaxially glabrous to very sparsely hairy on veins and base, margin glabrous to very sparsely hairy, petiolules prominent, 1–1.5 mm, region below apical incision usually with distinct, variously shaped white to pale green and translucent patch. *Peduncles* 1–6 flowered, longer than the petioles. *Bracts* 2–8, erect, up to 1.5 mm long, glabrous to sparsely hairy, usually with prominent calli. *Pedicels* slender, 20 mm long, pendulous in bud and in fruit. *Sepals* 5, lanceolate, acute, without calli, glabrous to very sparsely glandular-pilose, up to 9 × 5 mm. *Corolla* c. 20 mm long, with broad funnel-shaped yellow tube. *Petals* 5, claw yellow, ± half the length of the petal, lobes white. *Stamens* 10, in 3 whorls; 2 whorls per plant, lower whorl c. 3 mm long, middle whorl c. 5.5 mm long, longest whorl c. 9 mm long; filaments sparsely hairy, with mostly simple hairs and a few glandular hairs towards the base, with prominent blunt teeth on longest whorl; anthers oval, yellow. *Ovary* narrowly ovoid, 4–5 mm long, 5-loculed, glabrous, 5–6 ovules per locule; styles 5, separate, hairy with both simple and glandular hairs, reciprocally herkogamous with two stamen whorls, short-whorled styles curving outwards between filaments, mid- and long-whorled styles erect. *Stigmas* green, fimbriate. *Fruit* capsule slightly longer than sepals. *Seed* endospermous.

Diagnostic characters — Tall geophyte with thick, branched, succulent, bright apple green stems. Leaflets usually with prominent clear white markings just below the apical incision. The few-flowered inflorescences produce large, white flowers, with pedicels that are often distinctly darker in colour than the peduncle. It is closely related to other branched, umbellate species, such as *O. knuthiana*, *O. petricola* and *O. rubricallosa* and grows in fairly similar habitats. It can immediately be distinguished from these species by the combination of translucent white patches on the leaflets, thick stems, white corollas and ecallose sepals. This species flowers from August to September. The specimens collected near Kubus (Drijhout



Fig. 2 a. Typical habitat of *Oxalis hirsutibulba* in the Richtersveld Conservancy; b. *Oxalis hirsutibulba* herbarium specimen (Bayer 1507, NBG); c. flower - side view; d. flower - top view; e. leaves - adaxial side; f. leaves - abaxial side; g. bulb. — Scale bars = 1 cm.

2916) seem to lack the white to pale green and translucent patch at the apical incision.

Distribution — Only known from southern slopes in the western end of the Richtersveld Conservancy, Northern Cape, where it grows in shady crevices between granite boulders and in rock fields.

Additional specimens examined. SOUTH AFRICA, Northern Cape, Richtersveld Conservancy, Tierhoek camping site, 2816DD, June 2012, sterile; Dreyer, Roets & Oberlander MO1527a (NBG, STEU); Northern Cape, Richters-

veld Conservancy, 1.4 km north-west of Tierhoek campsite, June 2012, sterile; Dreyer, Roets & Oberlander MO1532 (NBG, STEU); Northern Cape Province, Richtersveld Conservancy, Vanderster Mountain, near Kubus, 2816BD, June 1980, flowering, Drijhout 2916 (NBG) South Africa.

DISCUSSION

Fifteen *Oxalis* species have now been confirmed as members of the *O. pes-caprae* clade, the only major lineage of *Oxalis* in



Fig. 3 a. Typical habitat of *Oxalis fenestrata* in the Richtersveld Conservancy; b. *Oxalis fenestrata* habit; c. flower; d. leaves; e. peduncles with prominently callose bracts (arrows); f. bulb (Drijhout 2916, NBG); g. excavated plants showing thick and fleshy, tapering, apple green stems. — Scale bars = 1 cm. — Fig. b & d provided by P.C.V. van Wyk.

Africa to be well-represented outside of the GCFR. This clade has seen dramatic increases in the number of constituent species since the first large-scale phylogenetic reconstructions of southern African *Oxalis*, where it could still be referred to as 'species-poor', containing only seven species (Oberlander et al. 2011). In conjunction with several other recent discoveries (Dreyer et al. 2013, Roets et al. 2013), and the inclusion of uncertain taxa such as *O. lasiorrhiza*, this is clearly no longer the case. Biogeographically, the two newly described spe-

cies have also helped shift the centre of diversity in this clade towards the extreme northern edge of the GCFR. (Eight spp. are found in the region: *O. fenestrata*, *O. cf. haedulipes*, *O. hirsutibulba*, *O. nivea*, *O. pes-caprae*, *O. petricola*, *O. rosettifolia* and *O. rubricallosa*; admittedly *O. pes-caprae* is quite possibly a recent introduction). All six recently-described spp. are endemic to the Richtersveld region, compared to three spp. endemic to the entire core CFR (*O. compressa*, *O. lasiorrhiza*, and *O. purpurata*). Both diversity and endemism factors may

strengthen hypotheses on the extra-GCFR diversification of this lineage (Oberlander et al. 2011). Better sampling of the poorly sampled Namibian *Oxalis* flora will be required in order to fully understand the radiation of this lineage.

The morphology of members of the *O. pes-caprae* clade varies considerably. Although the bulk of species in this clade form part of sect. *Cernuae* sensu Salter (1944), this section is based on a plesiomorphic character (umbellate inflorescences) spread across all three main clades of southern African *Oxalis*. In fact, this character has been partially lost twice within the *O. pes-caprae* clade itself (in *O. copiosa* and *O. lasiorrhiza*), and consequently must be used only as a rough first guide to phylogenetic placement of southern African *Oxalis* species. Other potential characters currently in use to delimit subsections of *Oxalis* sect. *Cernuae* (yellow vs non-yellow flowers, longitudinally grooved bulbs, apically beaked bulbs) are also plesiomorphic or highly variable across the phylogeny. Currently, no synapomorphic morphological characters have been identified for members of this variable clade.

Despite this variability, the unsampled *O. schaeferi* and *O. luederitzii* are on morphological and geographical grounds also likely members of this clade. *Oxalis schaeferi* is a Namibian species morphologically very similar to *O. knuthiana*, *O. petri-cola*, *O. rubricallosa* and the newly described *O. fenestrata*. This group of species shares the well-branched above-ground habit as a potential diagnostic character. Although this character does occur in other southern African *Oxalis*, it is fairly rare and found in taxa distantly related to, and morphologically very distinct from, the *O. pes-caprae* clade (e.g. *O. reclinata* Jacq.). Ecologically, these species also seem to have fairly similar habitat requirements, being confined to cooler, south-facing slopes or screes with greater water availability (very little habitat data is known for *O. schaeferi*, though). The case for *O. luederitzii* is somewhat less certain and awaits more data, although geographically, the only lineage of umbellate *Oxalis* taxa known from southern Namibia is the *O. pes-caprae* clade. This would make this clade the most parsimonious home for both *O. luederitzii* and *O. schaeferi*. Most other morphological (i.e. teeth present on the filaments, seven or more ovules per carpel, glabrous corolla) and palynological (finely reticulate tectum; Dreyer 1996) features are at least consistent with a placement in the *O. pes-caprae* clade.

Oxalis lasiorrhiza seems to be closely related to *O. pes-caprae* and *O. compressa*. It clearly differs from both these taxa in the larger flowers, much shorter peduncles and hairier plant body. Although the original (Salter 1935) and subsequent (Salter 1944) descriptions of this species clearly consider it to have a single-flowered inflorescence, the fairly common production of 2–3-flowered peduncles makes the placement of this species in the *O. pes-caprae* clade much less unexpected. It is only the second taxon capable of producing single-flowered inflorescences in the *O. pes-caprae* clade (*O. copiosa* also produces single-flowered inflorescences, a character that can vary even on the same plant). The longitudinally grooved bulb and endospermous seeds are consistent with a placement within the *O. pes-caprae* clade. Reduction to a single flower per peduncle is known from multiple other *Oxalis* lineages (e.g. sections *Oxalis* and *Palmatifoliae* (Lourteig 2000) and the core southern African clade (Oberlander et al. 2011)). The single-flowered inflorescence of *O. lasiorrhiza* can thus be seen as another, independent origin of this character.

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